WEATHER AND LONG-DISTANCE VAGRANCY IN RED-BILLED TROPICBIRDS

by W. Herbert Wilson

In a recent provocative contribution, Veit (1988) speculated that long-distance vagrancy of Red-billed Tropicbirds is an adaptive trait. I wish to take issue with several of his speculations. I will proceed by first discussing salient aspects of the biology of Red-billed Tropicbirds. Second, I will discuss the nature of long-distance dispersal in birds. Third, I will challenge the assertion of Veit that long-distance vagrancy is "of fundamental importance in the life history of Red-billed Tropicbirds." Lastly, I will present an alternate hypothesis to explain extralimital occurrences of Red-billed Tropicbirds in the northwest Atlantic that I believe is more parsimonious than the hypothesis of active northerly dispersal suggested by Veit.

Red-billed Tropicbirds breed in tropical and subtropical waters of the Pacific, Atlantic, and Indian oceans. The population closest to New England breeds in the Virgin Islands. A single egg is laid each year. Nesting occurs in cavities or under overhangs on cliffs that are inaccessible to predators and humans. Breeding pairs form long-term bonds, and pairs exhibit great nest-site fidelity. The oldest known individual was nearly seven years old. Food abundance and the availability of nesting sites seem to limit breeding success. On one of the Galapagos Islands, breeding pairs that cannot a find suitable nesting site wait until successful breeders have fledged their young and then use a vacated nesting cavity. For this Galapagos population, waiting for an available nesting site and breeding at a suboptimal time seem preferable to dispersing in search of new breeding sites. Red-billed Tropicbirds do forage widely in search of food, mainly fish (particularly flying fish) and squid. First-year birds tend to wander more than adults. However, these birds are nearly always associated with tropical and subtropical waters. In the western Atlantic, Red-billed Tropicbirds are regularly found in the Gulf Stream as far north as the Carolinas (Lee et al., 1981; Lee and Irvin, 1983). The occurrence of these individuals, mostly first-year birds, is not associated with storms.

Most long-distance dispersal of birds occurs in response to deteriorating conditions. Well-known examples include the Snowy Owl irruptions into the United States during winters of low lemming abundance in Canada and irruptions of Purple Finches into the southeastern U. S. during winters of low seed abundance in northeastern North America. Dispersal would also be expected from actively increasing colonies where nesting sites are all occupied or food is scarce. Veit (1988) cited Grant (1978) as an example of dispersal during times of plenty. However, this work on voles concerned dispersal on the

order of meters, hardly germane to consideration of dispersal between tropical oceans and the boreal waters of Massachusetts. Furthermore, this vole dispersal occurred in anticipation of deteriorating conditions. Finally, it is well established that young birds are more prone to long-distance vagrancy than adults.

I do not accept Veit's contention that long-distance vagrancy is "of fundamental importance in the life history of Red-billed Tropicbirds." Most life history features, such as number of eggs per clutch or age at first reproduction, can be subjected to a risk/benefit analysis. For instance, a warbler might increase her clutch size from four to five. Such an increase could have the benefit of producing an extra fledgling yet might carry the risk of overtaxing the abilities of the parents to provide food for the young, thus threatening the entire brood. The added physiological stress of finding enough food for an extra nestling might leave the adults in perilously poor condition to attempt migration to tropical wintering grounds. Thus, an investment in increased reproduction in the present year might translate into reduced reproduction during subsequent years. In the process of evolution, natural selection plays the role of arbiter among birds with different life history traits. The life history traits of those birds of a given species that produce the most offspring over their lifetimes will be selected for. If such a risk/benefit analysis is applied to northward long-distance vagrancy in Red-billed Tropicbirds, one is hard pressed to understand how this behavior could be maintained during the course of evolution. The obvious risk of such vagrancy is that migrations are physiologically taxing; there is a finite risk of never finding or returning to suitable breeding habitat.

The benefit is less obvious. Given that Red-billed Tropicbirds are not expanding their ranges northward into the temperate zone, it would seem that in virtually all cases, a northward vagrant would fail to find suitable new breeding habitat and would subsequently attempt to return to tropical waters. The time scale on which such vagrancy would reap benefits (establishment of new breeding populations) must be significantly longer than the typical generation time of these birds. Natural selections would not maintain a behavior that carries a significant risk yearly but offers a benefit only perhaps every thousand years. Because there would be a significant cost each generation (risk of dispersal away from potential nesting sites) but no benefit in the vast majority of years, genetic theory tells us that such a trait would be eliminated from the population. The cost would be particularly severe in Red-billed Tropicbirds, which produce only one young per year. Sending a lone offspring northward to explore new habitats seems highly risky given that the chance of success is vanishingly low.

Assessing the risk of long-distance dispersal is difficult. A recent study showed that Red Knots wintering in southern Argentina have significantly lower survivorship than the Red Knots from a disjunct population that winters on the

Gulf Coast of Florida (Harrington et al., 1988). The birds that winter in Argentina obviously undergo a much longer migration from their Arctic breeding grounds than the Floridian birds. These data are consistent with the hypothesis that long-distance migration carries a measurable risk.

Veit (1988) disputed the suggestion that the Red-billed Tropicbird seen on Martha's Vineyard in 1986 (Arvidson 1986) had made some navigational errors. I agree with his interpretation. However, I believe that the occurrence of the tropicbird was storm-influenced. On August 17-18, 1988, Hurricane Charlie followed the coast of the southeastern United States before veering toward Nantucket Island and rapidly dissipating. The tropicbird seen in Maine was first noted on August 31, 1986 (Jones, 1986), and the first sighting of the tropicbird at Martha's Vineyard (likely the same bird, in my opinion) was on September 16, 1986 (Arvidson, 1986). I do not regard the lack of apparent feather damage as an indication that the tropicbird(s) was not storm-carried (Jones 1986). The discovery of a dead Red-billed Tropicbird in New York followed the passing of a tropic disturbance along the Atlantic coast. A moribund specimen found in Providence, Rhode Island, in 1973, appeared after the passage of a storm as well.

The effects of storms and wind currents on vagrancy in birds are well known. McLaren (1981) showed that the relative occurrence of vagrant passerines in Nova Scotia and North Carolina was explicable solely from knowledge of wind patterns. A storm in 1937 carried a number of Fieldfares from Europe to Greenland, where subsequently these birds established a breeding population (Salomonsen 1951). Other familiar examples of long-distance dispersal impelled by weather phenomena include the invasion of Newfoundland and Labrador by storm-driven Lapwings in 1927 and 1966 and the appearance of numerous North American passerines and Monarch butterflies that were carried to the British Isles by a storm in the fall of 1968.

It is clear that long-distance vagrancy can infrequently pay large dividends for birds. There has undoubtedly been dispersal between the tropical populations of Red-billed Tropicbirds in three oceans. Such dispersal would involve easterly or westerly migration. However, northward migration, taking a tropicbird from a virtually aseasonal, tropical environment to a strongly seasonal environment, would seem to provide no adaptive advantage. I propose the most parsimonious explanation for the occurrence of tropicbirds in the northeastern United States is that such vagrancy is impelled by weather phenomena rather than by natural selection for a tendency to wander northward. I believe that any tropicbird found outside tropical and subtropical waters is, in fact, lost, due to the overriding influence of meteorological events.

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