EXPERIMENTS ON HOMING IN LAYSAN ALBATROSSES, *DIOMEDEA IMMUTABILIS*

HARVEY I. FISHER

Department of Zoology and School of Medicine
Southern Illinois University
Carbondale, Illinois 62901

It is legendary that breeding albatrosses return to the same nest site year after year. That certain species actually do so has been demonstrated, for example, in the Royal Albatross, *Diomedea epomophora* (Richdale 1950; Tickell 1968); Laysan Albatross, *D. immutabilis* (Rice and Kenyon 1962; Fisher 1969); Black-footed Albatross, *D. nigripes* (Rice and Kenyon 1962); and Wandering Albatross, *D. exulans* (Tickell 1968). Rowan (1951) reported that at least some Yellow-nosed Albatrosses, *D. chlororhynchos*, returned to the same site.

Studies in recent years have refined our views of this return of breeding birds. Fisher (unpubl.) has found that only members of unbroken pairs and males of broken pairs of Laysan Albatrosses return so precisely to the same site. Surviving females of broken pairs may nest at considerable distances, although usually in the same colony. The basis for the sexual difference in site attachment between survivors is apparently the fact that males maintain for life the small territories within which the females select the nest sites. A similar situation appears in the Royal and Wandering Albatrosses (Tickell 1968). There is no firm evidence that any Laysan Albatross, male or female, has ever nested on an island other than the one where it first nested.

Only the Laysan Albatross has been studied long enough to determine the age, site, and frequency of return of juveniles. Fisher and Fisher (1969) and Fisher (unpubl.) found very few instances of young hatched on one island breeding on another island. Most young settle to nest not far from their own hatching sites, as will be discussed later. This is contrary to the early suggestion of Rice and Kenyon (1962:532) that "innubile birds wander and eventually establish territories some distance from their hatching sites." Fisher and Fisher (1969) also established that juveniles usually visit the natal colonies several times in each of the pre-breeding years after the third year.

Nestlings also exhibit homing to the nest. Chicks 2–5 months of age regularly returned to the nest site when displaced as far as 75 yards (Fisher, unpubl.).

All the evidence thus indicates that Laysan Albatrosses of all ages are firmly attached not only to the island of their origin, but to the colony of origin, the vicinity of the nest of origin, and the nest site previously used. We also know from the experiments of Kenyon and Rice (1958) that Laysans will home very rapidly, sometimes from places outside the current range of the species. Matthews (1968: 63) has described these homing flights as the longest successful homing flights yet reported.

What we do not know is the age at which Laysan Albatrosses first acquire sufficient information to make possible a later return to the nest site, the colony, and the island. And we know nothing of the cues the albatrosses use for orientation or navigation.

When I first became interested in albatrosses and some of these problems in 1945, it seemed unreasonable to expect that a young Laysan could acquire the necessary cues for return to the colony and natal nest without actually flying over and away from that site. How could a chick, still bound to the earth and perhaps mostly hidden from its surroundings by dense vegetation or buildings, obtain the proper cues for a return by flying? I also believed that breeding birds used nearby topographical features—trees, bushes, rocks, runways, buildings—as cues for return to the specific nest site. The early experiments to test these views involved transporting flightless chicks to other islands, as well as gross modifications of the terrain within a nesting colony.

Parenthetically, I should add that another purpose in translocating young albatrosses was to see if we could establish other colonies, should military operations and the control program recommended by the U.S. Fish and Wildlife Service on Midway Atoll endanger the one-third of the world's population of Laysan Albatrosses that breed there. This aim was developed in spite of several past failures in attempts to establish or reestablish breeding populations of wild birds (McCabe and Hale 1960). Past attempts had involved interspecific adoption and/or establishment in an environment where there were no conspecifics currently breeding. Our attempts would in-

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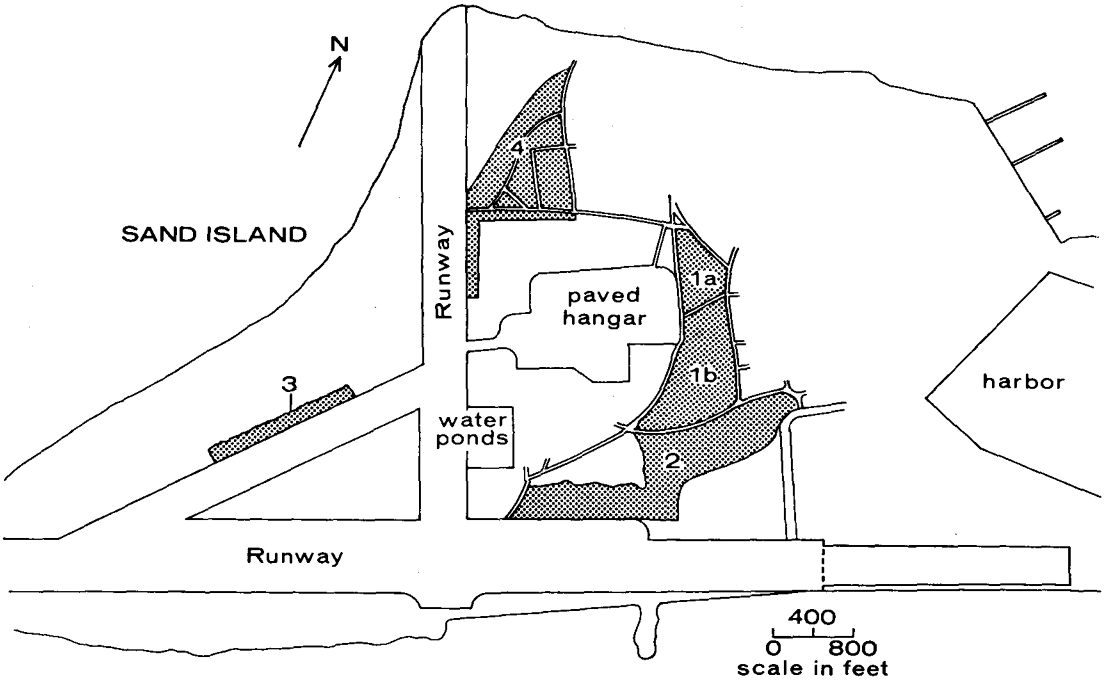

FIGURE 1. Sand Island, Midway Atoll, showing sites (1a, b, 2, 3, 4) of origin of Laysan Albatrosses used in the experiments.

clude only intraspecific adoption and establishment where at least small populations of Laysans were currently breeding.

The purpose of this report is to present evidence on homing by Laysan Albatrosses in various stages of the life cycle, and some views on cues and the age at which they are used. Although not all of the transported birds are yet of breeding age, most are beyond the age when males select territories and forever attach themselves to one place. Consequently, although the study is continuing, it is unlikely that any further accumulation of evidence will change substantially the results apparent now. The evidence is presented now at the urging of Mr. Frank Bellrose who suggested that the findings would be of current interest and aid in evaluating certain aspects of bird navigation. Moreover, it may stimulate the further reporting of our experimental birds by residents and the occasional ornithologist in the area. To encourage this, the numbers and colors of bands on transported birds are listed in the text.

DESIGN AND EXECUTION OF THE EXPERIMENTS

The design was established in major part by the natural and modified conditions on Midway, the location of other islands, and by the age at which we could move young birds. Availability of tugs, barges, trucks, planes, and personnel, and age of chicks determined the timing of the experiments. We could separate chick from parent only if the chick was nearly ready to leave the colony and be on its own, or if it was at an age to accept a foster nest and be accepted by foster parents. In Experiments 1 through 4, which involved transporting chicks, later recapture of the birds was facilitated by obtaining the young, whenever possible, from a single central area of Sand Island (fig. 1, area 1).

Experiments 1, 2, and 3 were designed to test the return to the natal colony in later years of fledglings ready to leave the nest but not yet capable of flight. The birds were essentially free of down (fig. 2) and approximately 5.5 months of age.

Experiment No. 1. This was a pilot experiment to test the feasibility of moving young albatrosses. It was so successful that the results are included. On 15 and 16 July 1961 we moved 991 fledglings to the south shore of Eastern Island, an airline distance of 3 mi. E. Trucks with stockracks were driven into the colonies in areas 1 and 2 of Sand Island (fig. 1) and the young lifted in. The trucks were then driven onto barges for the trip across the lagoon. It is important to note that these young birds had complete access to whatever topographic, celestial, or other cues may have existed during the period of transport.

The birds were released within 5 hr at the juncture of beach sand and brush and within 100 ft of the water in the lagoon in which many young Laysans were already paddling about. This release site was

FIGURE 2. A fledgling Laysan Albatross typical of those translocated.

chosen because the reef is near the land and the intervening water is shallow. Thus, the young would encounter fewer sharks and have a shorter distance to travel to deep water, both important factors in the mortality of young Laysan Albatrosses.

At the release site the birds were banded on the right leg with a standard numbered band (nos. between 667–40000 and 667–44481) and a blue plastic band. Nearly daily checks were made of the condition of the transported birds at the release area and of their spread along the beaches of Eastern Island. Searches for these birds in the areas of origin and release have been made in each egg-laying season since, 15 December 1964–1 June 1965, and 15 December 1968–1 March 1969.

Experiment No. 2. This experiment was designed to test the return of fledglings to the natal colony when they had no access to visual cues during transport.

On 24 July 1961 we moved 112 fledglings from area number 4 on Sand Island (fig. 1) to Green Island in Kure Atoll, an airline distance of 52 mi. NW. The young were placed in cardboard boxes in the colony, the boxes sealed, and then trucked to a seaplane for the flight. They were trucked approximately one-fourth mile across Green Island to the lagoon and, because there were no roads between the airstrip and the release area, they were carried by outboard motor boat to the sandy northeast tip of the island, where no Green Island Laysans were present. The birds were in the boxes approximately 8 hr. A standard band (numbers 667–44889 to 667–45000, inclusive) and a blue plastic band were placed on each leg.

Searches for these birds have been made as follows. At the site of origin, we searched weekly, 15 November 1964–1 June 1965, and three times between 15 November 1968 and 1 March 1969. At the site of release, James R. Fisher, a member of our group, checked the transported birds on 27 July 1961; James Hunt, a Coast Guardsman stationed on Kure, searched the island on 3 August 1961; and we have made four subsequent searches, once each in 1966 and 1967, and twice in 1969. Between 1963 and 1969, the Pacific Project of the Smithsonian Institution had one or two ornithologists on the island at virtually all times; they were working with albatrosses as well as other species and were informed of our experiment.

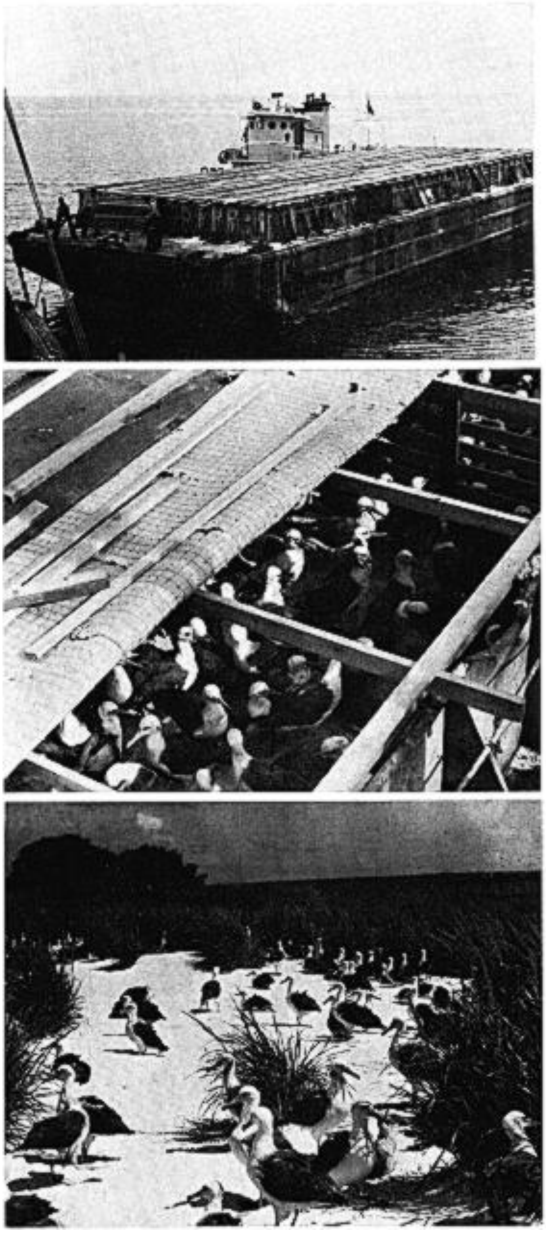

FIGURE 3. The move to Lisianski Atoll in Experiment No. 3: upper, the barge; middle, the young Laysan Albatrosses in the barge; lower, after release on the beach of Lisianski.

Experiment No. 3. The experiment was originally intended to test the return to the natal colony of fledglings moved a long distance and without access to visual cues. However, hot weather made some changes necessary, as is indicated below.

On 15 and 16 July 1962 we loaded 2021 fledglings for transport to the northwest shore of Lisianski Island, approximately 250 airline mi. SE of Midway. The young albatrosses were picked up from areas 1, 2, and 3 on Sand Island (fig. 1), and loaded into open stock trucks for the trip to the harbor where they were transferred, 200 birds to each of 10 slat pens (15 × 18 × 3.5 ft high) on a 30 × 90-ft steel barge (fig. 3).

Two inches of sand on the deck provided better footing and a dry surface for the birds, and the top was roofed with screen overlaid by roofing paper. We had intended to have the roof entirely closed to prevent any vision of the sky, but hot weather made some ventilation necessary. This was finally provided by small holes punched through the roofing paper with the claws of a claw hammer (fig. 3). The degree to which the birds could view the sky is thus open to some speculation. However, the barge was very unstable at sea and it would seem improbable that the birds could ascertain celestial relationships, at least in any manner comparable to that used by man.

At Lisianski on 17 and 18 July 1962 the albatrosses were put in discarded orange and onion crates and moved by small boat three miles across the reef to the shore. They were released on sand at the edge of the bunch grass cover of the island, above the high-water mark among the few fledgling Laysans reared on Lisianski (fig. 3). The birds carried band numbers in the series 697–01000 to 697–16500 and a red plastic band on the left leg. The longest possible period of confinement for any bird was 71 hr.

All materials used in the transfer were returned to Sand Island to prevent the introduction to Lisianski of any other foreign living materials.

We could not check on the dispersal on the island, or on the departure of the birds from it immediately after the transfer. Neither has any member of our group yet revisited the island. However, members of the Pacific Project and Eugene Kridler of the U.S. Fish and Wildlife Service have visited the island several times in the intervening years. They were aware of the significance of these birds to our work and presumably reported all banded birds found there.

Experiment No. 4. This experiment was conducted in order to test the return to the natal colony in later years of chicks which were moved at the age of three or four weeks and without access to visual cues. On 25 February 1965 we exchanged 97 chicks between the southcentral part of Eastern Island and area 1a of Sand Island (fig. 1). They were moved in closed, cardboard boxes and within 2 hr were placed in marked nests from which other chicks had been taken. Adoption was expected to be successful, as indicated by a few earlier, casual exchanges between nests in the same colony.

At the time of transfer the chicks were too small to retain standard numbered bands; they were marked with narrow red plastic bands. On 19 March 1965 we banded the survivors (63) on Sand Island (nos. 757–70000 through 757–70062). A wide blue plastic band was placed on the left leg, along with the numbered band. A wide red plastic band was placed with the narrow red band on the right leg. Unfortunately, the chicks moved to Eastern Island were banded earlier by a person not of our group, and I have been unable to determine the numbers used. Several of these chicks either lost their numbered bands because of too early banding or were never banded; in April we found the carcasses of several that had only the narrow red plastic band. Consequently, one-half of this experiment must be eliminated from consideration now and in the future.

Several searches of the Sand Island site were made prior to 31 May 1965. Later searches have been made as described for Experiment No. 1.

Experiment No. 5. This experiment was designed to determine how close the return of experienced breeding Laysan Albatrosses to the nest site in subsequent years would be when all landmarks in the vicinity of the nest site had been removed.

In the egg-laying seasons of 1961 and 1962 all nests in the permanent study plot (Fisher 1971) were marked with a numbered stake set 1 ft north of the rim of each nest. Stake numbers and band numbers of the pair using the nest were associated in the records. On 31 July and 1 and 2 August 1963, after virtually all of the young and adult Laysans were gone, we plotted the position of each nest site in the study area. At the same time we pulled all stakes, weeds, and grass and cut all brush and trees; the trees were hauled away, but the other vegetation was placed in windrows 10 feet apart. The small coral hillocks were leveled and the material shovelled into low places. Old nest sites were obliterated by raking.

The plot was then free of all standing vegetation and other landmarks. It was nearly as level as the 400-ft-wide runway which bordered it on the east. To the north and south there were grass and low weeds for a hundred yards and then a paved runway 400 ft wide. Old revetments with 25-ft ironwood trees bordered the south half of the west line of the plot; they constituted the only landmarks discernible to the human eye. They were 250 ft from some of the nests and more than 100 ft from nearly half of the 411 nests replotted in November and December 1963. Before the clearing was done, birds on the ground in the east half of the plot could not see the trees because of dense intervening brush.

Experiment No. 6. This experiment was structured to determine how close to the sites where they were hatched would be the nests of birds breeding for the first time.

Chicks hatched in 1961 and 1962 in nests plotted in Experiment No. 5 were identified with the nest of their natality. When the surviving chicks began to breed in 1968 and 1969, their nest sites were plotted, and the distance from the natal nest was measured. As an indication of movement into the plot by birds originating in the area which surrounds the plot on three sides, we banded 1122 chicks in the summer of 1961. Survivors moving into the plot to breed were identified in 1968 and 1969.

RESULTS

It is thought that the recaptures reported in this study represent minimum numbers; more than 99 per cent have been made by our group of workers. It is almost incredible that the various ornithologists working the Hawaiian chain during all these years have found so few of these albatrosses. However, the scarcity of recaptures by other workers may be but another manifestation of the closeness of attachment of Laysan Albatrosses to a restricted area. If the specific area where the birds were banded is not searched, one recaptures only vagrants.

Another event affecting the results of Experiments 1–3, which was beyond our control, was the bulldozing and paving of the south part of area 2 on Sand Island; birds originating here had no suitable place to return to. This continuing control program also included the killing of birds along the south edge of area 2 in 1964. There is no way of estimating the scattering effect of the "terrain modification" or the decimation of experimental birds.

Experiment No. 1. Of 991 fledglings moved, only 9 (1 per cent) died in transit. Forty-seven (5 per cent) were known to have died later on Eastern Island. Based on other studies, it seems likely that a nearly equal number of dead were not found. Consequently, perhaps 900 flew from the island. The rate of departure was similar to that of young from our permanent study plot; 90 per cent departed before 28 July and none was found on the island after 5 August. Before departure they scattered along the mile-long south shore of Eastern, tending to work upwind; only one was observed more than 100 yards inland. Seven, one of which was dead, were found before mid-August on the eastern and southern shores of Sand Island, three miles downwind.

In 1964–65, when they were 4.5 years old (from date egg was laid) but still 3 or 4 years from breeding, 164 birds were recaptured. These recaptures represented approximately 18 per cent of the number estimated to have departed successfully as fledglings. One was taken on Kure, one at sea, 47 at the site of release on Eastern Island, and 115 at the place of origin on Sand Island. Three were recaptured at both origin and release points; two of these were on Sand Island first, then on Eastern 9 and 42 days later; one was taken on Eastern first and on Sand the next day.

In 1968–69, when the birds were 8.5 years of age and starting to breed, 232 (26 per cent of number estimated to have departed as fledglings) were recaptured. Two were taken on Eastern Island, the remainder at or near their origin on Sand Island. Forty-six per cent of a group of 267 moved from area 1 were retaken there.

Experiment No. 2. All 112 fledglings transported to Green Island of Kure Atoll on 24 July 1961 survived the trip. A number flew into the lagoon as soon as released. Only 16 were found by James Fisher on 27 July, and James Hunt reported that the birds were gone within a week of release. He found one in the center of the island, one at the southwest tip, and one dead at the release site. The latter was the only known dead; perhaps 105–110 lived to fly away.

In 1964–65, 25 of these birds were retaken at the age of 4.5 years; this represented 24 per cent of the birds thought to have departed successfully in 1961. One was found at the release site on Green Island, one on Eastern, and 23 in the area of origin on Sand Island. One was recaptured on Kure in 1966.

In 1968–69 only seven birds were recaptured, all at the place of origin. Despite an almost continuous search by two ornithologists on Kure during this entire season, none of these experimentals was found. It should be mentioned that our own search of the place of origin in this season was limited by the press of other studies.

The months of first recapture of the 4.5-year-old birds in Experiments 1 and 2 were: Feb., 19 (10 percent); Mar., 65 (34 per cent); April, 77 (41 per cent); and May, 28 (15 per cent).

Experiment No. 3. Of 2021 fledglings loaded at Midway for transport to Lisianski, 118 died on the barge enroute and 66 died on the beach within 24 hr. This excessive mortality (14 per cent) was due to an improperly repaired hole in a forward compartment of the barge. The compartment flooded, the bow of the barge was thus lowered, and waves surged in, drowning some birds and so chilling others that they soon died.

The living birds were in good shape and within 24 hours had scattered along the entire west beach (1.25 miles) of Lisianski. Two were found on the eastern shore of the island the day following release. If the usual 90 per cent of the young to reach the beach survived to fly to sea, some 1600 of these transported birds left Lisianski.

In 1964–65, we found 50 of these 3.5-year-old birds, 40 on Eastern Island and 10 on Sand Island at their origin. Lisianski was not visited by us in 1964–65, but two recaptures in 1966 were reported. Four were found in 1966 on Sand Island and one on Eastern. Three were reported from Eastern in 1967.

In 1968–69, when the birds were 7.5 years of age, we caught 147 on Sand Island, none on Eastern Island. Lisianski was searched briefly in March 1969 by Eugene Kridler and David Olsen, but they found no transported albatrosses.

In all recaptures of albatrosses moved to Lisianski, note must be taken of the fact that the birds originated from far too large an area on Sand Island for us to make the same intensive search we made for birds in the other experiments. However, of a group of 87 birds that came from area 1 of Sand Island, 34 (38 per cent) were recaptured there in 1968–69.

The months of first recapture of the 3.5-year-

TABLE 1. Distance of 1963 nests of breeding Laysan Albatrosses from nest sites of former years (1961 or 1962) after removal of vegetation and other landmarks from the vicinity of the nest sites.

Distance from nest site (ft)	Constant pairs	Broken pairs	
	($n = 378$)	♂ ($n = 18$)	♀ ($n = 15$)
less than 1	78	1	0
1–3	297	7	0
3–6	3	10	1
more than 6	0	0	14[a]

[a] Distances ranged from 15 to 210 ft.

old birds were: Feb., 1 (2 per cent); Mar., 8 (16 per cent); April, 32 (64 per cent); and May, 9 (18 per cent).

Experiment No. 4. Only 63 of the 97 month-old chicks moved from Eastern to Sand Island nests on 25 February 1965 survived to be banded on 19 March. Only 47 were located on 28 March, 31 on 20 April, 30 on 28 May, and 27 on 31 May. Assuming that this rate of death persisted until the fledglings left the colony to go to the beaches, and that 10 per cent were lost there, it is likely that no more than 20 survived to depart the island.

No recaptures were made until late in the 1968–69 season when the birds were 4.5 years old. Seven were found then in area 1 of Sand Island, the area to which they had been moved. None was taken at the site of origin on Eastern, but since the survivors were few, they could easily have been overlooked. Thus, 35 per cent of the estimated number of survivors were known to have returned to the place of release.

Experiment No. 5. By the time the breeding albatrosses returned in November 1963, wind action, decay, and the growth of new vegetation had obscured the windrows of vegetation pulled or cut the preceding summer.

The plotting of nest sites in November and December 1963 was limited to nest sites of birds whose nests were identified in 1961 and 1962. The 411 sites were recorded in three categories: 1) those of constant pairs; 2) of males of 1961 from broken pairs; and 3) of females of 1961 from broken pairs. None of the survivors of broken pairs had been paired together and none of them bred in 1962. Birds with unbroken pair bonds returned as closely to the nest site as they did prior to the habitat disturbance (table 1).

Experiment No. 6. The results are given in table 2. Males tended to breed less than 50 ft from where they themselves were hatched; females selected sites approximately 80 ft from their natal nests. Sample sizes were small but representative: 1) distribution of returns ranged from 8 to 24 in each of 7 series of 100 bands used in the 2 years; 2) the returns from 1961 represented only 21 per cent survival vs. an expected 35 per cent, but a disproportionately small number of females were retaken. This is understandable since females usually leave the egg within 24 hr and are much less apt to be captured by us. Studies of non-experimentals indicate that we record approximately 30 per cent of the experienced breeding females in the egg-laying period (20 November–15 December). Therefore, if the 19 females taken represented 30 per cent of those that actually returned, some 50–60 of these females were in the plot and our total sample is 100±, and represents 33 per cent of the chicks banded for the experiment.

TABLE 2. Distance (ft) between natal nest and first breeding nest of Laysan Albatrosses.

	n	Mean	Mode	Median	Range
Males	50	60	40	41	8–166
Females	19	82	—	80	8–140

It is probable, since females do initiate nesting at a greater distance from the natal nest than males, that some few nested outside the area searched. That this number is small is indicated by the fact that only 22 of the 1122 chicks banded in the area surrounding the plot initiated nesting in the plot. The smallness of this movement is all the more remarkable when it is noted that the unmarked 600-foot border between the two areas traverses land densely occupied by nests.

SUMMARY OF RESULTS

These experiments on fledgling Laysan Albatrosses and chicks were carried out in the Leeward Islands of Hawaii, primarily on Midway. There were native, breeding populations of Laysans on the four islands used. The transport or exchange of birds, with the exception of two unusual situations, was effected with minimal mortality. The birds were released in apparently usual situations for departure, and normal numbers survived to depart, which they did at the same time as unmoved fledglings. They were recaptured in the expected months in later years (Fisher and Fisher 1969), and the numbers recaptured corresponded well with recaptures of undisturbed juveniles of identical age (35–46 per cent in experimentals and 42–51 per cent in controls). Thus no great percentage of unrecorded experimentals could be expected to be in areas other than those searched during recapture periods.

The total percentage of recaptures of experimentals of breeding age was comparable to recaptures of controls of the same age (26 vs. 25 per cent).

It may be concluded that the survivors among birds released after transport behaved in essentially normal fashion. Since 3124 fledglings were transported, with an estimated 2700 surviving to depart from the islands, and since some 500 different birds were later recaptured at or near breeding age, the numbers are sufficient to be meaningful.

Recaptures at 3.5 or 4.5 years of age were predominantly at the natal colony rather than at the release point (83 vs. 17 per cent). At 7.5 and 8.5 years, all but two recaptures were in the natal colony, indicating perhaps that some of the younger birds were initially "confused" by being moved and that they later regained the area of origin.

Direction of transport was not a factor; birds returned equally well from 3 mi. E, 52 mi. NW, and 250 mi. SE. It is unfortunate that the absence of islands within a reasonable distance to the northeast and southwest of Midway prevented releases in those directions, for all transport was in a generally SE-NW direction, following the line of islands and roughly parallel to or identical with the line of movement of many undisturbed juveniles. However, this unavoidable weakness in design may not have been serious. Many juveniles island-hop on their way southeast in the chain but few do so when they move northwest to the primary ocean feeding grounds. In 1964–1965 we color-painted albatrosses on Sand and Eastern Islands. Ornithologists of the Pacific Project on Kure also painted birds taken on Kure. By agreement we used different colors and took special note of birds from the other island. March of 1965 showed typical results. By that time we had painted more than 10,000 birds; some 4000 were painted on Kure. We recaptured hundreds of Kure birds on Eastern, but the ornithologists on Kure, who handled more than 3000 juveniles in March, retook only one Midway bird.

It is also evident that presence or absence of native, non-transported Laysan Albatrosses played no part in the return of the experimentals to their natal islands. Birds transported to a site on Green Island, where there were no young Laysans, returned to Sand Island, as did birds moved to Eastern and Lisianski, which already had numbers of fledglings ready to depart.

Juveniles without access to visual cues during transport returned to the place of origin as well as those that could see the land, the sea, and the sky. It is evident that the Laysan Albatross can surmount the problem of absence of celestial and landscape cues during transport.

Of the survivors of chicks exchanged between nests on different islands at the age of one month, 35 per cent returned at 4.5 years to the site of release. None was taken at the point of origin. However, the numbers were few, and we still do not know certainly where they will breed; perhaps they were only temporarily "confused" as mentioned above. Many did recognize the strangeness of the foster home (*e.g.*, they wandered away from the foster nest), indicating that recognition of the home colony and natal nest may occur prior to one month of age.

The suggestion is, however, that month-old chicks have not yet acquired the proper cues for homing. This, combined with the successful homing of fledglings moved at 5.5 months, indicates that the requisite cues may be established between 1 and 5.5 months of age.

Experienced breeding birds returned closely to the nest sites of former years after the landmarks within the colony had been destroyed.

Birds breeding for the first time established themselves near the nest site where they were hatched. Males returned more closely than females (40–50 ft vs. 80 ft).

DISCUSSION

Any bird transported beyond the distance it can see, if it is to return to its home, must have learned the cues for "home," must remember them, and must know where home is in relation to its present location. Those requirements apparently necessitate a genetically coded memory combined with the ability to navigate by celestial cues or unknown cues combined with some sort of "early memory" or a combination of these factors.

The problem for these Laysan Albatrosses was more than that posed by most homing experiments, indeed more than are naturally faced by most other species of birds. Laysans are truly pelagic during the non-breeding periods of their lives; the only lands they ever visit are the small breeding islands far from continental shores. The North Pacific Ocean is unmarked by seascape cues yet discernible by man. Juveniles do not usually return to the colony until sometime in their second year and perhaps only one in ten does so then (Fisher and Fisher 1969:201). It is possible, but I think unlikely, that juveniles return only to the vicinity of the island or fly over it without alighting, and thus are not recaptured in these early years. Therefore, it would appear that most juveniles must retain for three or more years, without the reinforcement of use in returning, whatever cues for homing they may have acquired before departure as fledglings. But perhaps this ability to remember is not unusual in birds, for Skinner (1950) showed that pigeons could remember an intricate visual pattern for as long as four years.

An additional troublesome facet of albatross homing is that juveniles return the first time in April and May and each year thereafter come to the colony at least a week or so earlier. Thus, by the breeding age of eight or nine years, they return in late November or early December. If they use celestial cues for navigation, the birds each year must adjust for the seasonal difference encountered. This learning of new seasonal patterns of celestial cues probably ceases in experienced breeding birds which always return in November. However, the adults, which may fly 1000 or more miles from November into July to seek food during incubation and later for the chick, evidently adjust for seasonal change each year or perhaps remember the seasonal celestial cues experienced in the pre-breeding years.

It would seem that the first return of the solitary juvenile would be the most difficult. The juvenile comes back six to eight weeks earlier than the date of its departure as a fledgling (Fisher and Fisher 1969). It encounters seasonal change and presumably uses cues gained at least two years earlier. However, this may not be as difficult as first thought might indicate. Meyer (1966) has demonstrated long-term remembrance of suntime by pigeons, and there is one constant in the sky—the inclination of the sun's arc. The latter is the same at the natal colony when they leave and arrive because the young depart and first return at times nearly equidistant from the summer solstice. Thus, determination of latitude may not be difficult. Longitude is another matter; the young are thought to be concentrated in the northwest portion of the Pacific (Fisher, unpubl.) and at a variance from the natal colony of as much as 50–60° longitude. The only plausible speculation about their ability to determine longitude seems to be that at sea they retain the local sun-time of the natal colony. Indeed, it may be these two factors, memory of the inclination of the sun's arc and local suntime imprinted so early in life that also "force" the birds into the firm and life-long attachment with the natal colony, discussed in the beginning of this paper.

At present the above explanation appears to be the most likely one for the return to the natal colony of birds moved in the absence of visual cues. It is not possible to eliminate navigation by some sort of geophysical grid, especially in view of the fact that these albatrosses return to volcanic islands, largely submerged though they may be. The Emperor Seamount Chain courses north and west from Midway to the tip of the Kamchatka Peninsula and lies east of the main concentrations of Laysan Albatrosses. Who yet knows what kind of "drift fence" or string of signposts these submerged peaks may constitute? Albatrosses may use magnetic fields, in spite of the findings of some still confusing avian experiments, especially when one considers the responses of living things to direction, force, and change in the electromagnetic environment documented by the studies of Frank A. Brown, Jr., and his associates at Northwestern University. But we do not know of any avian structure or process likely to function for navigation in magnetic or other fields of nonvisual forces. The possible exception is the olfactory organ which is well developed in procellariiform birds (Bang and Cobb 1968). The olfactory bulb is large and the anterior nasal chamber is designed so that air passes over the olfactory epithelium; Black-footed Albatrosses respond to odor as evidenced by changes in heart and respiratory rates (Wenzel, preprint). Further, procellariiform species have a strong and unique musky odor. That the odor of a heavily populated bird island carries far to sea is attested to by the diaries of many captains of sailing vessels. Laysan Albatrosses are concentrated on land in the North Pacific only in a 800-mile-long string of islands. When one considers these bits of evidence, one cannot disregard the possibility that odor may be important in homing, at least over the shorter distances, to an albatross island, but not to a specific island.

Certain structural and functional aspects of the avian eye lead us to suspect, at least, that it could aid in detailed and minute orientation and navigation as well as in ordinary visual reception of grosser land or sea marks. Experiments on avian species other than albatrosses have demonstrated a great visual acuity. Pigeons can resolve lights flickering 150 times per second (Granit 1959; Dodt and

Wirth 1953), and they can distinguish between movement and non-movement of an artificial sun arcing at the rate of 15 degrees per hour (Meyer 1964). Polyak (1957) has shown that Golden Eagles can resolve four seconds of arc. There is some evidence to indicate the presence of special retinal cells perhaps capable of detecting movements of the magnitude of 0.1 degree (Maturana and Frenk 1963, 1965), as also demonstrated in some insects (for example, the locust, Horridge 1966).

I believe we may disregard the possibility that cloud columns over the islands act as signal beacons for these albatrosses. The atolls used for breeding are too low and small to have constant or consistent formations.

Laysan Albatrosses might use the direction of prevailing winds to return to the vicinity of the natal island, as Bellrose (1966) has suggested for waterfowl. Kuroda (1957) believed that wind currents provided a means for certain members of the Procellariiformes. His "Pacific Circular Route" (p. 441) might apply to this albatross. Although the general wind currents in the North Pacific are fairly constant on a seasonal basis and might possibly be used to return to the region of the Hawaiian chain of islands, they are neither sufficiently constant nor specific enough for use in returning to a certain island. One might think that, once the albatrosses reached the chain, they could island-hop until they recognized the topography of their natal island. Fisher and Fisher (1969) indicated that significant numbers of juveniles, but few adults, appeared on other islands. However, on their flights *toward* the home island, pre-breeding birds visit mostly, if not solely, those islands lying northwest of the natal island in the chain. Thus Midway birds are found on Kure rather frequently but seldom on Pearl and Hermes, Lisianski, or Laysan Islands. Juveniles from the latter islands do appear on Kure and Midway. Consequently, a Midway bird encountering Laysan Island would not recognize it or be in any better position to proceed to Midway. Further, the birds in these experiments could have no memory of the topography of Midway, as observed from the air, and much less of the natal colony on Midway. These experimentals, it seems, would be forced to land and explore each island on foot to find the set of topographic data they might remember from fledgling days. There is no evidence that even juveniles do so. Fisher and Fisher (1969) did suggest that non-experimental juveniles retraced the terrestrial departure route used as fledglings between beach and colony, when they returned in pre-breeding visits. The experiments being discussed indicated that this was not a necessary part of homing to the natal colony, and breeding birds come directly upwind to the colony.

Identification of the natal colony and the return to the specific nest site impose great problems. Bellrose (1966:94–96) believed that migrating waterfowl employed landscape features to make pinpoint returns to specific water areas frequented in previous migrations. He considered that the sun and/or stars were used, when visible, for directional guidance over regions devoid of significant landscape cues and at night. He felt that under overcast skies the wind provided directional guidance to home areas. Nestling Laysan Albatrosses spend approximately 5.5 months in the vicinity of the nest, and this must be the period in which they obtain the necessary cues for return. However, the presence on Eastern of unusual numbers of Sand Island juveniles moved to Eastern and Lisianski four and three years earlier indicates that the cues may not have been completely or entirely accurately established by the age of 5.5 months. Since the survivors among the "confused" birds (of Eastern Island) have now settled down to breed in their natal colonies, they must have resolved the problem between their fourth and eighth years, perhaps by trial and error search until they recognized the landmarks of "home." Furthermore, the return of the surviving exchanged chicks to the foster colony in subsequent years indicates that the cues were acquired after a month of age. It is possible that they, as the "confused" transported fledglings moved from Sand to Eastern, will later seek their natal colonies on Eastern. If they do, it will of course show that they possessed the cues prior to one month.

If the exchanged chicks as well as the remainder of these "confused" transported birds do regain their natural home site, the experiments may well have accidentally demonstrated another aspect of the time or accuracy of acquiring cues. Earlier it was stated that determination of latitude appeared to be easier for the birds than determination of longitude. All the experimental transported birds originated on Sand Island and the exchanged chicks originated on Eastern Island. Eastern and Sand are at the same latitude and the experimental areas on the two islands lie on the same fractional degree of latitude and about two minutes apart in longitude. Lisianski is two degrees to the south and five degrees east. Green Island of Kure is less than one degree northwest. Thus, if the ability to determine latitude is acquired earlier or more accurately, one would expect all transported fledglings to home in first on the correct latitude (that of their origin). They did; few birds were ever found at Kure or Lisianski, located at latitudes different than Sand Island's. But at the same latitude and different longitude (Sand vs. Eastern) the birds were at least initially confused. At three and four years of age, one-third of the recaptures of Sand-to-Eastern Island transfers were on the latter island and four times as many Sand-to-Lisianski birds were taken on Eastern as compared with Sand.

The early development of topographic recognition of colony and home nest area is undoubtedly abetted by the behavior of the adults feeding chicks. Adults will only feed the young on or in the immediate vicinity of the nest site, and as the multidirectional wanderings of the chicks increase with age this means returns from different compass points and increasingly greater distances. It would be difficult to devise a better method for instilling recognition of the nest site and for training of chicks to return to it. The restlessness of chicks in strange nests indicates the probable effects of this training before one month of age; many of the chicks wandered from the foster nest even though being fed. These observations may indicate knowledge of home and an attempt to seek it even at this early age. The moot question is whether they sought to return by using topographical, celestial, or other cues. Hamilton (1962) found that ducklings raised in an environment void of directional cues learned to use the sun and stars to locate water sources. Unfortunately, he did not initiate test observations until the ducklings were three weeks old.

The results of Experiment No. 6 may also indicate that topographic cues are not necessary. Young raised in the plot before the landmarks were removed returned after the terrain was changed to breed near the nests in which they were hatched. On the other hand, they might have homed even more closely in the presence of the original landmarks. The experiment should be repeated in an undisturbed colony.

Experiment No. 5 showed that experienced, breeding Laysan Albatrosses can also return very closely to the exact nest site of former years in the absence of all formerly existing landmarks. They homed as closely as control birds returning to an undisturbed setting.

Although in Experiments No. 5 and 6 one cannot discount the possible use by some birds of the trees remaining near the plot, the trees were originally obscured or invisible from many nests because of intervening vegetation. Such distant cues, if they are indeed used, are quite different than the proximity of the base of a tree, shrub, building, or runway edge, and they require a higher degree of visual acuity. But, since many young and many pairs that could not have used these tree cues in former years returned in the absence of nearer topographic clues, it is plausible that the trees were not over-ridingly significant. This leaves as cues the usual assemblage of hypothesized, yet virtually unproven, ones: odors, magnetic fields, celestial markers. Odors can be eliminated as a possibility, I think, despite the great development of the olfactory apparatus in albatrosses. The nests are so close in many instances that incubating birds often defecate on each other, the chicks wander and defecate away from the nest, and, most importantly, our activities of clearing the plot (pulling weeds, dragging brush, and raking) rather thoroughly mixed the top sand and debris of adjacent nests. Time and the natural forces of wind and rain would also tend to eliminate such nest-site specifics. Magnetic fields are even less likely cues for return to the nest than for returning to the island of natality.

I think some kind or kinds of celestial cues are the primary guides by which these experimentals returned to the nest site. This does not mean that celestial navigation is necessarily the usual or only way undisturbed birds return, but these experiments and repeated field observations lead me to think that it is. Birds that nested alongside buildings continued to nest in the same places after the buildings were removed. When males first return to the colony they neither land at the territory nor proceed directly to it. They often alight a hundred or more feet away, pause, look at the sky, wander off course, pause, look at the sky, change course, and thus zigzag to their former nest sites. Females on their first return of the season do some of this "surveying," but not as much, and the reason may be that they soon recognize the mate which has usually preceded them to the territory.

The male tends to maintain the same central position in his territory from year to year, and the female could use this position as a cue to the nest site of former years. The fact that some females make the first seasonal return precludes postulation of any absolute sexual difference in ability to home in on the region of the territory, but I have never observed a female resting for long in the future nest site or any other place in or near the territory until after her mate has made his first return of the season. (See also Fisher and Fisher 1969:180.) She often returns by herself from the postcopulatory honeymoon at sea to initiate nest construction, but this of course occurs after the first reunion at the nest and probable identification of the current topography at the nest site. My hypothesis is that the male is the primary and usual factor in the pair's constant return to the same site, that he uses celestial cues to home in on the territory, and that the female uses his position to locate her nest site. When the time of first seasonal arrival is reversed, she uses celestial cues to reach the general area of the territory but can not, or at least does not, identify the exact nest site until her mate has taken up his position.

To suggest the use of celestial cues to pinpoint a territory, nest site, or food storage place seems preposterous in the current state of our knowledge. Perhaps it is best simply to record the event, without speculation, as Tickell (1962:12) did for the Dove Prion, *Pachyptila desolata.* This species burrows through the snow to the exact nest site, even though the topography of the entire area is obliterated by snow drifts. And Swanberg (1951) observed that the nutcracker, *Nucifraga,* spends only a few minutes hiding nuts in the ground but is able to return unerringly months later even when the site is snow-covered. Perhaps we must agree with Adler (1963:575) who concluded, after original studies and a review of the literature, that navigation probably requires sensory capacities beyond those already demonstrated and perhaps still undiscovered cues.

Our efforts to establish breeding colonies of Laysan Albatrosses by transporting fledglings obviously failed, as past attempts with most other species have. Bellrose (1958) indicated that small percentages of female Wood Ducks, *Aix sponsa,* hand reared and displaced as far as 200 miles at an age of 6–8 weeks, returned to the release site to breed the following year. Mauersberger (1957) also reported a measure of success, with Pied Flycatchers, *Ficedula hypoleuca.* However, in view of these albatross experiments, it is possible that at least the flycatchers returning to the release area were only temporarily confused. I am not aware that in his review of the experiments, Mauersberger reported any birds breeding there.

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