VAGRANT BIRDS: PASSIVE OR ACTIVE DISPERSAL?

by Richard R. Veit

Wilson (1988) raised some important issues regarding the causes of vagrancy in birds in response to my speculations about Red-billed Tropicbirds (Veit 1988). My purpose in this article is to address these issues. Our two most important points of contention are 1) whether or not a strategy of long-distance vagrancy could be favored by selection, i.e., could be adaptive, and 2) how strong an influence weather patterns have on the long-distance dispersal of birds. I will clarify my meaning of the "adaptiveness" of long-distance vagrancy and will argue that the influence of weather on the occurrence of vagrants has been greatly overemphasized.

My premise is that vagrant birds in general are the outer fringes of population-level dispersal episodes involving entire populations or at least numbers of individuals. These occur on different time and space scales than the massive incursions, such as those of Snowy Owls or winter finches that are ordinarily referred to as irruptions. Thus, I think what probably happened in the fall of 1986 is that a number of Red-billed Tropicbirds dispersed northward, and we were fortunate enough to have found two of them. The ones that we saw were those that remained in the same place long enough to be discovered.

How can a strategy of long-distance vagrancy be adaptive? Wilson stated that long-distance vagrancy would be unlikely to evolve as a strategy on the grounds that too great a risk would be incurred by those individuals that undertook lengthy flights. In other words, long-distance dispersers would have lowered fitness as compared with that of more sedentary individuals. Such a reduction in fitness would only result if the tendency to disperse long distances is under the control of a single gene or group of linked genes. That is, individual birds possessing the allele for long-distance dispersal always disperse long distances, whereas those with the "nondispersal" allele never do.

I did not mean to suggest that dispersal behavior is under the control of a simple Mendelian system such as this. Instead, I think that the behavioral abilities of birds are such that a bird can "decide" what kind of dispersal strategy to adopt based on an evaluation of environmental conditions. There is considerable evidence in support of this contention, as Wilson himself alluded to: "Most long-distance dispersal of birds occurs in response to deteriorating conditions." For example, the Great Gray Owls that dispersed southward during the winter of 1978-1979 are most unlikely to have differed genetically from those that remained within their customary northern range. Rather, all Great Gray Owls probably have sufficient behavioral flexibility to initiate dispersal under what they perceive to be deteriorating environmental conditions. I do not see why this option should not be available to all birds, including Red-billed

Tropicbirds. Because long-distance dispersers enhance their fitness by escaping deteriorating habitats, their behavior is adaptive.

To what extent is the dispersal of birds governed by wind circulation patterns? Wilson supports the overriding importance of weather to bird dispersal by quoting McLaren's (1981) fascinating paper on the incidence of vagrant birds on islands off Nova Scotia. Wilson states that McLaren showed that the occurrence of vagrants was "explicable solely from a knowledge of wind patterns." McLaren did no such thing.

McLaren's first assertion was that the frequency with which vagrants occur on islands off Nova Scotia is higher than at other islands farther south along the east coast. He compared the incidence of vagrants at Sable, Seal, and Brier islands, Nova Scotia, with their incidence at more southerly islands ranging from Nantucket and Martha's Vineyard south to Dog and St. George islands, off the northwestern panhandle of Florida. My interpretation of McLaren's analysis is that vagrants occur more frequently at islands more isolated from the mainland. That is, if Sable Island were located 125 miles off North Carolina, it would attract just as many vagrants as it does from its current position.

To explain his perceived increased incidence of vagrants in Nova Scotia, McLaren provides a series of maps of airflow at an elevation of constant pressure (1000 millibars) and suggests that this pattern explains why vagrants tend to appear more often in Nova Scotia than elsewhere. He gives no analytical proof of this assertion, nor does he explain why birds should follow patterns of average airflow. Furthermore, McLaren himself points out that most vagrants appear during periods of fine weather; that is, when winds are moderate. Such an observation is consistent with Able's (1972) finding that most migrating passerines choose nights when wind speeds are light to moderate for migrating. This suggests that migrating passerines, vagrant or otherwise, choose nights to fly when winds will not displace them from their intended course.

Weather maps have often been rather arbitrarily used to show that gross circulation patterns can account for the dispersal of birds. Murphy and Vogt (1933) described how a pattern of wind circulation (northeasterly winds extending across the North Atlantic) coincided with a major southward incursion of Dovekies in the fall of 1932. They did not, however, suggest that the weather pattern was the *cause* of the Dovekie irruption. Rather, they stated that a major irruption had to be underway in the first place, before the storm appeared. Despite Murphy and Vogt's analysis, a dogma persists on the East Coast that Dovekie flights are caused by storms.

The problem with the use of weather maps to explain dispersal is that an assessment of the "unusualness" of the presented pattern is virtually never made. For example, I am sure that one could select a weather map of North America during January of 1979 (just before Great Gray Owls exploded into New

England) showing a predominantly northwesterly airflow across the entire North American continent and then conclude that the owls were brought south by the wind. Such a conclusion would be ludicrous, but it would not be qualitatively different from inferring that Dovekies are carried south by storms. The winds that supposedly transported the Dovekies twenty-five hundred miles outside their normal range in 1932 had maximum sustained winds of forty miles per hour. Since Dovekies put up with winds of this strength two to three times per week during their nesting season in the arctic, it is ridiculous to assert that such a pattern would transport them so far. Much more serious storms occur almost every year in the North Atlantic, yet Dovekies are not transported south by them. The great Dovekie flight of 1932 was an irruption in just the same sense as are southward flights of crossbills, Snowy Owls, or Northern Shrikes.

Some of the most detailed analyses of the influence of wind circulation patterns on bird migration were prepared by Bagg (1957, 1958) for the "Changing Seasons" column of *Audubon Field Notes*. In his classic discussions, Bagg showed how the early arrival in New England in spring of migrants such as Indigo Buntings and Rose-breasted Grosbeaks often happened soon after the passage of storms. His observations are often misquoted or misinterpreted. He *did* say that early spring migrants tend to arrive in New England following the passage of storms, but he *did not* say that the birds were transported by the storms. Rather they take advantage of the strong southwesterly airflow that follows the storm. Bagg also showed that bad weather, especially rain, often forces migrating birds to alight. Therefore, the largest "waves" of migrants are often seen by birders during periods of bad weather. Such observations create the illusion that migrant birds are transported by storms. When we find large numbers of grounded migrants during a rainstorm, we can conclude that weather conditions are appropriate for grounding migrants. We should not conclude that the weather conditions are ideal for migrating.

My interpretation of Bagg's findings is that migrating birds likely choose nights with favorable winds (i.e., tail winds) on which to travel, but the weather patterns themselves do not cause dispersal. When tropicbirds are picked up exhausted on New England beaches immediately after hurricanes, then certainly the hurricane has influenced the dispersal of those individuals. It is curious, though, that tropicbirds appear in New England after some hurricanes, but not others. Perhaps northward dispersal has to coincide with the passage of a hurricane for tropicbirds to be carried to New England.

In the Pacific both Red-billed and Red-tailed tropicbirds disperse vast distances north of their breeding range each year, when there are no storms. I have been studying dispersion of birds on a series of cruises off the southern California coast for the last two years. These cruises monitor environmental change in the California Current system four times a year. I have seen Red-

tailed Tropicbirds within three hundred miles of the California coast in both 1987 and 1988. Red-tailed Tropicbirds do not nest any closer to California than Hawaii, twenty-five hundred miles away, and there were no hurricanes that came within a thousand miles of California in either of the last two years. Therefore, these tropicbirds are dispersing northward without any help from the weather.

A few pairs of Red-billed Tropicbirds nest on the Alijos Rocks, roughly five hundred miles south of the U. S. border off Baja California (Pitman 1985). The next closest place to southern California where Red-billed Tropicbirds breed are islets in the Gulf of California and the Revillagigedo group off the southern tip of Baja California (A.O.U. 1983). Both these island groups are about eight hundred miles distant, by sea, from southern California. But numbers of Red-billed Tropicbirds are seen off southern California each year; I have seen seven or eight on each of two cruises taken in late summer, and many of these are adults. Thus, Red-billed Tropicbirds ordinarily disperse hundreds of miles north of their nesting range each year *without* the assistance of hurricanes. In fact, the winds off Baja California blow almost unremittingly from the west or northwest, so Red-billed Tropicbirds off southern California are dispersing northward against the prevailing wind.

Were the Vineyard and Maine tropicbirds the same? The assertion that the Red-billed Tropicbirds at Martha's Vineyard and at Mt. Desert Island, Maine, were the same individual carries the implicit assumption that birders find and report all birds present in a given area during a given period of time. This assumption is certainly false. To see this, it is only necessary to compare numbers of birds of a given species reported by birders within a given area with aircraft censuses covering the same area at the same time. For example, the largest number of Pomarine Jaegers *ever* reported off the coast of California is about 250 in one day (Garrett and Dunn 1980). Yet Briggs et al. (1987) have demonstrated that fifty thousand are likely to be present on any given day during the months of September or October. Similar estimates of abundance for New England have been made by Powers (1983). In the fall of 1987, 11,707 Brown Pelicans were counted during an aircraft census of the southern California coast between Point Conception and the Mexican border in December, and 12,718 were found between Point Conception and Bodega Bay (D. L. Jaques, personal communication). Yet no group of birders could expect to *see* that many even during a coordinated census. Nine Christmas Bird Counts that year recorded 3493 between Santa Barbara and San Diego.

The reason that Wilson and others assume the two tropicbirds were the same individual presumably centers on their perception of the low probability associated with the occurrence of any Red- billed Tropicbird in New England. The New England occurrence of a Red-billed Tropicbird is thought to be

improbable because they have only appeared at infrequent intervals in the past. However, we do not know how rare Red-billed Tropicbirds were in the ocean off New England during September 1986. In my opinion, a small irruption of tropicbirds occurred at that time, and the two reported sightings are the fringe of a dispersal episode that was otherwise undetected. The reason that the individual at Martha's Vineyard was seen was that it stayed in one place for such a long time. Others may have flown north until they encountered land and then headed out to sea again. The probability that we would find more than two birds from a dispersal episode lasting a few days would be very low. Too often, we assume that we see all the birds that occur.

Should we expect vagrancy always to conform to previously documented patterns? Many readers will dismiss my speculation of the occurrence of an irruption of tropicbirds in September 1986 as improbable on the grounds that such an occurrence has not previously been recorded. Compilers of bird records and rarities committees tend to assume the same point of view, i.e., records of birds outside their normal range are suspect unless they fit a previously documented pattern. I think that the expectation of such patterns runs counter to our knowledge of bird population dynamics and dispersal abilities.

Major irruptions of birds such as Snowy Owls, winter finches, or three-toed woodpeckers are believed to be caused by extreme environmental change within those species' normal ranges. Drastically reduced food supply after a period of abundance is usually cited as the culprit. My theory is that vagrant birds have similarly dispersed in response to environmental change. The change in their environment is on a smaller scale or has occurred over a more extended period of time. If Red-billed Tropicbirds fly to New England in response to some sort of environmental disturbance and such disturbances occur only at infrequent intervals, then we may not be aware of any previous pattern of vagrancy, because the environment has not previously changed in the same way that it has this time. There is no previous pattern of occurrence of Red-footed Boobies in California, yet at least five were seen during the fall of 1987. There was no previous pattern of occurrence of Western Reef Herons in the Americas before 1983, but the accumulation of records from Nantucket, Barbados, and Trinidad show that this species is now dispersing much farther than it did in the past. These new patterns probably could reveal important insight into alterations in the condition of distant environments.

Environmental changes are unquestionably occurring at an accelerating rate. If birds in general respond to environmental changes by altering their dispersal behavior, then it will clearly be of practical value to learn how their dispersal behavior changes and to pay particular attention to the extended

dispersal of species not previously known to wander great distances from their normal ranges.

DeSante (1983) has rigorously demonstrated the increasing frequency of occurrence of vagrant birds at the Farallon Islands, off San Francisco, California, over the years 1968-1978. He also speculated that this change might reflect habitat destruction within those species' normal ranges. If this hypothesis is true, then documentation of the occurrence of vagrants will provide an especially useful tool for the monitoring of environmental change in a world that is rapidly altering.

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