

THE AUK

A QUARTERLY JOURNAL OF ORNITHOLOGY

VOL. 100

JULY 1983

NO. 3

"REPLACEMENTS" OF LANDBIRD SPECIES ON SOCORRO ISLAND, MEXICO

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ABSTRACT.—The endemic dove *Zenaida graysoni* of Socorro Island, an oceanic island in the Pacific south of Baja California, became extirpated between 1958 and 1978, and the endemic mockingbird *Mimodes graysoni* diminished during the same years and was approaching extinction by 1981. The mainland Mourning Dove *Z. macroura* became established on Socorro between (probably) 1971 and 1978, and the mainland Northern Mockingbird *Mimus polyglottos* between 1978 and 1981. Superficially an instance of replacement of island endemics by mainland relatives through competitive exclusion, the case is actually more complicated. We argue that extermination of the endemics was probably caused by predation by feral cats introduced in 1957 or later. There is no evidence of any actual competition between the pairs of species, and their preferred habitats overlap only slightly. We attribute the nearly concurrent establishment of the two invading species, known to have occurred frequently as casual visitors to Socorro and other islands, largely to the provision of fresh water made available as a result of human settlement. Our data show that simple comparison of island species lists compiled at intervals is an inadequate base for theories of island species turnover. Received 24 May 1982, accepted 4 October 1982.

"When a species native to a large area is successfully introduced into a new small area, the related species which is native in this area and with which the former comes into competition is soon supplanted."—J. Grinnell (1925).

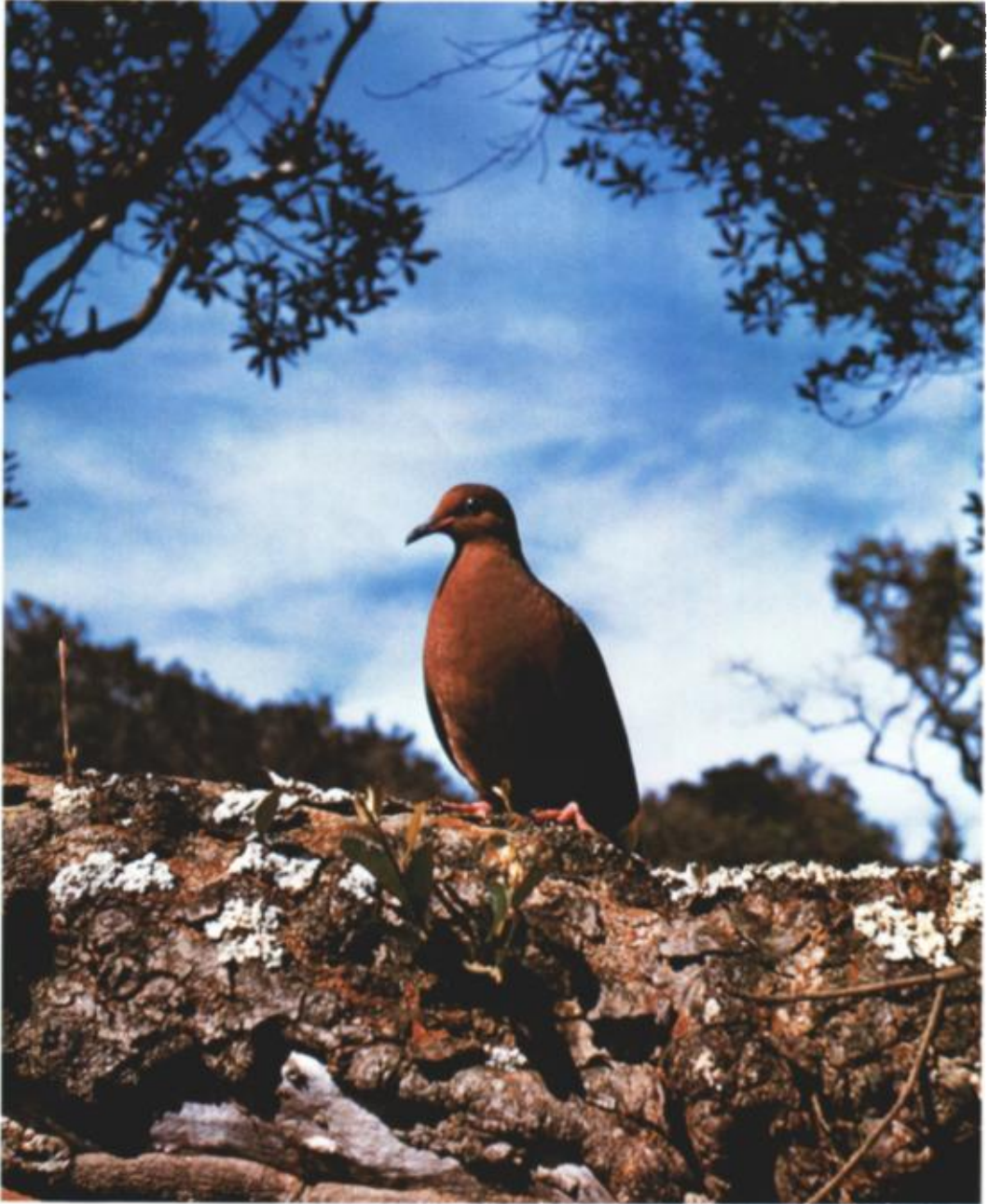
"Things are seldom what they seem."—Little Buttermilkcup.

RECENT interest in island biogeography owes its origins principally to the work of MacArthur and Wilson (1967). They proposed (1) that the size of an island's fauna is predictable from knowledge of its area and its distance from other source faunas and (2) that, although species composition might be in a state of flux as a result of the establishment of newly colonizing species and the extinction of former inhabitants ("turnover"), the number of species comprising the fauna tends to remain relatively constant ("equilibrium").

The MacArthur-Wilson model has been widely extended and refined (e.g. Diamond

1969, Power 1972, Hunt and Hunt 1974, Lynch and Johnson 1974, Jones and Diamond 1976, Marshall et al. 1982) and applied to conservation problems (Diamond 1975, Temple 1981). It is important to recognize that the data on which the model is based are simply faunal lists made at different periods, of which a disproportionate number have been based on the ornithological literature. As Gilbert (1980) has shown, however, there are many reasons for doubting the validity and application of those data. Further, recent paleontological studies (e.g. Pregill and Olson 1981, Olson and James 1982) have cast serious doubt on the concept of an equilibrium number of species for any island.

Although the causes of turnover are not an explicit part of the MacArthur-Wilson model, it is clear that those authors regard competition as an important cause of extinction (MacArthur 1972). It follows, therefore, that the loss or gain of a species may be directly related to a change



FRONTISPIECE. Socorro Dove (*Zenaida graysoni*) in its natural habitat on Socorro Island, 10 March 1957; elevation 550 m. Photograph by Reid V. Moran.

in the status of another, often closely-related, form.

In this paper we document two cases of turnover that involve replacements in an island avifauna by closely related taxa. These exchanges are so striking that they would appear to be "textbook" examples of competitive exclusion. Field data obtained during the period of replacement, however, show that the competitive exclusion hypothesis is untenable.

Socorro Island, largest of the Revillagigedo Islands of Mexico (ca. 210 km²), lies approximately 400 km south-southwest of the tip of the Baja California peninsula. Formed by volcanic eruptions, it is a true oceanic island, never having been connected to the mainland. The resident avifauna, omitting seabirds but including one heron, consists of only 10 forms, all of which are endemic at the subspecies (7), species (2), or generic (1) level. The bird life of the island is well known as a result of several early expeditions, long-term studies by B. H. Brattstrom (Brattstrom and Howell 1956) that have been continued to the present, and two recent expeditions (1978, 1981) by the authors (Jehl and Parkes 1982). One of the most interesting findings of the recent expeditions was the discovery that the status of two endemics, the Socorro or Grayson's Dove (*Zenaida graysoni*) and the Socorro Mockingbird¹ (*Mimodes graysoni*), has changed dramatically in the past 25 yr. The dove has evidently become extinct, and the mockingbird appears to be on the verge of extinction. Concurrently, two mainland relatives of the island endemics, the Mourning Dove (*Zenaida macroura*) and the Northern Mockingbird (*Mimus polyglottos*), have become established and are now thriving.

This situation, in which island forms have disappeared while their close relatives from the mainland have become established, represents the most dramatic case of replacement known in birds, and we have little doubt that ecologists comparing faunal lists made in 1958 and 1981 would invoke the competitive exclusion hypothesis to explain it. But they would be in

error. Here we review the histories of the endemics and the invaders, and we argue that the competitive exclusion hypothesis is untenable for Socorro Island.

THE DOVES

The Socorro Dove (*Zenaida graysoni*) is a highly distinctive bird. Larger than the well-known Mourning Dove (*Z. macroura*) of the North American mainland, with ruddy rather than buffy underparts, a different pattern of tail markings, and different vocalizations, it has been treated by some authors as no more than a race of the Mourning Dove, of which it is an obvious derivative. It is perhaps 15–20% heavier than the Mourning Dove, and, in accordance with a frequent pattern of variation in island birds, has a longer bill and much longer (29%) tarsi than the mainland dove, but shows little difference in wing and tail length. The Socorro Dove was discovered in 1867 by Edward Grayson and his father, A. J. Grayson, an early naturalist and explorer of the Mexican islands. The Graysons found this dove in the vicinity of the cove that bears their name on the southwestern corner of Socorro. (Place names on Socorro may be found on the map presented by Jehl and Parkes 1982.) A. J. Grayson (1872) called his probable new species the "Solitary Dove," as he never saw more than one or two at a time; the Mourning Dove, except when nesting, is highly gregarious. Grayson and most subsequent observers commented on the incredible tameness of the Socorro Dove; apparently, it was not uncommon to have one walk across one's shoes or enter one's tent (R. Moran pers. comm.), and Grayson as well as Villa (1960) noted that doves could be captured by hand.

Anthony (1898) reported that in May 1897 the dove "did not seem to be at all common, but was perhaps more abundant in the higher parts of the island." Kaeding (1905), who accompanied Anthony but published separately, stated that it was "not common, evidently breeding May 2nd." This evaluation as uncommon was probably based entirely on observations at lower elevations. McLellan (1926), who published information on the birds studied by the California Academy of Sciences Expedition, which visited Socorro 2–12 May 1925, stated from the field notes of the taxidermist of the expedition that *Zenaida graysoni* was "very numerous . . . , being particularly abundant on the

¹ This species is known in much of the literature as "Socorro Thrasher," but it bears little external resemblance to the true thrashers of the genus *Toxostoma*; its general appearance and behavior (including vocalizations) are more like those of the true mockingbirds (*Mimus*).

higher wooded levels, and ranging almost to the top of the island"; the central peak, Mount Evermann, reaches about 1,130 m. Thirteen of the doves were captured alive "with an ordinary fisherman's landing net tied on the end of a stick about six feet long" (Hanna 1926). Brattstrom and Howell (1956), in a comprehensive review of the avifauna of the Revillagigedo Islands, noted that the Socorro Dove was "common around rocks at low elevations in March 1953, but in November 1953 it was rare in such places and common above 1500 feet." Data from specimen labels in several museums also indicate that most doves were collected at 500 m or higher. Villa (1960) visited several localities and habitats on Socorro in January 1958 but did not specify exactly where he saw the dove. This is unfortunate, as he was the last to report this species. R. Moran had seen and photographed several in March 1957 (see Frontispiece); neither he nor Villa had any indication that the dove was declining.

In April 1978, our field party of six, including R. Moran and B. Brattstrom, failed to find any trace of the Socorro Dove, but our searches were made at elevations below 600 m. Instead, we found that the Mourning Dove had become established since 1958 (and perhaps since 1971, when Brattstrom had last previously visited the island); these were the first records for Socorro. It was common and widely distributed in open dry wooded areas and adjacent scrub and meadows on the south and east sides of the island as far north, at least, as the airstrip. We saw scattered flocks of up to 40 Mourning Doves between Bahía Braithwaite and the airstrip, and some were seen as high as 500 m. Some were courting, and their calls, heard commonly in the early evening, were indistinguishable from those of mainland birds. The calls of the Socorro Dove are quite different (Baptista et al. MS) and would have been easily recognizable. We also saw courtship flights and found two active nests and one deserted nest. The species was unequivocally established.

Our failure to find *Zenaida graysoni* prompted a second expedition, in April 1981. Not only did we revisit many areas studied in 1978, but our party of four (including R. Moran and a local guide) spent two days and nights camped in the forested areas of Mount Evermann, at 500 m and 650 m, where the species had been most abundant. Although we made thorough searches in each of the major habitats of the

island, and even climbed above the forest to the crest of Mount Evermann, we found no trace of the species. Furthermore, the personnel of the military base on Socorro were unfamiliar with this dove. We have concluded that *Zenaida graysoni* is extinct in the wild state.

In 1981 Mourning Doves seemed even commoner than in 1978 in the dry lowlands, and over 100 were seen at one time in trees bordering Laguna Escondida, where they flocked and drank. In 1978 we saw no Mourning Doves above 500 m, but our observations there were very brief; in 1981 a few were present and calling in open areas within the forest up to about 650 m.

THE MOCKINGBIRDS

The Socorro Mockingbird (*Mimodes graysoni*) is even more distinctive than the Socorro Dove. The latter is rather clearly derived from the mainland Mourning Dove, whereas the mockingbird, placed in its own monotypic genus, has no obvious mainland relative. Anatomically it appears in some ways to link the true mockingbirds (*Mimus*) with the thrashers (*Toxostoma*) (Gulledge 1975) and may be a relict of a primitive form ancestral to both. Its voice is more like that of a mockingbird (J. Barlow pers. comm.), as is its general appearance.

Like the dove, the Socorro Mockingbird was formerly widespread and tame. McLellan (1926) wrote that it was "the most abundant and most widely distributed species on Socorro. They were particularly numerous about the spring at Grayson's Cove, and in the heavily wooded cañons." Hanna (1926), a participant in the 1925 expedition, wrote that in the densely forested canyons on the upper slopes of Mount Evermann, "the trees were teeming with bird life . . . the curiosity of the mockingbirds was uncontrollable. They would hop up and peck, jay-like, at our knapsacks or boots. . . . This fearlessness of the birds is one of the most striking features of far away, uninhabited islands such as this." In March 1953, Brattstrom found this species "common at lower elevations on Socorro . . . at that time they seemed to prefer open areas with a few shrubs." In November of the same year, *Mimodes* "appeared to be rare at lower elevations on the south side of Socorro but common in forested areas at higher elevations and in canyons on the north side of the island" (Brattstrom and Howell 1956). Villa

(1960) reported that during his 1958 visit the mockingbirds, like all of the other Socorro species, were extraordinarily tame, to the extent that one pair fed from his hand, and one flew to his shoulder and sang. He stated that mockingbirds were abundant in the higher wooded parts of Socorro, and "siempre nada huranos con el hombre" [= never shy towards man].

By 1978 *Mimodes graysoni* appeared to be almost entirely restricted to the vicinity of large fig groves near the coast. Away from the coast our party found only two near the airstrip in 2 days of field work, whereas in a relatively small area of fig groves at Playa Blanca there were as many as five, somewhat wary but readily seen. This favored habitat is very restricted. In 1981 most of our time was spent searching for the dove, and we spent little or no time in most of the areas where mockingbirds had been present in 1978, except for Playa Blanca. Here Parkes, using playback of songs recorded in 1978, elicited a distant response from one point, and later lured into the open what may have been the same individual. But for the lure of the playback, we would not have detected this species at all. The Socorro Mockingbird now is absent or exceedingly rare in most of its former range, and we consider the prospects for its survival dim.

On 10 April 1978, Brattstrom saw a Northern Mockingbird (*Mimus polyglottos*) at Grayson's Cove, and Parkes and Brattstrom saw two, about 300 m apart, in open country below the airstrip 2 days later. These were the first records of this mainland species. By April 1981, Northern Mockingbirds were abundant on the southeast side of the island, in open and scrubby areas up to about 400 m. On 6 April we saw at least 30 individuals and found a nest containing a large juvenile.

DISCUSSION

The successful establishment of immigrant birds on Isla Socorro, 400 km from the nearest mainland, must be a rare event, as all 10 of the resident nonmarine species are endemic, from well-marked subspecies to one distinct genus. It is thus especially notable that two, or 20%, of the resident species appear to have been replaced by mainland relatives in a period of less than two decades.

What events led to the extinction of the So-

corro Dove and the impending disappearance of the Socorro Mockingbird? An obvious "explanation" is that the "fragile" island endemics were replaced by more "vigorous" mainland stocks via the process of competitive exclusion. The theory underlying this explanation is discussed by Mayr (1963: 74-76), with citations of various examples. If the competitive exclusion explanation were appropriate to Socorro, it would be remarkable that the replacement events took place virtually simultaneously and congruently in two very different types of birds. Full data for the critical years are unavailable, but there is sufficient information about the birds and the island ecology to support an alternative explanation. At least one and perhaps both endemics were largely gone prior to the arrival of the mainland species. Thus, we think that the process involved was a simple one of immigration and colonization that had no direct effect on the insular forms.

FACTORS PROMOTING EXTINCTION

Although the causes of the decline of the endemic taxa on Socorro can never be known with certainty, a number of possible contributing factors can be analyzed.

Human factors.—Although there had been a few temporary settlements on Isla Socorro (Richards and Brattstrom 1959), by 1956 Brattstrom and Howell described it as uninhabited. In 1957 the Mexican Government established a small military garrison and weather station near Bahía Braithwaite. The presence of humans had no direct effect on the avifauna; in fact, Villa (1960) reported that in 1958 the soldiers were protective of the local birds, with the exception of the Red-tailed Hawk (*Buteo jamaicensis socorroensis*), which they persecuted because it killed other birds for food. The hawk, nevertheless, persists in fair numbers to this day (Jehl and Parkes 1982). The military garrison expanded in the late 1970's, in part to accommodate construction of an airstrip on the island, which was completed in 1980. The base commander in 1978-1981 was particularly solicitous of the wildlife on Socorro and took actions to help in its preservation.

Sheep were introduced on Socorro in 1869 and are still abundant. Although parts of the island appear severely overgrazed, creating new, open field environments that were probably not present a century ago, the impact of

the sheep on the endemic avifauna has been minimal, as there was no apparent change in either abundance or wariness of birds from Grayson's time through 1958. Soldiers are permitted to hunt feral sheep in many parts of the island, even to the crest of Mount Evermann, but do not disturb birds during their hunting trips, and we certainly have no reason to implicate either the sheep or their hunters in the decline of the dove and the mockingbird.

The Socorro Dove has been maintained in aviaries for many years (and now survives only as an aviary bird). To the best of our knowledge, the last wild-trapped doves were removed from the island in the mid 1940's. In view of the tameness of the doves, it is conceivable that some were caught by soldiers and maintained as pets. In view of the species' former wide distribution, the small size of the garrison, the infrequency of collecting trips, and the species' persistence until the late 1950's, we see no serious possibility that overtrapping depleted the dove population. There is no evidence that the Socorro Mockingbird was ever kept in aviaries, although it is possible that some were trapped by local inhabitants; in 1981 we witnessed a soldier capturing a fledgling Northern Mockingbird for a pet. Trapping is even less likely to have affected the population of *Mimodes graysoni* than might be true of the dove.

Environmental factors.—Despite two decades of human occupancy on Socorro, we have observed no environmental changes of sufficient magnitude to have caused the decline of the dove and mockingbird. The island is large and extremely rugged; human activity near the airstrip, the garrison, and the small agricultural areas is so restricted as to leave by far the majority of the island undisturbed.

Biological factors.—One might postulate that the mainland Mourning Dove was able to swamp the endemic form by interbreeding, in effect hybridizing it out of existence. At a lower taxonomic level, this is what happened to the endemic subspecies of Madagascar Turtle-Dove (*Streptopelia picturata rostrata*) on most islands of the Seychelles after the introduction of the mainland Madagascar subspecies *S. p. picturata* (Penny 1974). The Socorro Dove has, in fact, hybridized with the Mourning Dove under captive conditions. There is no evidence, however, of introgression in the present dove population. This is based on the examination of

several specimens collected in 1978 and on careful scrutiny of hundreds of doves at close range in 1981. The mockingbirds are so distinct that we doubt that they would hybridize under any circumstances.

We cannot exclude the possibility that the endemics succumbed to diseases introduced by the immigrants, but that seems unlikely because the ranges and habitat preferences of the species involved are so different (see below) that contact, if any, would have been minimal.

Predation.—There are no native mammals on Socorro Island and only two raptorial birds, one of which is the tiny insectivorous Elf Owl (*Micrathene whitneyi graysoni*). The other is the endemic subspecies of Red-tailed Hawk. Although this hawk on the mainland is primarily a mammal-feeder, on Socorro it feeds on birds, land crabs, and probably lizards. Villa (1960) reported that the hawk was adept at catching Common Ground-Doves (*Columbina passerina socorroensis*), and the crop of one collected by the 1925 expedition contained a Socorro Dove (McLellan 1926). In April 1981, Parkes found remains of a Mourning Dove and a Common Ground-Dove at Laguna Escondida; both had probably been killed by hawks. The Red-tailed Hawk, the Socorro Dove, and the Socorro Mockingbird long coexisted successfully, as evidenced by their taxonomic distinctness from mainland relatives. It is unlikely that any recent shift in predation by the hawk could have been involved in the decline of the other two species.

Human settlement of the island in the late 1950's was responsible for the introduction of domestic animals, and cats have become feral. No cats were reported on Socorro prior to establishment of the military base. The size of the present feline population is not known, but it may be considerable. We found a nest of cats in 1978, far from settlement, and in 1981 we found the remains of several Townsend's Shearwaters (*Puffinus auricularis*) high on Mount Evermann, within the woodlands formerly occupied by the Socorro Dove. This shearwater spends the day at sea, returning to the island only after dark, and is thus vulnerable only to a nocturnal predator while ashore. The only nocturnal predator capable of killing a shearwater or a dove is the cat. The tame, ground-dwelling doves and mockingbirds would have been easy prey for cats, by night or day.

We infer that feral cats were responsible for

the extinction of *Zenaida graysoni* and the near-extinction of *Mimodes graysoni*. We base this conclusion in part on a broader examination of the fauna (Jehl and Parkes 1982), in which we show that the relative abundance of tree-dwelling birds on Socorro has increased whereas all the ground-nesters have declined. The arboreal endemic wren (*Thryomanes sissonii*) and warbler (*Parula pitiayumi graysoni*) are not only abundant but retain the traditional fearlessness of the insular avifauna. By contrast, the ground-nesting towhee (*Pipilo erythrophthalmus socorroensis*), although still present in fair numbers, is neither as abundant nor as tame as reported by all observers prior to 1978.

Competitive exclusion.—Although we accept the possibility that *Zenaida macroura* invaded Socorro prior to the disappearance of the endemic *Z. graysoni* (we lack firm data for the period between January 1958 and April 1978), and we know that *Mimodes graysoni* was declining during the three-year period in which *Mimus polyglottos* became established, we do not believe that competitive exclusion was involved. Indeed, we agree with Pregill and Olson (1981: 91) that “ecological doctrine and good sense revolt at the idea that a species with a long history of adaptation to a particular environment would be at a competitive disadvantage with newly arriving colonists.”

In *Zenaida*, direct physical exclusion of the island species by the mainland species is unlikely for several reasons. First, the Socorro Dove is considerably larger than the Mourning Dove and, in the experience of aviculturists (L. Baptista pers. comm.), is dominant to the smaller species in all interactions. It is a very feisty species and aggressive toward *macroura* when they are caged together. Second, the absence of direct competition is indicated by the very different habitat preferences of the two species. The Socorro Dove is a ground-nesting species, and its principal habitat was the fig forests at higher elevations. That habitat today is not used by the tree-nesting Mourning Doves, which occur in abundance at lower elevations in more arid situations in open woodlands, similar to their preferred habitat on the mainland. We see no possibility here for any competition.

Similarly, the preferred habitats of the island and mainland mockingbirds are dissimilar. Although the island endemic species formerly occurred over most of Socorro, it preferred forested areas. Before the arrival of the Northern

Mockingbird in 1978, *Mimodes graysoni* was already confined almost exclusively to dense fig groves and canyons along the coast. The invading species, like the Mourning Dove, is found in open farmland and fields with scattered groves or isolated trees. Only once, in 1978, did we see a Northern Mockingbird in the habitat of the Socorro Mockingbird; not only is it unlikely that the recent immigrant competes in any way with the endemic species, but it is probable that the populations of the two species have not even been in contact since the arrival of the Northern Mockingbird.

It is thus our contention that feral cats have depleted or eradicated the ground-nesting endemic birds on Socorro and that the invasion by two related mainland forms bears no causal relationship to the decline of the endemic insular species. Indeed, under present environmental conditions on Socorro it seems possible that the native and invading species could coexist.

It would be logical to ask how the Mourning Dove and Northern Mockingbird were able to withstand cat predation, especially immediately after their immigration while their populations were still low. Unlike their endemic relatives, both species nest in trees—and the arboreal birds of Socorro Island remain as abundant as ever. Although the Northern Mockingbird and, especially, the Mourning Dove forage on the ground, the open habitats they prefer would make stalking them by day-hunting cats more difficult than would have been true of the Socorro Mockingbird and Socorro Dove.

In a similar study, Diamond and Veitch (1981) compared the abundance of native and exotic (introduced by man) bird species in disturbed forest on the mainland of New Zealand and in relatively undisturbed forest on islands in Hauraki Gulf. They concluded that “exotic bird species were not able to achieve their present penetration into New Zealand forest until the forest structure had been disturbed by browsing and logging, or until native species had been decimated by predation, disease, and these habitat changes.” On Socorro, as we have shown, reduction of the endemic avifauna is not related to the limited habitat disturbance created by sheep. On the other hand, both the Northern Mockingbird and Mourning Dove chiefly inhabit those areas that have been most heavily grazed. Thus, the sheep may have cre-

ated suitable habitat for the invaders, resulting in additions to the avifauna but without any correlated loss.

FACTORS PROMOTING SUCCESSFUL COLONIZATION

Mourning Doves are very strong fliers and are among the land birds most frequently seen off southern California, often many miles at sea (Jehl pers. obs.). The species has been recorded from all of the islands off California and Baja California, and we have no doubt that it has reached Socorro frequently, even though it had not been seen there by ornithologists prior to 1978. The species became established twice previously on the Revillagigedos, having evolved into the endemic *Zenaida graysoni* on Socorro and *Z. macroura clarionensis* on Clarión. Mourning Doves have been seen on San Benedicto but cannot become established there because of the absence of fresh water. Similarly, there are records of the Northern Mockingbird from most of the California and Mexican islands, including Guadalupe and Clarión, indicating a fair dispersal ability over the open seas.

Given the dispersal potential of these two species, especially the dove, how can we explain the colonization of both on Socorro in an interval of two decades? There is no evidence that either species was introduced by man, and this was confirmed by our conversations with military personnel.

One factor is competitive exclusion, but rather than the invading mainlanders prevailing over the insular forms, the invaders may have been prevented from colonizing by the locally adapted (and, in both cases, larger) island forms. This situation would persist for millenia, until (a) the insular endemics were in very low numbers or had already become extinct through some agency other than competition—in this case, predation by the newly introduced cats—or (b) habitat changes, or the restriction of island forms to certain habitats, created a vacant "niche." As Pregill and Olson (1981: 92) put it, "we see no reason why a species adapted to a particular set of conditions on an island would not persist indefinitely, provided that its environment did not change." This is essentially what Diamond and Veitch (1981) found in their New Zealand study.

Exclusion by the endemics might have con-

tributed to the failure of the mainland birds to colonize Socorro until 1958–1978, but another event was probably much more important. The establishment of the military base, though of minimal significance to the ecology of the island as a whole, did affect the immediate environment of the settlement. Not only were domestic animals introduced, but also food and ornamental plants, and this required the establishment of a fresh-water system. Socorro is a desert island; the only regular sources of fresh water are several intertidal springs, which are exposed for only brief periods each day. The Graysons survived being shipwrecked only because they landed, by chance, near the spring at Grayson's Cove. Other than the springs, the only natural sources of drinkable water (there are some hot springs high on Mount Evermann) are rain-filled pools; these are temporary and seasonal, and may be absent in dry years.

The principal dispersal of land birds is that of immature individuals in the autumn, a well known phenomenon that accounts for many "out of range" and unusual distributional records. During migratory flights "water requirements rather than energy reserves in some instances may limit flight range" (Blem 1980: 204). Furthermore, "long-range migrants unable to obtain fresh water may have a severe tendency to dehydrate" (Blem loc. cit.). Therefore, the rapid discovery of fresh water within a few hours of reaching landfall is probably critical to the survival of migratory or lost birds. At Socorro in fall the rain pools are dry, and the possibility that waifs will discover the localized sources of intertidal water during the brief hours they become available each day seems very small. Some desert species are able to survive for long periods without fresh water, but Mourning Doves, despite their widespread distribution in arid regions, require water daily and are unable to subsist on 50% sea water (Bartholomew and MacMillen 1960). No data on the osmoregulatory abilities of the Mockingbirds are available, but there is no reason to suspect that they are exceptional.

With the establishment of the military base, with its human families and their domestic animals, gardens, and orchards, fresh water that could be used by migrants became available year round. Survivorship of newly arrived birds would be greatly increased, and species that could find an appropriate vacant "niche"—such

as the open field habitats created by overgrazing sheep—would have a much improved opportunity to become established.

We have no direct evidence from Socorro for the critical water theory, but there appears to be a comparable situation on Guadalupe Island. The Mourning Dove was considered to be accidental there prior to 1952 (Howell and Cade 1954), having been recorded only once, in the 1880's. Subsequently, doves were reported in August 1956 (1), November 1964 (1), and February 1967 (24), dates compatible with the timing of the fall dispersal. By 1970 the species was widespread and nesting, and in August 1981 the population numbered in the low hundreds (Jehl and Everett MS). The colonization was approximately synchronous with that on Socorro, but probably not because of any change in the abundance or dispersal patterns of mainland populations. In the late 1960's the military garrison at the south end of Guadalupe was enlarging, and leaks from the freshwater system were common in the village, providing an attraction for the endemic House Finch (*Carpodacus mexicanus amplus*), often considered a full species (Jehl pers. obs., photos). Habitat conditions on Guadalupe are such that doves are among the very few species that might be expected to become established. Although the Northern Mockingbird has not become established there, it has reached that island. One was convincingly described to Jehl on 22 February 1969, the first record since two were seen by Bryant in March 1886 (Jehl and Everett MS).

CONCLUSIONS

Double invasions of islands by mainland stocks of birds are not uncommon (Mayr 1963), but they must almost always be studied inferentially, long after the invasions occurred. We were fortunate to visit Socorro during the actual establishment of one species, the Northern Mockingbird, and have been able to narrow the establishment of the Mourning Dove to a period of 20 years or (probably) less. Furthermore, we have first-hand knowledge of the ecological conditions on the island and of the habitat preferences of the species involved in the turnover.

At their present rate of population growth, Mourning Doves and Northern Mockingbirds can be expected to expand their range to in-

clude much of Socorro in the near future. Had we not visited the island in 1978 and 1981 but 20 years hence, we might have found that the size of the avifauna remained constant but that two endemic forms had disappeared and their mainland counterparts had become widespread. This simple comparison of species lists would have led us to the "acceptable," but incorrect, conclusion that the Socorro situation was a classical case of replacement via competitive exclusion.

In an important review of the zoology of West Indian vertebrates, Pregill and Olson (1981) documented the inadequacies of theories of island biogeography that were constructed without an historical and paleontological perspective. Our data from Socorro confirm their skepticism and show that an historical perspective of as little as a decade may be critical for interpreting turnover on oceanic islands; for near-shore islands annual censuses are necessary (Diamond and Jones 1980).

So long as the testing of theories of island biogeography is based primarily on comparisons of faunal lists from different periods and does not incorporate information about ecological conditions, habitat preferences of the endemic and "replacement" species, and extraneous factors such as, on Socorro, the establishment of feral cats and the provision of supplementary water supplies, interpretation of turnover data will be hazardous, if not impossible (see also Lynch and Johnson 1974). Because such data are not available for most islands, we advocate great caution in extrapolating comparisons of faunal lists to general descriptions or theories regarding processes of faunal change.

ACKNOWLEDGMENTS

Most of the cost of the 1978 expedition was covered by grants from the M. Graham Netting Research Fund and the Edward O'Neil Field Fund of the Carnegie Museum of Natural History. Additional funding was provided by Hubbs-Sea World Research Institute. The 1981 expedition was sponsored by Tom and Dorothy Hawthorne of San Diego, California, with additional support from the M. Graham Netting Research Fund. Permission to conduct these studies was granted by the Mexican government. We thank Dr. Jorge Carranza Frazer for his interest in our studies and Capt. F. Urtaza of the Mexican Navy for support and hospitality on our visits to Socorro.

This paper has benefited from the comments of E.

Connor, J. Diamond, N. K. Johnson, B. G. Murray, Jr., and D. M. Power, all of whom have sufficient confidence and courtesy to sign their reviews.

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