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THE BIOLOGY OF STORM PETRELS IN THE
GALÁPAGOS ISLANDS*

By

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ABSTRACT: Between November, 1965 and July, 1967, studies were made on the biology of *Oceanodroma castro* and *O. tethys* in the Galápagos Islands.

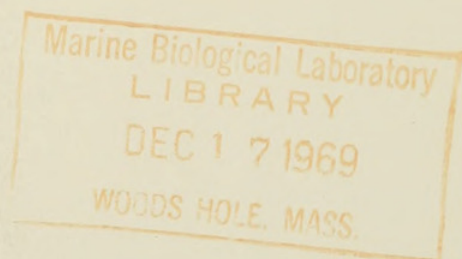
Oceanodroma castro is a widespread species in subtropical parts of the Pacific and Atlantic oceans. Although there is considerable size variation between breeding populations, the species is best treated binomially. Four specimens collected in the Gulf of Guinea may however belong to a distinct race.

In the Galápagos Islands *O. castro* has two breeding seasons a year but there appeared to be two entirely separate populations, each breeding annually, one in the hot season, one in the cold. Even nonbreeders and failed breeders remained faithful to their annual cycle in the four seasons studied. A detailed study of the breeding biology showed marked differences in the seasons but little correlation with breeding in the hot or cold seasons. There was a decline in nesting success with date of laying within each season. The cause of this was obscure but it did not appear to be food shortage or predation of the adults by *Asio galapagoensis*. Wing molt occurred away from the breeding grounds and took most of the time between breeding seasons. This need not indicate that birds were prevented from breeding more rapidly as other factors might also be important.

The factors preventing nesting throughout the year are obscure, but presumably there was some advantage to a pair in breeding when the majority of individuals did so, which more than compensated for losses due to competition for food and nest sites. Predation is probably important in the synchronization of breeding.

Oceanodroma tethys is a diurnal species when visiting land. The colony studied on Tower Island was occupied by approximately 200,000 breeding pairs. Large numbers of birds frequented the colony throughout the year but all but a few eggs were laid from May to July. The vast numbers of birds flighting at the colony out of the breeding season were apparently nonbreeders as adults would have been away replacing their wing feathers. No apparent reason for the flighting was found. In another colony

* Contribution of the Charles Darwin Foundation for the Galápagos.



at Isla Pitt, there were no birds present during the nonbreeding season. The nesting colonies were extremely crowded and the low nesting success (less than 23 percent) was mainly due to intense intraspecific competition for nest sites.

The third species of storm petrel was *Oceanites gracilis*. This is ecologically distinct from the *Oceanodroma* species as it is an inshore feeder. There was probably little competition between *O. castro* and *O. tethys* as the former feeds on fish and cephalopods by day, the latter on smaller fish, cephalopods, and crustacea caught by night. Their feeding areas may also be different.

INTRODUCTION

Three species of storm petrels are seen in the waters around the Galápagos Islands, the Madeiran storm petrel (*Oceanodroma castro*), the Galápagos storm petrel (*Oceanodroma tethys*), and Elliot's storm petrel (*Oceanites gracilis*). The last species has not been found breeding but the results of gonad examination (Loomis, 1918), and the fact that it appears to be resident and an endemic race, show that it must breed in the archipelago. Ecologically however it is quite distinct.

My wife and I were resident at the Charles Darwin Research Station in the Galápagos from November, 1965, to July, 1967, and for the majority of the time we were engaged on studies of the two *Oceanodroma* species. Observations were also made on the other species of sea birds present in the archipelago but these will be published separately except as far as they concern the storm petrels.

There has always been confusion regarding the names of the various islands in the archipelago (Slevin, 1959) and I have compromised and used the names now in commonest usage. However for the sake of completion I give below the alternate names for those which have both Spanish and English names but are not direct translations. The alternate names are given in brackets and the official Ecuadorian title in *italics*. The islands are *Santa Cruz* [Indefatigable]; *Isabela* [Albemarle]; *San Cristóbal* [Chatham]; *Española* [Hood]; *Genovesa* [Tower].

OCEANODROMA CASTRO

Oceanodroma castro is a widespread species in the subtropical parts of both the Atlantic (summary in Bannerman, 1941) and Pacific oceans. It is known to breed in Hidejima and possibly Sanganjima off the eastern coast of Japan (Austin and Kuroda, 1953), Kauai in the Hawaiian Archipelago (Richardson, 1957), several islands in the Galápagos Archipelago (Loomis, 1918; Lévêque, 1964), the Azores (Hartert and Ogilvie-Grant, 1905), the Salvages (Lockley, 1952), Madeira (Bannerman, 1914), Cape Verde Islands (Murphy, 1924), Ascension (Allan, 1962), and St. Helena (Haydock, 1954). It may also nest on São Tomé in the Gulf of Guinea (Amadon, 1953) but there is no reason to suppose that it nests on Cocos Island, Pacific Ocean (Murphy, 1936). The only detailed breeding study is that of Allan (1962) on Boatswainbird Island off Ascension.

SUBSPECIATION

The classification of storm petrels is extremely difficult and has been the subject of much splitting and discussion. Several races of *O. castro* have been described, all on insufficient specimens, but their validity was successfully challenged by Austin (1952).

During the present study I examined far more specimens from Galápagos (the race "*bangsi*" of Nichols, 1914) than anyone previous and I also measured the skins of *O. castro* in the American Museum of Natural History, the Peabody Museum (Yale), Museum of Comparative Zoology (Harvard), California Academy of Sciences (San Francisco), the Los Angeles County Museum, the Smithsonian Institution (Washington), and the British Museum (London). It seemed therefore desirable to attempt to reassess the amount of variation shown by this species. All measurements were made by myself (thus reducing error caused by differing techniques). Austin (1952) had a larger sample of birds from Japan but it has been thought advisable to use my own measurements; they are, however, similar to those of Austin. The state of specimens and the time available for the work meant that totals of different measurements varied and details are given in table 1. Wing and bill lengths were measured on all but the few molting and damaged specimens. The depth of the bill at gonys, at nostrils, and at its minimum depth just in front of the nostrils and the length of the gonys were also measured but no marked differences were noted. Although any such measurement was likely to be inaccurate, an attempt was made to define the rump patch. The rump patch was measured in the mid-dorsal line from the base of the white, even if hidden by covering feathers, to the furthest limit of the white on the most posterior black-tipped feather. As there were no demonstratable sexual differences in any measurements the results have been lumped.

Included among the measurements are four birds from, or very near to, São Tomé in the Gulf of Guinea. The full details (measurements in mm.) of these specimens collected by Correia and now in the American Museum of Natural History are:

Male collected 10 December 1928. Wing 155, bill 17.0, rump patch 24. Gonads small. This is in extremely fresh juvenile plumage.

Male collected 10 December 1928. Wing 160, bill 17.3, rump patch 25. Gonads swelling.

Male collected 14 December 1928. Wing 160, bill 15.5, rump patch 25. In fresh plumage, gonads large.

Female collected 16 November 1928. Wing 171, bill 16.8, rump patch 26. Plumage fresh.

Dr. Dean Amadon has very kindly examined the details of other birds collected by Correia on São Tomé and it seems as though these petrels may well have been collected from the shore as other land birds were from the same locali-

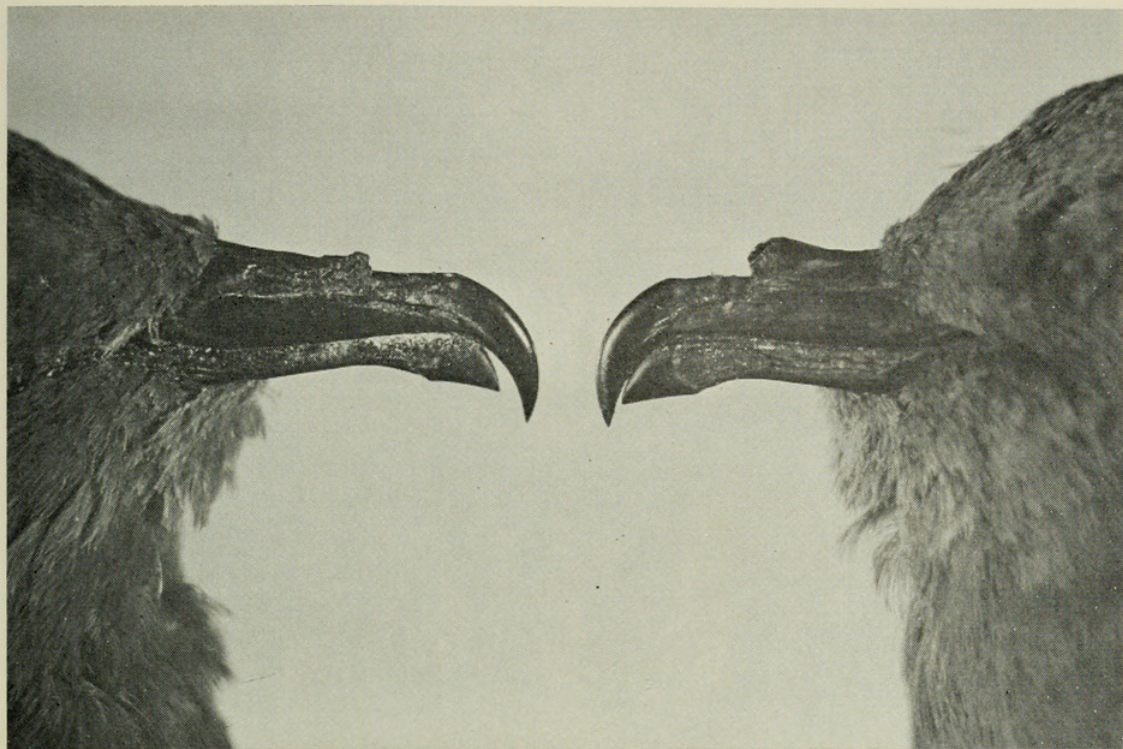


FIGURE 1. A comparison of the bill of a specimen of *Oceanodroma castro* from the Gulf of Guinea (on the left) with the slightly shorter bill of a bird from the Azores (right). The bill of the Gulf of Guinea bird measured 16.8 mm. The nostrils of the left-hand bird may have collapsed with shrinkage due to drying.

ties. There are however no definite data as to whether "chummed" at sea or caught on land. Correia was a very experienced collector and it is more than likely that he would have mentioned the fact if they had definitely been breeding.

Three of these birds are extremely large in wing and bill length (fig. 1), the female having a wing much longer than any other examined, and all have by far the smallest area of white in the rump of all examined (fig. 2). The differences between all four birds and those from the Cape Verde Islands are significant at the 5 percent level. It therefore seems likely that a subspecies of *O. castro* may be found in the Gulf of Guinea (possibly at Isla das Cabras where the white-tailed tropic-bird (*Phaethon lepturus*) probably breeds (Snow, 1950) but it would be premature to describe a new race on only four specimens, before a breeding colony has been found.

Although this species shows considerable variation between the isolated breeding populations, especially in wing length, the differences are however not significant except for the Gulf of Guinea birds. I agree with Austin (1952) and Bourne (1955) that the existence of geographic variation should be recognized but that the species is best treated binomially. The populations are probably distinct with little mixing. There is a suggestion that the tropical populations are



FIGURE 2. Photograph to show the relatively small rump patch in two specimens of *Oceanodroma castro* from the Gulf of Guinea (the two right-hand birds) contrasted with two birds from the Azores (on the left).

larger than those of more temperate regions (especially if, as suggested by Bourne (1955), the Azores have warmer surface waters than Madeira).

An interesting point concerning differing populations is the occurrence of white feathers in the normally dark parts of the plumage, usually about the head. Baptista (1966) found white feathers in four birds from the Galápagos Islands out of 30 Pacific skins he examined, but I noted only three among 143 Atlantic skins. Admittedly he may have been looking more closely than I did, but there seems to be a regional difference. Allan (1962) did not mention any such birds. In the Galápagos Islands I noted only conspicuous white markings as I was unwilling to disturb my birds more than necessary. Among 1015 birds handled, there were six with very obvious white patches on the head and neck. Two of these birds had white on the head which increased from one season to the next whereas another obtained its white area in a molt between successive breedings

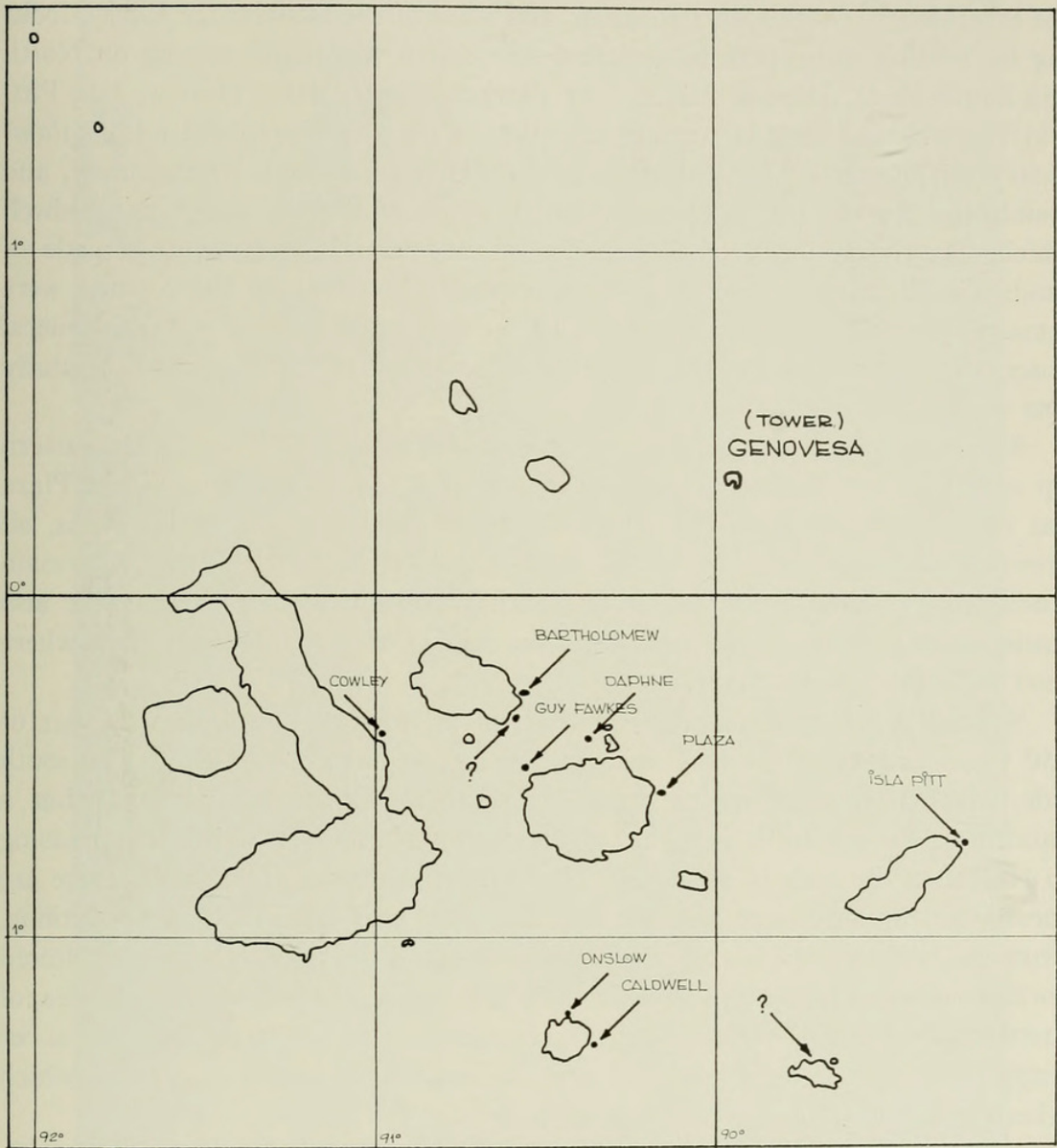


FIGURE 3. Definite and possible breeding colonies of *Oceanodroma castro* in the Galápagos Islands. The present study was undertaken on Plaza.

which suggests that the white may be associated with age. These markings are erratic and form no pattern except that they occur mainly on the head. Similar markings were noted on a single *O. tethys*.

HABITAT AND METHOD OF STUDY

The first Galápagos breeding record of *O. castro* was made by Beck on Cowley Island in 1906 (Loomis, 1918) and Lévêque (1964) also found it nesting on Plaza and Daphne (for locations see fig. 3). Between November, 1965, and July, 1967, I visited all the main islands and most of the climbable isolated rocks with

the exception of Culpepper, Crossman, and some of the Baimbridge Rocks, looking for nesting storm petrels. *Oceanodroma castro* was found nesting on North and South Plaza, Daphne major, Guy Fawkes, Cowley Islet, Onslow, Isla Pitt, and Tower. Dead birds or remains in pellets of the short-eared owl (*Asio (flammeus) galapagoensis*) were also collected on Hood, Caldwell, Bartholomew, and Bainbridge Rocks; the species may well nest on all of these excepting Caldwell which, like the majority of the smaller isolated islands and rocks, is made of sandstone-like lava so smooth as to be virtually holeless. All the colonies were reasonably small and well spaced out, as appears typical of the species. General observations were made at several of the colonies but the main part of the study was undertaken on South Plaza.

The Plazas are two small islets of basaltic lava about 400 yards off the eastern tip of Santa Cruz. Both are inhabited by sea birds but, as the larger South Plaza has more birds and lacks the extremely dense thorn scrub of North Plaza, all previous observers have restricted their activities to South Plaza. My main studies, likewise, were carried out on South Plaza, but regular checks were also made on the northern island and so, for the sake of brevity, the term Plaza where used will signify South Plaza.

South Plaza is an elongated island about a half mile long by an average of 150 yards wide with the long axis running approximately east-west. The south side, which is exposed to the prevailing southeast winds and where all but a handful of the sea birds nest, has cliffs mainly 30–60 feet high but decreasing to 10 feet at the ends of the island (fig. 4). At the bases of the cliffs there are considerable quantities of boulders due mainly to cliff falls, which still continue. From the cliff tops the island slopes gently down to the sea on the very sheltered northern shore. The western third of the island has a covering, dense in places, of thorn scrub. Cacti (*Opuntia* species) are common in this area and also occur singly or in small groups scattered over the rest of the top of the island, which otherwise has only low ground vegetation.

Five species of sea birds nest on Plaza, the swallow-tailed gull (*Creagrus furcatus*) (on the cliffs, among the boulders, and rarely inland), Audubon's shearwater (*Puffinus lherminieri*) and *Oceanodroma castro* (both of them in holes in cliffs and boulders), red-billed tropic-bird (*Phaethon aethereus*) (in cliff holes), and a few brown noddies (*Anous stolidus*) (on exposed cliffs). Masked and blue-footed bobbies (*Sula dactylatra* and *S. nebouxii*) and frigates (mainly *Fregata magnificens*) are always to be seen on or around the island but none nested. Other nesting species were the finches (*Geospiza fortis*, *G. fuliginosa*, *G. scandens*), the yellow warbler (*Dendroica petechia*), and a single pair of yellow-crowned night-herons (*Nyctanassa violacea*). An egret (*Casmerodius egretta*), one or more grey herons (*Ardea herodias*), and one or more individuals of *Asio galapagoensis* were regularly present, and the owls may well have bred on

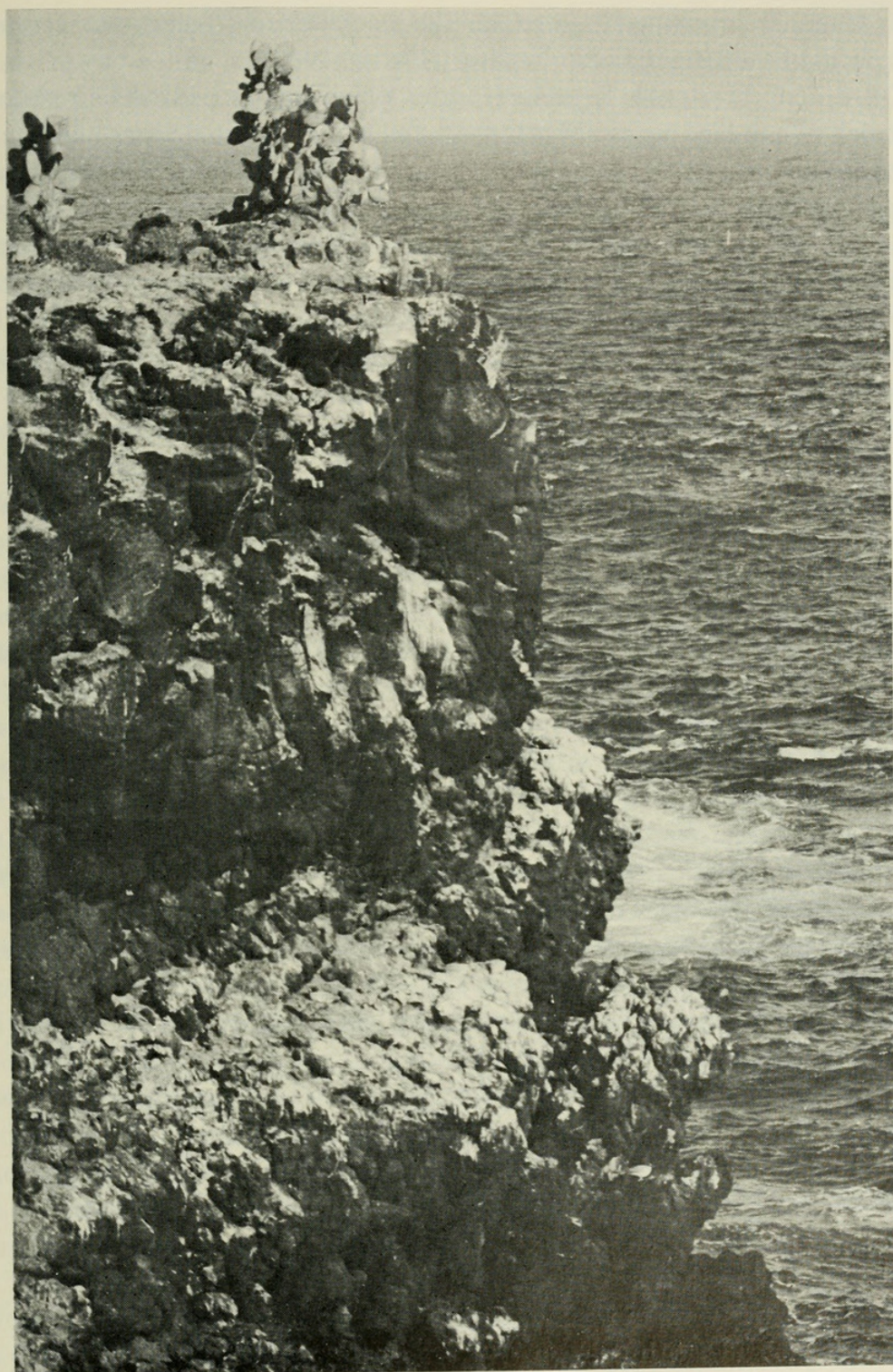


FIGURE 4. Part of the south-facing cliffs on Plaza Island during the hot (and calm) season. *Creagrus furcatus* nests on the flatter area (one bird can just be seen incubating in the guano covered area), while *Oceanodroma castro*, *Puffinus lherminieri*, and *Phaethon aethereus* nest in the cliff holes and among the boulders. The guano is mainly due to *Sula nebouxii* and *S. dactylatra* which however do not breed on Plaza.

North Plaza. A surprising absentee was the mockingbird (*Nesomimus parvulus*), which would be a potential nest predator (Harris, 1968).

There were three other large vertebrates which were known to be responsible for losses of sea-bird nests. The largest and most numerous was the sea lion (*Zalophus californianus*), whose population was in excess of a thousand, mainly on the north side but with haul-outs of unemployed males near the east and west tips. Plaza supports the densest colony of land iguanas (*Conolophus subcristatus*) remaining in Galápagos and also a smaller colony of marine iguanas (*Amblyrhynchus cristatus*). The former species is restricted to the flatter area of the island, the latter usually to the sea cliffs, but both species are not infrequently found in the nesting holes of sea birds.

NEST SITES

The nest sites of *O. castro* varied greatly in the Galápagos but the preferred site appeared to be a hole in a cliff or under a boulder, deep enough to hide the bird from sight but not so deep as to exclude all light. Direct access to the sea is extremely important and very few birds nest far from the cliff edge or the sea. Of 171 nest sites examined on Plaza, 55 were in holes in cliffs, 27 in holes at top of cliff, 38 in boulders at cliff base, 38 among boulders or large stones on cliff top, 6 in the back of small caves, 5 in holes excavated by the birds in soil, mud, or seal guano, and 2 inland under boulders. Of the cliff nest sites, half were under substantial overhangs and only 10 allowed a clear view of an incubating bird. These figures are probably biased towards the shallower sites, as these are more easily found, but it is unlikely that many birds nest in very deep holes. On Onslow there were very few holes indeed and birds nested very much more in the open than on Plaza. Onslow was not visited during a breeding season, but out of season there were many abandoned eggs and also the remains of adults eaten by owls (*Asio galapagoensis*). In a colony such as this, the incubating birds must be very liable to predation.

The total population of any small nocturnal species is extremely difficult to determine, but on Plaza it was thought that about a third of the available nest sites had been found by the end of the study, which would put the number of occupied holes in the cold season at about 600 and in the hot season approximately 300. However the data on owl predation and the estimate of the annual adult mortality taken together, suggest that my estimates were too low.

Regular monthly visits were made to Plaza. At least 10 days a month were spent on the island (with only one exception), usually divided into a stay of a week or more, with several day visits timed, as far as possible, so that never more than 10 days (or a week at peak breeding times) elapsed without the nests being checked. In all a total of 208 days was spent on Plaza.

All holes with birds found were given a description and a number which was painted on the rock alongside. The number of holes used in the study increased

throughout the period, from 74 at the end of the first breeding season to just over 180 at the end of the study. Some birds were also found in burrows of *Puffinus lherminieri*, which was the subject of a separate study (Harris, 1969). Birds were marked with numbered bands and examined for wing molt and state of development of the brood patch. When time allowed, they were also weighed and measured. Birds were sexed by cloaca inspection after the laying of an egg, and adults of some pairs marked with spots of paint on head, wings, and tail, so that incubation spells could be followed without handling the birds. Luckily, and unlike some other storm petrels, such as the British storm petrel (*Hydrobates pelagicus*), this species does not desert readily, so that it was possible to handle and even weigh some birds daily during incubation. Eggs were measured and young were weighed daily to obtain growth rates and twice daily to get weights of feeds and feeding frequencies.

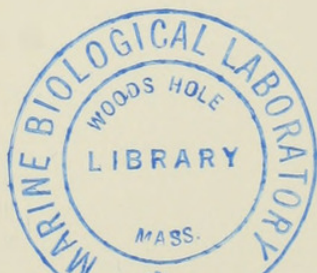
The majority of the nests were examined every day, but in some awkward or dangerous areas they were checked only two or three times a month. The terrain was such that night work was hazardous and restricted to a little mist-netting and a few searches for holes or specific birds. This part of the study was very similar to that on Ascension by Allan (1962). However, unlike those of Ascension, the adult and young petrels here were subject to much predation by owls, and young were also taken by herons (*Ardea herodias*) and the red crab (*Grapsus grapsus*). Some eggs and chicks were also destroyed by the two species of iguana.

GENERAL BIOLOGY

Virtually nothing is known about the biology or distribution of this species at sea except that it is seldom seen on or from ships, so that our knowledge of its biology is restricted to the breeding grounds. However, it does appear to feed well away from land, presumably mostly by day.

In accordance with the strict conservation measures now enforced in the Galápagos, no attempt was made to collect large numbers of birds for the examination of stomach contents, but during the study 15 stomachs, mainly from birds injured or killed by owls, were collected. Of these 14 had fish-eye lenses (up to 19) or otoliths, and 4 had cephalopod remains. One cephalopod beak was identified as belonging to a myopsid (probably sepiolid) of estimated weight 3–4 grams. Two adults netted in April regurgitated fish of lengths 50 and 37 mm., and the droppings of a young bird on Plaza in August contained a single fish otolith and a smashed cephalopod beak. This evidence indicates that the main food is small fish (probably mainly of the size of the regurgitated sample to judge from otolith size) and squids, all caught on or near the surface.

The inside of the mouth of *O. castro* has large numbers of relatively big backwardly pointing spines (fig. 5), and is well adapted for catching and holding slippery prey. The stomach is large, approximately 55 mm. long by 38 mm. (width when cut open and flattened) and capable of large distention. The intestine



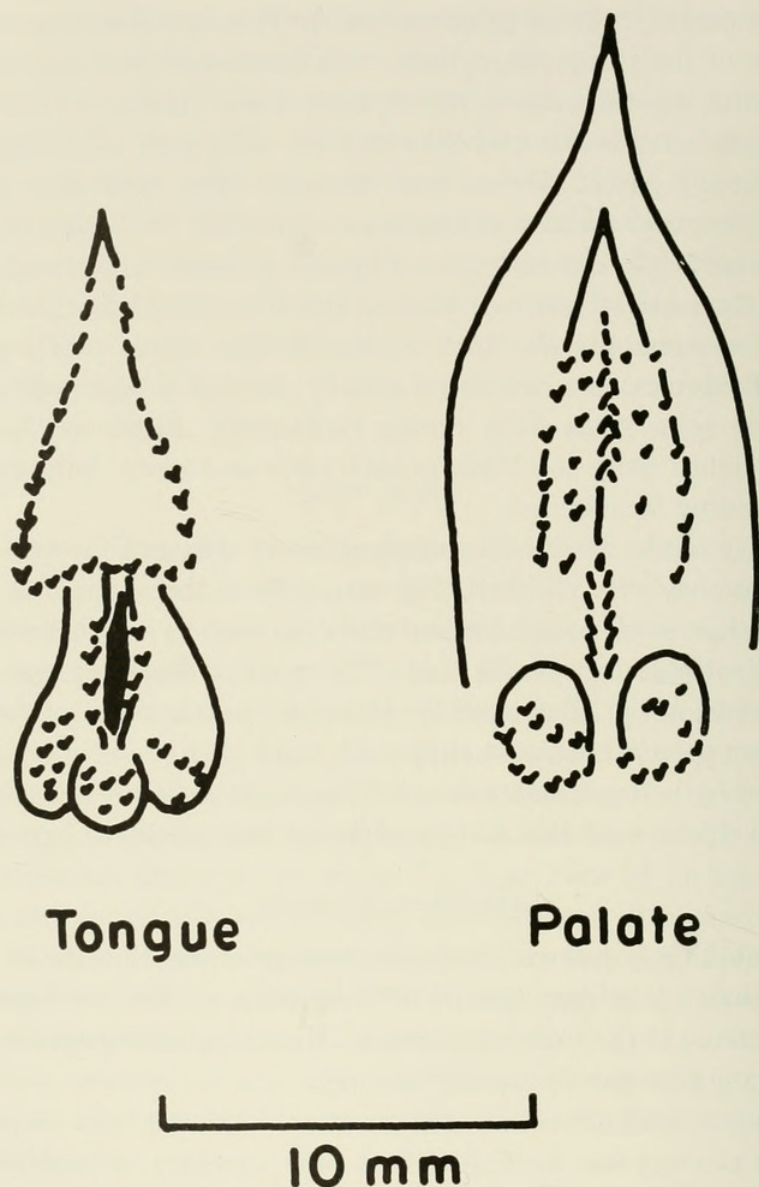


FIGURE 5. Tongue and palate of *Oceanodroma castro* to show backwardly pointing spines.

measured about 250 mm. The roughly dissected flight muscles of a bird of 33 grams, weighed 6 grams or 18 percent of the body weight.

As the method of feeding is presumably similar to that of other species of *Oceanodroma*, that is, catching prey at or just below the surface of the sea, it is hardly surprising that birds show injuries to the feet, presumably due to predatory fish. A sample of 100 birds examined closely included 7 with injured feet. The injuries were holed webs (2), only a single toe left on a foot (2), distal half of a foot missing (2), and leg missing completely from outside the body (1). Injuries seen in other birds were a badly torn web (1), a leg missing outside body (1), and a bird unable to straighten a leg (1). Allan (1962) found similar in-

juries in $3\frac{1}{2}$ percent of his birds. These injuries did not seem to affect the reproductive success of the birds concerned.

THE BREEDING CYCLE

The majority of sea birds have fixed annual breeding cycles, usually assumed to be timed to coincide with the maximum availability of food for egg formation, feeding, and/or survival of young. However, in a small but varied group of equatorial species, breeding occurs at intervals of less than a year. In some species, such as *Anous tenuirostris* and the sooty tern (*Sterna fuscata*) (Ashmole, 1962, 1963) on Ascension, it seems clear that the time between the starts of successive layings is that needed to complete the breeding processes and undergo a molt, a period of just under 10 months in *S. fuscata*. In a few other parts of its range, *S. fuscata* has breeding seasons at 6-month intervals, and on Christmas Island (in the Pacific) successful breeders nest annually, but those which lose their egg or young chick may return for the next cycle 6 months later (Ashmole, 1965).

Oceanodroma castro is a widespread species, but since it breeds on isolated islands and is nocturnal when visiting land, there is a dearth of precise data on its breeding cycle, except on Ascension, where there is an annual cycle with all but a few eggs laid from October to December (Allan, 1962). The Blossom collections taken on Ascension in 1925 (now at the Peabody Museum) include some young birds from eggs which must have been laid August-November which perhaps fits with the contention of Allan that there is a fixed annual cycle. The few eggs from St. Helena were of October and November origin (Benson, 1950; Haydock, 1954; Stonehouse, 1963b).

In the Cape Verde Islands, breeding is recorded in the first half of the year (Bourne, 1957) whereas in the Salvages it is probably a little later with no breeding found at the end of April (Ogilvie-Grant, 1896), and fresh and incubated eggs and very few small young in July (Lockley, 1952; Dr. C. Jouanin, personal communication).

In the Madeiran group, eggs have been found in every month but May (Bannerman, 1914 and Jouanin, personal communication), and Schmitz (Bannerman, 1914), thought that there was no definite breeding season. Bannerman (1914) interpreted the same results as suggesting that there are two breeding seasons, June-September and October-December, involving different individuals and a few birds laying in between. Lockley (1952) spent the 4 days 10-13 July 1939 at the colony at Chao Deserta and found birds present but no nests. Roux and Jouanin (personal communication) visited Baixo in July, 1967 and found the birds with fresh eggs, incubated eggs, and rarely with very young chicks. It is therefore uncertain whether there are two seasons a year, one season with some out-of-season nesting (as Ascension), or a less than annual cycle. Further north

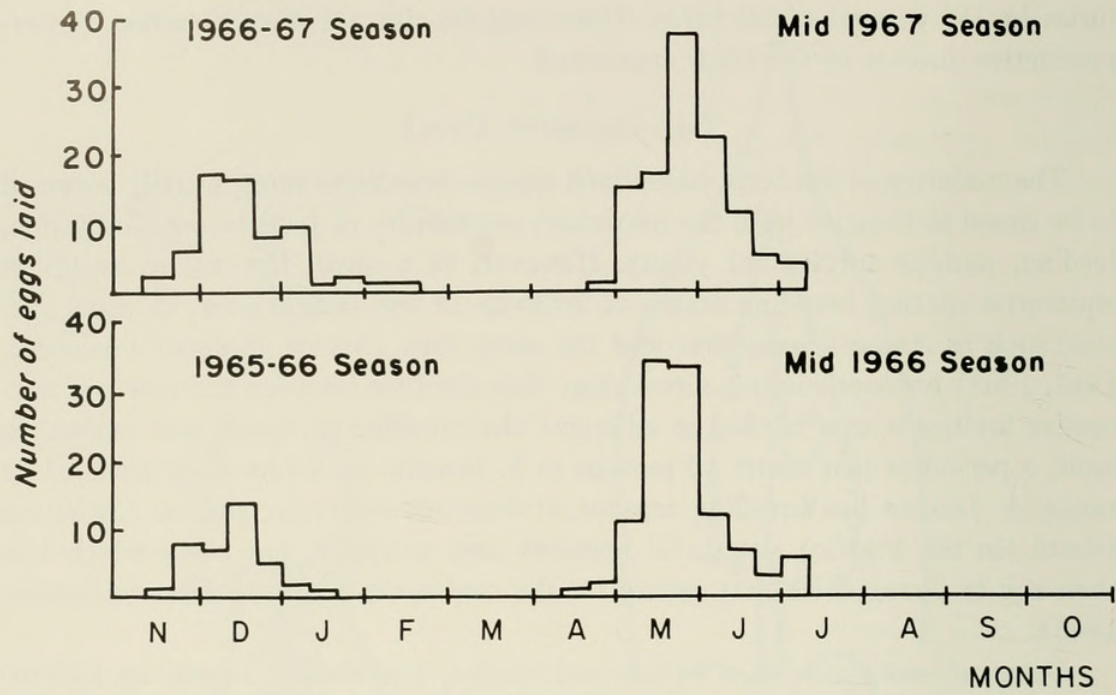


FIGURE 6. The distribution of egg-laying dates of *Oceanodroma castro* in the study burrows on Plaza November, 1965, to the start of July, 1967.

in the Azores no breeding was found 1 June, but birds were coming ashore to breed in September (Hartert and Ogilvie-Grant, 1905).

In Japan the birds arrive at the colonies in late May, breed through the summer, and leave in October (Austin and Kuroda, 1953). The scant Hawaiian data of several barely flying young found in October in the late nineteenth century, suggest a similar cycle (Richardson, 1957).

For many years it was thought from the single breeding record quoted by Loomis (1918) that egg laying in Galápagos took place May-July, but a single

TABLE 2. The numbers of birds ringed for *Oceanodroma castro* on Plaza in one season and of retraps from one season to another. The figures in brackets after the number of birds handled is the number of possible nonbreeders in the sample.

	Birds handled in season							
	1965-66	Mid-1966	1966-67	Mid-1967	1967-68	Mid-1968	1968-69	Mid-1969
	118	305	213	410	15	0	17	18
	[30]	[113]	[66]	[221]				
Retraps from season								
1965-66		0	64	0	5		8	0
mid-1966			0	150	0		0	10
1966-1967				0	5		6	0
mid-1967					0		0	6

chick found by Brosset (1963) indicated an egg laid around December. Snow and Snow (1966) have since shown that on Plaza there were two breeding seasons a year, with eggs laid March-June and December-January. They thought that the same birds were probably involved in successive cycles, and also that the December-January season was subsidiary, with less birds breeding and a lower nesting success.

Details of all eggs found on Plaza between November 1965 and July 1967 are shown in figure 6, and it should be stressed that the same burrows were often used by different birds in successive cycles, a few in all four seasons for which records are available (see later). There were four sharply demarcated cycles, two in the hot seasons (November to February) and two in the cold (May to July). Note that the two peaks do not come quite at 6-month intervals, but closer to 5 and 7 respectively, the significance of which is not known.

All birds ringed as breeders and nonbreeders in one season and retrapped in another are shown in table 2, which indicates that each individual bird had an annual cycle and that there were no recorded interchanges of birds between the cold and hot seasons. Unfortunately, only 12 adults and a single chick of this species had been ringed previously on Plaza (in the cold season of 1960 by Lévêque) and only one of these was recorded. This, however bred again in the cold seasons of both 1966 and 1967.

The species has such a long breeding cycle, involving at least a 3-week pre-egg period, 6 weeks' incubation, up to 3 months feeding the young, and with the need to fit in a complete molt as well, that it is clear that successful breeders could not nest in successive seasons during the same year. But the faithfulness of failed breeders and nonbreeders to the same cycle was unexpected and contrasts markedly with the results for *S. fuscata* where it breeds twice a year on Christmas Island (Ashmole, 1965).

This complete separation of birds nesting in the hot and cold seasons, if associated with young birds returning to breed at the same season of the year as they were raised, could potentially give rise to separate forms of the same species. However, no morphological differences were found between adults at different seasons, though there was a slight and constant difference in egg breadth (see later).

CLIMATIC FACTORS

Although the Galápagos Islands straddle the equator, the climate is only subtropical owing to the modifying influence of the Humboldt Current.* An account of the rather complicated currents is given by Abbott (1966).

Figure 7 shows the average monthly surface water temperature taken by the

* The 1965 temperatures were in a year when the Humboldt Current lessened allowing 'El Niño' or warm current to affect Galápagos. The phenomenon was responsible for a very large mortality of sea birds from the guano islands of Peru.

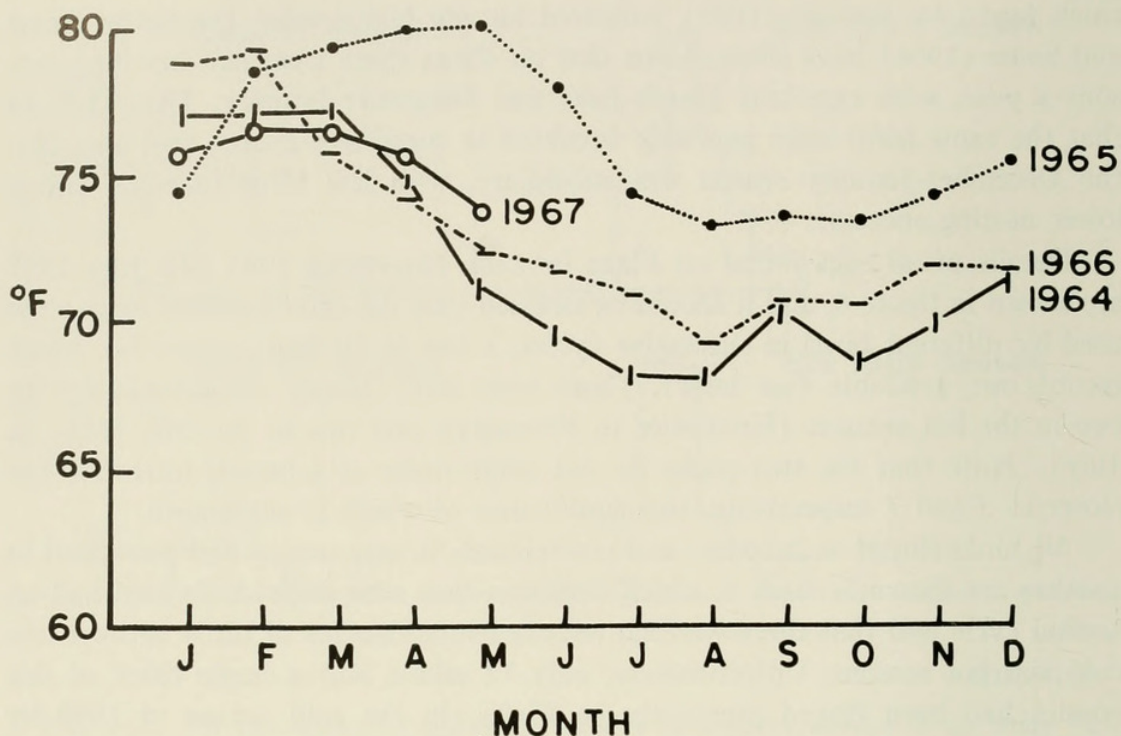


FIGURE 7. Surface water temperatures taken at Academy Bay, Santa Cruz, Galápagos, by the Charles Darwin Research Station.

Charles Darwin Research Station at Academy Bay, Santa Cruz—about 18 miles from Plaza. Despite a regular fluctuation in water temperatures I was unable to detect any large-scale seasonal variation in surface plankton, although the samples show that it appears to be very variable both in time and place. As a general rule, the seas and winds are calmest during the warm months, and strongest during the cold season, but there is little correlation of breeding success with time of year.

ACTIVITY OF NONBREEDERS

In all sea bird populations there are large numbers of nonbreeding birds which may or may not frequent the breeding colonies. In some instances, as in the Manx shearwater (*Puffinus puffinus*) and *H. pelagicus*, the total number of nonbreeders visiting the colonies throughout the breeding season may be a substantial proportion of all the birds there (Harris, 1966a, and personal observations).

Unfortunately netting at night was all but impossible, so observations of nonbreeders were almost entirely restricted to those roosting in burrows by day. However night observations and estimates of the number of birds calling in flight agree very closely with the three seasons' results given below. Detailed observations were made in all four seasons but only three seasons are treated here as many fewer burrows were available in the 1965-66 season. In the other

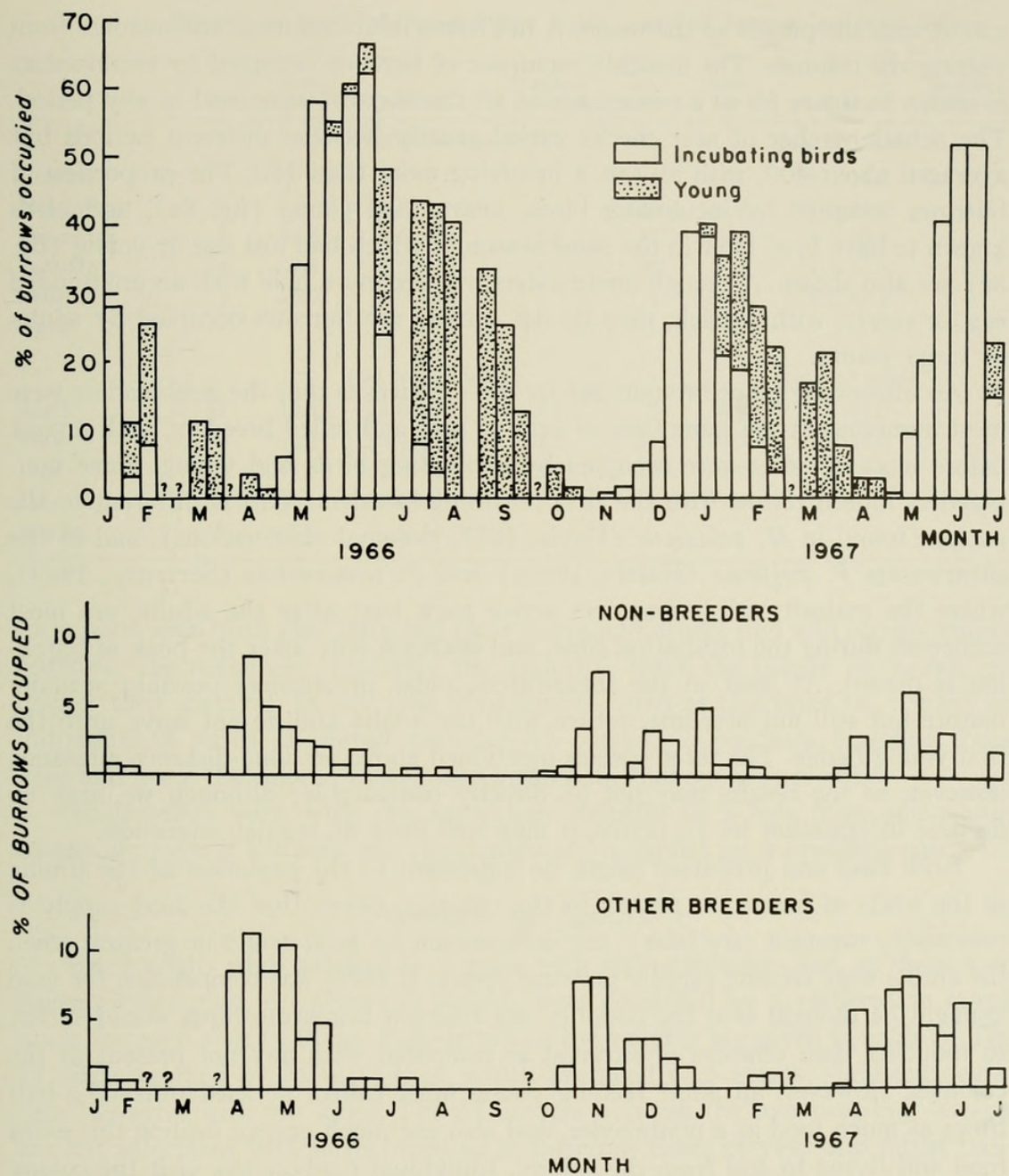


FIGURE 8. The percentages of the study burrows of *Oceanodroma castro* occupied January, 1966, to July, 1967, by a) incubating birds (unstippled area) and unattended young (stippled), b) nonbreeders, and c) breeders before laying or after losing egg or young.

seasons, 43 percent, 43 percent, and 64 percent of all burrows had nonbreeders roosting in them at some time, and, as the burrows were checked on only about 1 day in 3, the true proportion must have been much higher.

The visits by nonbreeders were not scattered throughout the year but were closely correlated with the reproductive cycles of the breeders, and to a lesser

extent with the phases of the moon. A full moon inhibited most nonbreeders from visiting the colonies. The monthly incidence of burrows occupied by nonbreeders is shown in figure 8b as a percentage of all the burrows examined in any period. The actual number of nest checks varied greatly between different periods but averaged about 400, with all but 8 involving more than 150. The proportion of burrows occupied by incubating birds, unattended young (fig. 8a), and birds known to have bred later in the same season or which had lost egg or young (fig. 8c) are also shown. Although nonbreeders will occupy a hole with an unattended egg, or rarely, with a chick, they do not usually use burrows occupied by adults or large young.

An interesting point brought out by these figures is that the nonbreeders were most numerous at the same time of year as pre- and failed breeders, with a peak before most burrows were occupied by incubating birds and young. Some nonbreeders indeed return with the first returning breeders. This is different to the pattern found in *H. pelagicus* (Davis, 1957, personal observations), and in the shearwaters *P. puffinus* (Harris, 1966a) and *P. tenuirostris* (Serventy, 1967), where the majority of nonbreeders arrive back long after the adults, are most numerous during the incubation time, and decrease only after the peak of hatching is passed. At least in the shearwaters, older prebreeders possibly sexually mature but still not breeding, return with the adults and do not leave until the first young fledge. The three species mentioned above are long-distance migrants, however, so the results may not be directly comparable; although we have no definite information for *O. castro*, it may well have no regular migration.

Both food and predation might be important in the evolution of the timing of the visits of immature petrels to the colonies. Given that the food supply is reasonably constant (see later), any competition for food would be greatest when the adults were feeding rapidly growing young. If there was competition for food it might be thought that the possibly less efficient immature birds would suffer, so reducing their chances of survival as compared with any not present at the colonies. However, an adult feeding young must collect at least one-and-a-half times as much food as a nonbreeder, and also use much energy finding this extra food and flying to and from the colony. Individual nonbreeders visit the colony only infrequently and can spend most of their time on the feeding grounds. As it appears unlikely that a nonbreeder is only half as efficient at feeding as a breeder, the first result of any competition for food would be food shortage for the nestlings. The adults themselves look after their own needs before those of their young (Harris, 1966b).

Predation by owls is important in this colony (see later) and perhaps the nonbreeders, by returning with the displaying adults, increase their own chances of survival as the predators would take proportionately many fewer birds than if the return was spread over a longer time. Of these nonbreeders, some presumably

TABLE 3. *Weights in grams of Oceanodroma castro found in burrows on Plaza Island.*

	No.	Aver- age	Range	Standard deviation	No.	Aver- age	Range	Standard deviation
1965-66 season					1966-67 season			
October					5	42.1	39.0-44.5	2.2
November					39	39.2	33.0-45.5	2.7
December	6	42.5	35.0-53.0	5.6	37	38.7	31.5-50.0	3.8
January	16	47.3	41.0-55.0	4.8	20	40.2	32.5-56.5	4.2
February	2	46.0	38.0-54.0		4	39.5	28.5-41.5	4.7
April					1	39.5		
Mid-1966 season					Mid-1967 season			
April	33	39.3	31.0-49.0	3.1	3	40.8	38.5-43.0	
May	34	41.3	34.5-54.5	4.7	52	39.7	32.0-48.0	3.5
June	102	45.3	33.5-54.0	5.1	27	41.5	34.0-50.5	4.5
July	4	44.4	39.0-46.5	1.1	1	39.0		
August	3	42.7	40.5-44.5					

form pairs with birds that have lost their mates and others find and occupy empty burrows; the remainder, probably the majority, leave the colony so do not endanger their survival. In any long-lived species, such as this must be, it pays an individual in terms of overall reproductive output, to postpone breeding for a year and leave the colony, rather than reduce its chances of survival.

Nonbreeders were, with two exceptions, faithful to a hole from one season to another even if the hole was simultaneously occupied by a breeding pair.

WEIGHTS OF ADULTS

Many adults were weighed to .5 gram with spring balances but, as these soon became inaccurate, the observed weights were corrected by a calibration graph made for each visit to Plaza. Full details of the weights are given in table 3. The 12 birds weighed by Allan (1962), which averaged 43.5 grams, standard deviation 5.0, agree with my series. The differences between the four breeding seasons are not associated with birds breeding at different times of year and might indicate some difference in the availability of food (but see later).

In all four seasons, the average weight increased as birds started incubating and had food stored in the stomach, reached peaks during January and June, and then decreased when the birds had small young.

There were no significant differences in the weights of adults before laying, failed breeders, and intruders.

VISITS TO BURROWS

General observations showed that as soon as birds returned for the start of a season, some might remain in the burrows by day. In extreme instances, adults

TABLE 4. Days spent in nesting burrows by *Oceanodroma castro* storm petrels during 5-day periods before laying. There were also birds present on five days (4 with both birds) between 61 and 72 days before laying.

	56-60	51-55	46-50	41-45	36-40	Days before laying					11-15	6-10	1-5
						31-35	26-30	21-25	16-20	11-15			
No. of possible days	179	183	163	185	168	237	179	301	296	370	273	325	
% days male only	1.1	1.7	0	3.2	1.8	4.2	6.7	4.9	5.4	3.8	4.0	7.4*	
% days female only	0	0	0	.5	0	2.1	2.8	3.9	.3	1.9	.7	.3	
% days both together	.6	.5	1.2	2.2	3.0	5.1	8.9	11.0	6.1	.8	2.2	0	
% including unsexed birds	2.8	5.5	1.8	5.9	9.5	14.3	18.4	21.0	17.2	6.7	8.0	10.8*	

* This does not include 16 birds found in burrows immediately prior to laying.

stayed in burrows still occupied by the previous season's young. This was however rare as there was little overlap between successive seasons.

There were no detectable differences in the occupation of burrows before laying in the four seasons, and all the results are treated together in table 4. The longest recorded interval between birds first roosting in the burrow by day and laying was 72 days, but in several burrows no birds were found until the egg was laid. After these early visits, the frequency of birds in the burrows increased rapidly to a maximum 3–4 weeks before laying and then decreased to a minimum 2 weeks before laying. This decrease was most marked in the females, which were presumably far away at the time feeding hard in order to form the large egg. There is however no well-marked "honeymoon period" as in *P. tenuirostris* (Marshall and Serventy, 1956) when both birds are away from the colony. The longest recorded stay in a burrow was 5 days by a female which was joined by the male for 3 days. It was common to find both birds together in the burrow by day.

The male continued to roost in the burrow occasionally, perhaps so as to keep possession, right up to the time of laying, even though it might have been expected that he would have been away building up his reserves in preparation for the first incubation spell. In the 5 days immediately prior to laying, birds of known sex were found in the burrow in 41 instances—only one of these was a female, which returned 2 days before laying. Of the males, 16 were found the day before the egg was laid (and it might be assumed that they were waiting for the first incubation spell), eight were 2 days prior, six were 3 days, three were 4 days and seven were 5 days prior to laying. Normally the female leaves after laying the egg and the male incubates. In some instances, however, probably when the male has not returned, she may either incubate for 1 or 2 days or leave the egg. It may well be that the arrival of the male at laying time is a matter of chance and perhaps at this time he is feeding near the colony by day and visiting the nest site most nights. The data of Pinder (1966, fig. 4) for the Cape pigeon (*Daption capensis*) lend support for this view.

BEHAVIOR

On Plaza the species flies only at night and in only a single instance, about 30 minutes before dusk, was a bird seen near the island by day. The first birds arrived ashore about 1850 hours, that is, 50 minutes after sunset, but birds were never heard calling before 1900 hours. The peak activity was normally 2200 to 2400 hours on nights without moon but just before dawn on nights with a full moon. The effect of the moon was very marked, especially affecting the numbers of calling birds. The calls have been well described by Lockley (1952) and Allan (1962) and were uttered both in flight and from the burrows.

Birds usually flew close to the cliffs and rarely over the flat top of the island

and there appeared to be two types of display. One was directed toward the holes, usually to a hole with a churring occupant. Presumably unattached birds are attracted by these calls emitted by a bird with a hole but not a mate. In several species of storm petrels, adults can be attracted by a tape recording of these churrs. (Huntington, personal communication and personal observation). The second display was aerial and usually between two birds which chased each other in reasonably constant circuits. This was very noticeable when nets were used, as some pairs would circle time and again, just missing the net, until one, or usually both, were caught. In one display, two birds repeatedly went through a 2-foot gap between the net and the cliff face until one was caught; the other then did its usual circuit before joining its mate in the net.

A single mating was observed by day in a very open nest site. The prior display was not observed, but the whole subsequent procedure was silent. Throughout the mounting, which lasted at least 3 minutes, the male gently pecked the female's head, moving from side to side across the head with special emphasis at the base of the upper mandible. The egg was laid 33 days later.

DEVELOPMENT OF THE BROOD PATCH

Little is known of the molt of the brood patch in sea birds and the only observations on petrels appear to be those of Allan (1962), who thought that no bird molted its brood patch later than 20 days before laying, that some started at least 40 days before laying, that the actual molt might be completed in no more than 4 days, and that vascularization was complete 5 days before laying.

In the present study there were 249 observations on birds prior to laying, 267 on nonbreeders, 44 on birds which had lost the egg, 10 on those with young, and 3 on those which had lost young. With a few exceptions, incubating birds were not examined. There was no apparent difference between the sexes so the results have been lumped. Similarly there was no difference between the various seasons.

The state of the brood patch was classified and scored as follows:

Score 0. No sign of brood patch.

Score 1. Brood patch half defeathered.

Score 2. Brood patch defeathered but unvascularized.

Score 3. Blood vessels just visible.

Score 4. Fully vascularized, with blood vessels "knotted" and obvious.

No special note was made of oedema, but it was apparently only present in incubating birds. Apart from a netted sample which is discussed separately, all birds were taken from burrows and their breeding state was known. Any dubiously breeding birds have been omitted. The laying dates of most breeders were known to within 2 or 3 days, and if not so exactly, then the mean date was used between a check without and with egg provided that the interval was less than 8 days.

Although it is realized that the scores 0-4 are probably not equivalent in

TABLE 5. *State of brood patch in early and late nesting representatives of Oceanodroma castro in relation to days before laying. State of brood patch 0 = no trace, 1 = half de-feathered, 2 = defeathered but unvascularized, 3 = blood vessels just visible, 4 = fully vascularized.*

	State of brood patch and numbers of birds											
	Early breeders						Late breeders					
	0	1	2	3	4	Average	0	1	2	3	4	Overall Average average
Days before laying												
46+	1	2		1		1.3	2	3	9	1		1.5
41-45	2		1			.7	1				1	1.2
36-40	4		3			.9			9			1.5
31-35	4	1	8	2		1.5	6		4	4	1	1.6
26-30	11	4	8	1	2	1.2		4	13		2	1.5
21-25	5	4	9	4	2	1.7		1	7	4	1	2.0
16-20		2	12	5	1	2.3		5	13	4	2	2.2
11-15		1	3	3	3	2.8			2	2		2.7
6-10		1	1	2	8	3.4			3		1	3.2
1-5				4	10	3.7			1	3	5	3.6

time or metabolic effort to the birds indicated, an average score for each 5-day period prior to or after laying was calculated and used below.

BREEDING BIRDS

At least some birds lose the feathers from the brood patch immediately after, or perhaps even before, coming to the colony at the start of a season. Of 10 adults caught more than 50 days before laying, only two were without a brood patch, and one even showed some enlargement of the blood vessels. However, these birds may have been slightly anomalous, as many other individuals come back without any trace of a brood patch. The progression of the losing of the feathers and vascularization is shown in table 5.

It is difficult to find how long the various stages take as individual birds were irregular in their roosting in the holes. But the process is certainly very variable, as some birds have fully vascularized brood patches more than 6 weeks before laying, but others not even when the egg is laid. The minimum observed time for vascularization of a defeathered brood patch was 7 days. I agree with Allan (1962) in finding that all birds had lost all the feathers of the brood patch at least 20 days before laying, but this is hardly surprising, as most nonbreeders also reach this stage. My minimal observed time for defeatherization was 12 days. The most complete record for any bird was (1) 32 days prior to laying, no brood patch, (2) 23 days prior to laying, defeathered but nonvascular brood patch, (3) 18 days prior, partially vascularized, and (4) 2 days before laying, a fully vascularized brood patch.

TABLE 6. *State of brood patches in nonbreeding members of Oceanodroma castro. Details of brood patch numbers as table 5.*

	Numbers of birds with brood patches					Average
	0	1	2	3	4	
October	1					1.0
November	4	4	23	2		1.7
December	1		40	12		2.2
January			20	5	1	2.3
February			2	1		2.3
March	1					0
April	8	1	4			.7
May	11	5	66	10	3	1.9
June			21	7	2	2.4
July	1		7	2	1	2.2
August			1			2.0

There is evidence to suggest (table 5) that birds laying early in the season arrive back with brood patches less developed relative to the date of laying than do later nesters, and that this is associated with quicker development.

Regrowth of the feathers of the brood patch usually started about a week after hatching, but the process was again variable and the numbers of birds examined small. Ten birds netted on Tower 16 February 1966 consisted of five birds with brood patches unvascularized, four with feathers growing, and a single bird with no brood patch. At least six of these were probably feeding young, as they regurgitated large quantities of food.

NONBREEDERS

The majority of nonbreeders (184 out of 267 observations) had defeathered but unvascularized brood patches, while many fewer (39) showed signs of vascularization. A few birds (7) had fully vascularized brood patches identical with those of breeders. The brood scores (table 6) show that there is a cyclic fluctuation related to the 6-monthly breeding. Unfortunately, I know little of birds coming ashore by night, but a sample of 36 birds caught at night, 2 and 3 June 1967 consisted of two birds with no brood patch (one bird had bred a year previously), 32 with it defeathered (one bird had bred a year previously), and two with it fully vascularized (one had an egg about to be laid). This gave an average brood score of 2.0, or 1.9 if the breeder is omitted, which is significantly lower than that for 30 birds taken from burrows in June (2.4). This is probably explained by the birds spending time in aerial display at this stage of the breeding cycle being younger than those which were overstaying in the burrows.

TABLE 7. Egg measurements (in mm.) of eggs of *Oceanodroma castro*.

	Number	Average		Standard deviation	
		Length	Breadth	Length	Breadth
Galápagos 1965-66 season	16	31.2	22.8	1.8	.80
mid-1966 season	72	31.5	23.5	1.3	.75
1966-67 season	45	31.1	22.6	1.4	.71
mid-1967 season	61	31.4	23.6	.95	.66
Cape Verde Islands (Bannerman, 1959)	2	31.0	23.8		
St. Helena (Haydock, 1954)	8	33.3	24.2		
Madeira (Brit. Mus. and Jouanin)	9	32.8	24.9	1.1	.48
Ascension (Stonehouse, 1963a)	44	32.2	23.5	1.3	1.0
Salvage Islands (Jouanin)	5	32.7	25.0	.91	.51

THE EGG-STAGE

The egg was always laid at night and then either incubated by the male (32 instances), by the female (23 instances), or left unincubated (6 instances). The male took the first long incubation stint and the female only waited for him to appear before departing; if he did not arrive soon she either incubated for 1 or at the most 2 days or departed at once. The male took over from the female the night after laying in at least five cases.

The single egg was white, often with a ring of faint pink marks (as in other storm petrels) at the blunt end which soon disappear with incubation. The measurements of 194 eggs from Galápagos and some from other colonies are shown in table 7. The differences between the seasons and the colonies are not significant. The extreme measurements of the Galápagos eggs (in mm.) were 34.8×22.1 , 28.0×22.3 , 32.7×24.9 , 28.3×21.0 (which was also the overall smallest egg) and 34.0×24.0 (overall largest). Twenty-eight newly laid eggs averaged 8.5 grams, range 6.0 to 11.1 (standard deviation .93). Five newly laid, and hard boiled, eggs had yolk: albumen weights of 2.3 : 4.3, 2.5 : 4.9, 2.4 : 4.9, 3.6 : 6.8, 2.8 : 3.8. The shell weights were from .3 to .7 grams but my balance was not very accurate in this range.

The female usually weighed least immediately after laying, 20 individuals weighed the morning after laying averaged 39.8 grams, range 36.5 to 45.5 (standard deviation 2.6). One bird caught after laying in 2 successive years weighed 36.5 and 38.0 grams. This postlaying weight is still slightly heavier than non-breeders (average 38.9 grams) and only just under that of adults in the prebreeding period, 40.3 grams), which suggests that the female obtained the food reserves for the egg during the prelaying period at sea. The female is probably lighter than nonbreeders if the weight of the enlarged ovary is excluded. The egg was approximately a fifth of the female's weight (20 eggs, range 17 to 24 percent, average 21 percent) as compared to 26 percent in *Oceanites oceanicus* (Roberts, 1940)

and *Pelagodroma marina* (Richdale, 1943–44), 25 percent in *H. pelagicus* (Davis, 1957), and 20 percent in *Oceanodroma leucorhoa* (Huntington in Lack, 1967). The measurements of eggs laid by individual females in two seasons showed less variation than those of the population as a whole.

Birds were extremely faithful to their burrows, and this could sufficiently explain this tendency to have the same mate in successive years. In only 10 instances was a bird ever caught in a different hole from that where it had been ringed. Two of these refer to a pair which were found breeding in the 1966–67 season in a hole 12 feet away from that occupied in the 1965–66 season. It is impossible to say if they moved as a pair or met again by chance in a new hole. One other breeder was found a second season in a hole a few feet from where it had previously bred. Four nonbreeders in one season were retrapped in another season in other holes, all within 10 feet; two of them were breeding with unringed birds. A single bird was caught once in each of two seasons in shearwater holes 150 yards apart. The remaining two cases referred to two holes only 6 inches apart in a smooth vertical rock face and could easily have been due to birds entering the wrong hole.

All other retraps between seasons (194 birds) and within a season (many thousands) were in holes where the birds had been ringed. Obviously birds could have moved into burrows inaccessible to me but it is unlikely that burrow desertions occur at all frequently if both birds of a pair remain alive. Richdale (1965) found similar results in *Pelagodroma marina*.

The laying dates of pairs were not influenced by the success or otherwise of the breeding attempts in the immediately previous season even if there had been a late chick present when the first adults returned for the new season. This suggests that the gap between breeding cycles was sufficient for all the prelaying activities. Pairs which had bred before laid an average of 4 days before new pairs but this difference was not significant.

The relative shortness of my stays on Plaza (maximum 13 days) did not allow many individual incubation spells to be calculated directly and the results are biased towards the shorter spells. Observations were however made on color-marked birds and the results showed that the normal spell was 4 to 7 days with, rarely, a prolonged stay of at least 11 days, or as short as 2. Such long stays are however very unusual as most birds leave the egg long before this if not relieved by the mate. Another method of calculating the average incubation spell (table 8) is by observing the proportion of nests where changeovers have occurred overnight, with the proviso that the observations are spread over enough nights to avoid bias due to many pairs changing over together. The average spell appeared to be 6 days as compared with 2 days in *Oceanites oceanicus* (Roberts, 1940), 3 to 5 days in *Pelagodroma marina* (Richdale, 1943–44) and 3 days in *H. pelagicus* (Davis, 1957).

TABLE 8. *Number of change overs from one day to the next in incubating members of Oceanodroma castro.*

<i>Year</i>	<i>Month</i>	<i>Number examined</i>	<i>Number with different bird</i>	<i>Average incubation spell (days)</i>
1966	January	62	11	5.6
1966	June	392	62	6.3
1967	January	103	21	4.9
1967	May	25	6	4.2
1967	June	170	24	7.1
1967	July	43	8	5.4
	Total	877	146	6.0

As reported by Allan (1962), a strange bird may rarely be found in a burrow with an egg when the normal adults are missing. In this study such birds were never actually incubating, the egg being cold, and were certainly nonbreeders prospecting for holes.

Some birds were weighed daily during incubation and the observed weight losses are shown in figure 9, the average loss being 1.6 grams a day. Expressed another way, for a normal incubation spell a bird must have stored food reserves equivalent to a quarter of its normal weight. Three birds were weighed on a day before a changeover and then the first day of their next incubation spell, the gains were 9.5 grams (in 5 days), 5.5 grams (7 days) and 8.5 grams (8 days) or 23 percent, 20 percent, and 12 percent of the weight of the birds at the end of the spell. Two of these increases were less per day than the daily losses during incubation, and it was unfortunate that the incubation spells of these returning birds were not known, as they may have been shorter than average. The weight of a returning bird did not increase, presumably after a minimum level, with the length of time spent away from the nest, suggesting that birds came back as soon as they had sufficient reserves to undertake another incubating spell.

The average incubation period for 62 eggs was 42 days, with extremes of 39 and 51 days, much longer than the 38 days obtained indirectly by Allan (1962) but in line with the 43 days (39–48) for *Oceanites oceanicus* (Roberts, 1940), 41–42 days for *Oceanodroma leucorhoa* (Huntingdon in Palmer, 1962), and 41 days for *H. pelagicus* (Davis, 1957). In all these species, the incubation period may be prolonged because of eggs being left unincubated for several days at a time.

As yet there appears to be only a single published record in a procellariiform of a repeat laying in the same season after the loss of an egg. This was in *P. puffinus* (Harris, 1966b) but Britton (personal communication) has now found another instance of repeat laying in this species. Huntington (in preparation) documents a case of repeat laying in *O. leucorhoa*.

On Plaza the situation was complicated owing to competition for nest sites,

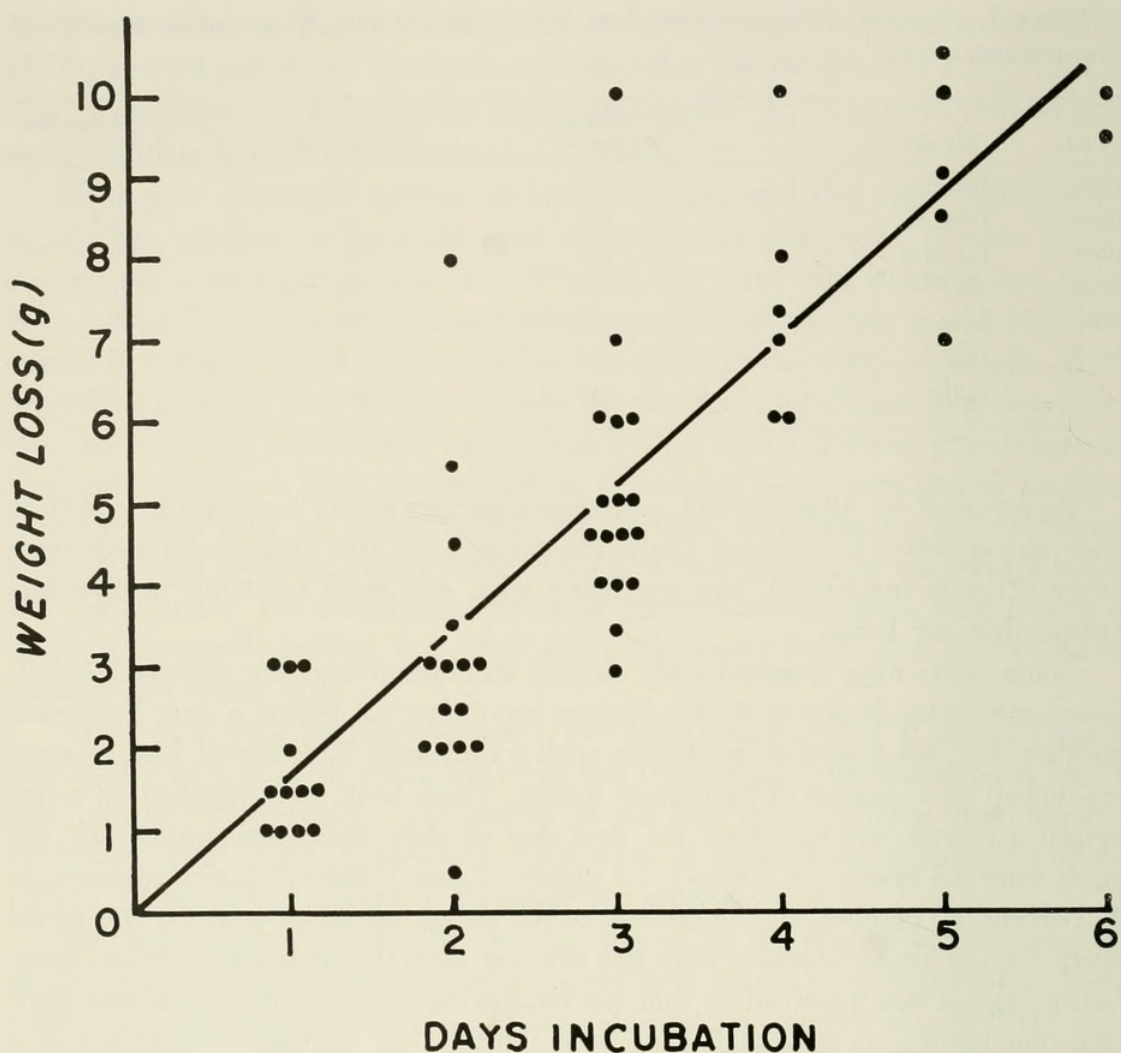


FIGURE 9. Daily weight losses in incubating individuals of *Oceanodroma castro*.

and in several instances two pairs were known to have laid in the same burrow during the same season. There were however six instances where repeat laying was a possibility but in no case was it certain.

In the first instance, an egg was accidentally broken when the female was incubating the day after an egg appeared in a burrow. Unfortunately the cloaca of the bird was not examined in detail but, as she had had a fully vascularized brood patch 20 days before, it is probable that she had laid this egg. This same female, with a swollen and distended cloaca, was found on a fresh egg a month later. This was the latest egg to be laid that season. No other bird was seen in the burrow. The second case was a female found with a vascularized brood patch and a broken egg a month before laying another egg.

The third was of a male incubating an egg which was broken after 3 days' incubation, almost certainly by a representative of *P. lherminieri*, which was also

using the nest hole; the female (its mate from a previous breeding) was on another egg 6 weeks later, the last egg to be laid that season. No other bird was seen in the hole.

The other cases refer to males, with fully developed brood patches, found on eggs which were almost immediately lost, and later on another egg, 27, 31, and 36 days respectively after the losses. There was no evidence to suggest that one of the birds early in the season had deserted and the remaining bird had to delay breeding while finding a new mate (Davis, 1957). It is impossible, however, to be sure that a nonresident had not visited the burrow and laid an egg which was then taken over by the resident pair, but the birds having had vascular brood patches very early (which on average occurred only 2 to 3 weeks prior to laying) suggested that some were probably true second eggs. Allan (1962) had similar occurrences in two burrows but was unable to prove repeat layings.

Two eggs were laid in two other holes but these were probably a result of 2 pairs. The numbers of birds found in a burrow did not affect the nesting success; this agrees with Allan's (1962) suggestion that once ownership was established it was well nigh absolute.

Nothing in the data suggested that females laid at the same date each year or that the nesting success of the pair using the site 6 months previously affected the date of laying.

THE CHICK-STAGE

Hatching was a very variable process, taking from 3 to about 7 days from the first denting of the shell. Davis (1957) suggested there was a changeover during chipping, but with short incubation spells as in *H. pelagicus* this is inevitable.

The only observations I have on the behavior of the adults near hatching were on those marked during incubation. These showed that there was no changeover prior to hatching, but once the chick emerged, changeovers were more frequent as the adults gave food to the young and probably depleted their own food reserves in the process. Many young were brooded for only 2 to 3 days, as compared to 6 in *H. pelagicus* (Davis, 1957), 2 to 4 in *Pelagodroma marina* (Richdale, 1943-44), and 1 or 2 in *Oceanites oceanicus* in a very cold climate (Roberts, 1940); it was rare to find an adult with the chick after this time.

GROWTH OF THE YOUNG

Growth of the young of many procellariiformes tends to be erratic, presumably due to scarcity and fluctuations in the available food, and the long fledging period has doubtless been evolved to cope with a food supply of this kind (Lack, 1948). If, however, a reasonable sample of chick weights are lumped, a uniform and typical growth pattern is found. This shows a steady increase to a maximum

much higher than the adult weight, and then a gradual fall-off towards fledging. I have suggested (Harris, 1966b) that this large accumulation of fat reserves serves two complementary functions in allowing the adults to leave the colonies earlier than if they had to supply less food regularly but for a longer time and the chicks to have a better chance of surviving if the adults are forced to leave them due to food shortage. The former point is probably most important to a migratory species; the latter to some tropical species as *P. lherminieri* in Galápagos, which suffer from frequent food shortages (Harris, 1969).

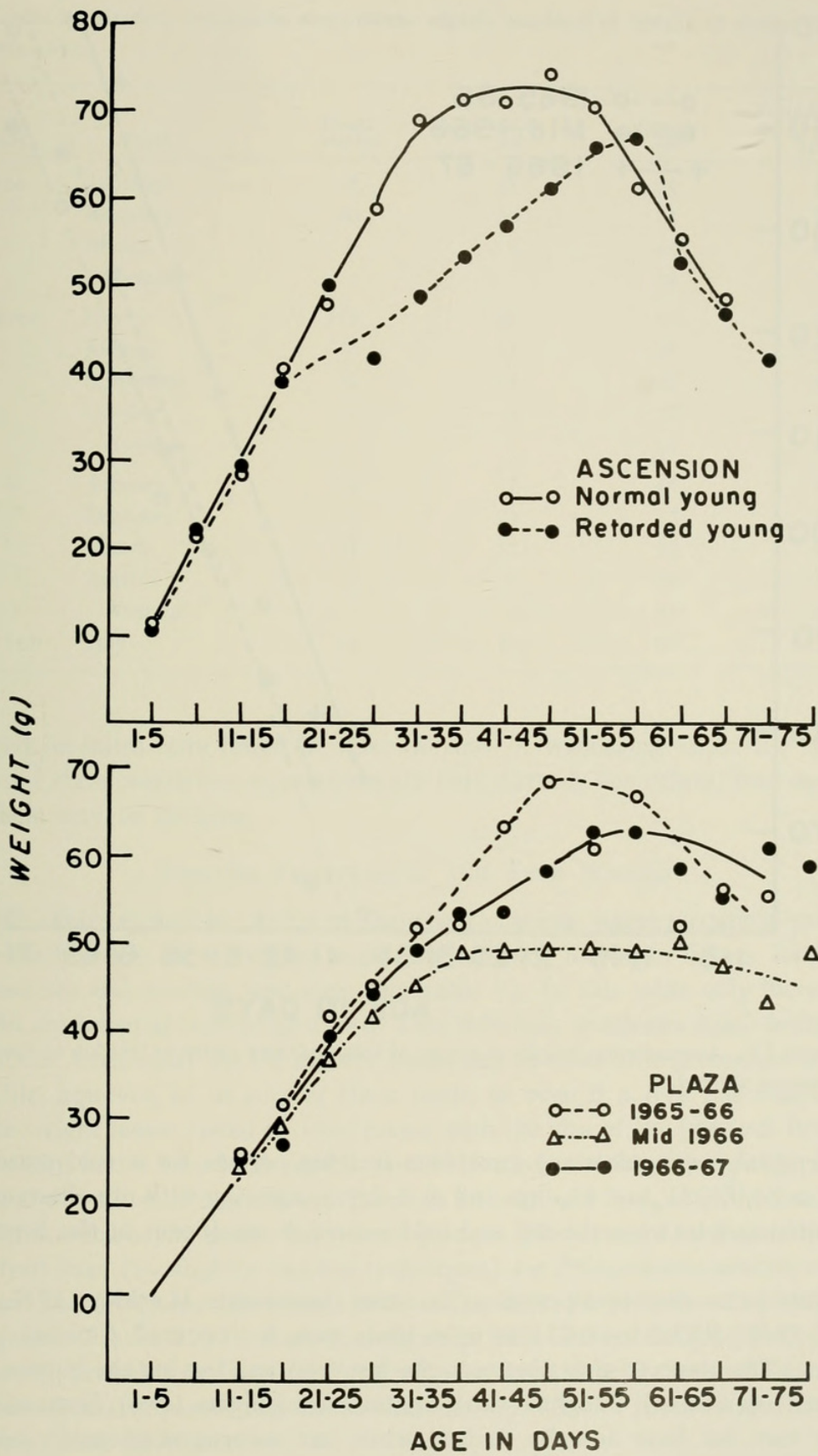
Unlike Allan (1962), I did not find it possible to readily separate the young into normal and retarded groups (though there were some of the latter so aptly described by him as 'Mohawks'); the average growth curves for the three seasons (fig. 10) include all young which survived to an age when they might have fledged, and also young lost earlier due to predation. As far as possible, evening weighings have been used, as they were less affected by larger-than-average feeds, but for some instances when this was not possible, some morning weighings are also included. Any errors from the last cause are slight because the average decrease between morning and evening weighings was just under 2 grams. The growth curves for my three seasons and that given by Allan (1962) differ considerably, in fact the mid-1966 growth curve is far below that of "retarded" young on Ascension. These differences are also apparent in the maximum weights attained by the individual chicks. Surprisingly, these marked differences in growth are not correlated with corresponding differences in feeding frequency, weight of feeds, or nesting success. It is impossible to say if the "quality" of the food presented to the young varied from season to season, something which has yet to be demonstrated in any sea bird.

Wing lengths of chicks were also measured and showed a slightly different pattern (fig. 11) in that the growth lines in the 1965-66 and mid-1966 seasons were almost identical despite dissimilar weight curves, whereas the 1966-67 chicks appear slightly advanced. I have too few data on actual fledging weights for any comparison between seasons.

The fledging periods obtained varied in their accuracy, the majority having a possible error of ± 2 days. Eight for the 1965-66 seasons averaged 69 days (range 60-72) and 11 in 1966-67 averaged 71 days (65-72). These from the hot seasons (average 70, standard deviation 4.0) were longer than the 58 days quoted by Allan (1962), but the 25 from the 1966 cold season (average 78, range 66-107, standard deviation 9.5) were longer still. Snow and Snow (1966

→

FIGURE 10. The average growth curves of young of *Oceanodroma castro* on Plaza in the 1965-66 season (ten young), mid-1966 season (37 young), and 1966-67 season (16 young). The growth curves for young on Ascension are plotted from Allan (1962).



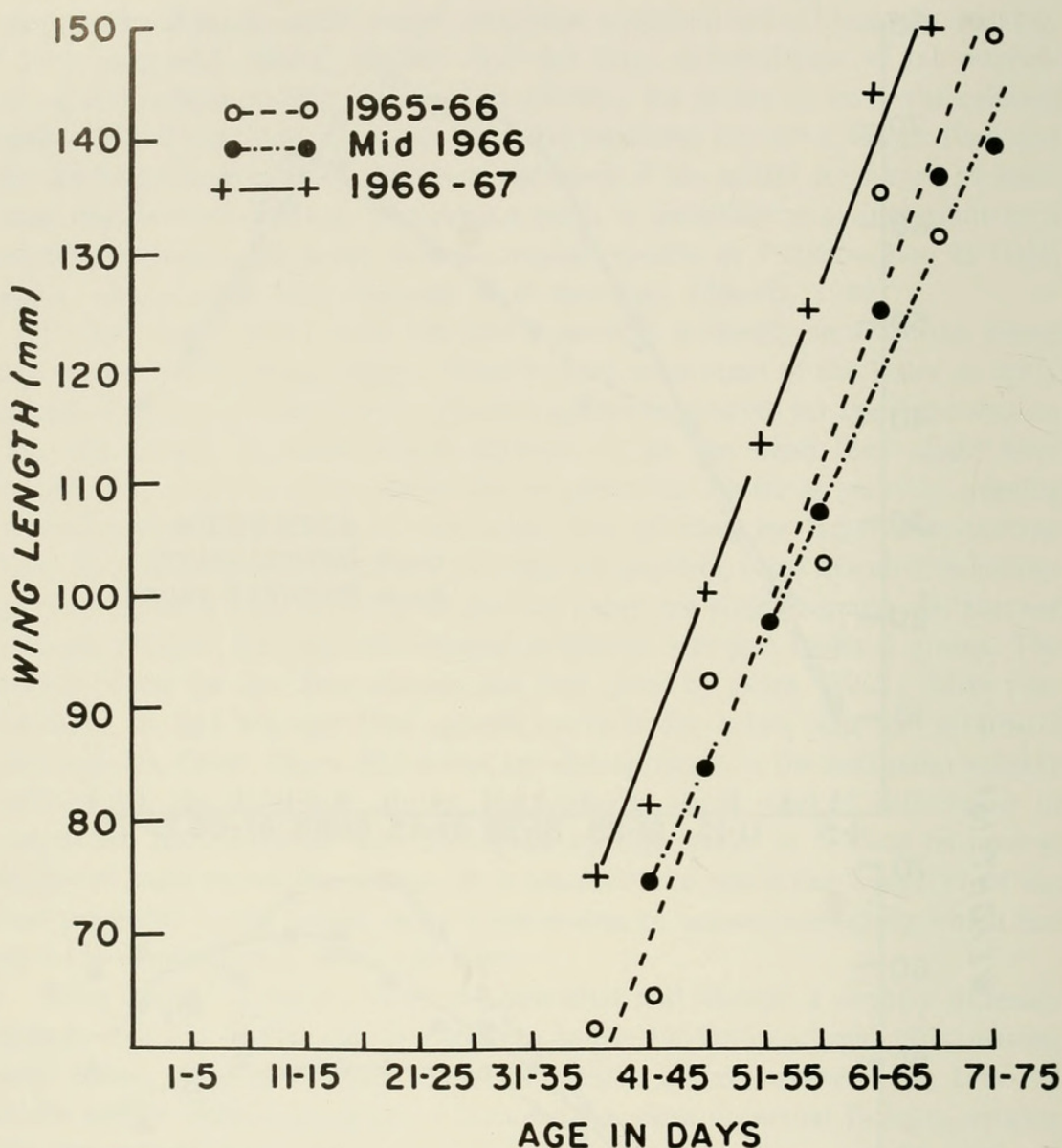


FIGURE 11. Average wing lengths of young of *Oceanodroma castro* in relation to age in the three seasons studied.

and personal communication) gave four fledging periods for a cold season on Plaza as 86, 84, 83, and 81 days (all ± 7 days), agreeing with my observations. The difference between the hot and cold seasons is significant at the 5 percent level.

There is no desertion period as in some shearwaters (Lockley, 1930; Serventy, 1958; Richdale, 1963) as most birds were fed up until 2 nights before fledging. The observed times between the last feed and leaving the burrow were 1 night (seven cases), 2 nights (two), and at least 5 nights (two). Some of these young may not have actually fledged when last seen as occasionally almost-

TABLE 9. Feeding frequencies and average nightly increases in weight of young of *Oceanodroma castro*.

Season	Month	Young weighed	Number fed	Percent fed	Average increase in weight (grams)
1965-66	January	36	23	64	6.8
	February	30	22	73	7.3
	March	9	4	44	8.4
	Average			65	7.2
mid-1966	July	112	67	60	5.7
	August	56	31	55	6.2
	September	70	36	51	6.0
	October	10	3	30	4.7
	Average			55	5.8
1966-67	January	16	7	44	6.6
	February	65	24	37	6.7
	March	61	32	52	4.9
	April	18	7	39	3.9
	Average			44	5.6
mid-1967	July	32	23	72	5.1

fledged juveniles were found in other burrows or wandering about the colonies. Some of these wanderers were obviously half-starved, but others were doubtless on their way to fledging.

FEEDING FREQUENCIES AND FEED WEIGHTS

All easily accessible chicks in sheltered locations where accurate weighings were easily made, were weighed night and morning to obtain figures for feeding frequencies and average feed sizes (see table 9). In this table only increases in weight are taken as indicating a feed. This obviously overlooks small feeds which might not even make up for nightly losses due to metabolic processes. It is impossible, however, to be sure of these feeds, or even if a feed has taken place, as the weight losses varied to some extent with the size of the previous feed, that is if a bird had a very large feed it would then lose weight very quickly. If anything above a loss of 2 grams was taken as indicating a feed, then the percentage of nights when a young was fed was 69 percent. The average feeding frequencies and feed sizes (by slightly varying techniques) for *Pelagodroma marina* were 72 percent and 6.4 grams (Richdale, 1943-44), and for *H. pelagicus* 83 percent and 6.4 grams (Davis, 1957). Both these species have shorter fledging periods than *O. castro*, probably because the food supplies were richer or nearer the colonies in these more temperate regions, so that the feed size, or the feeding frequency, or both, must be higher.

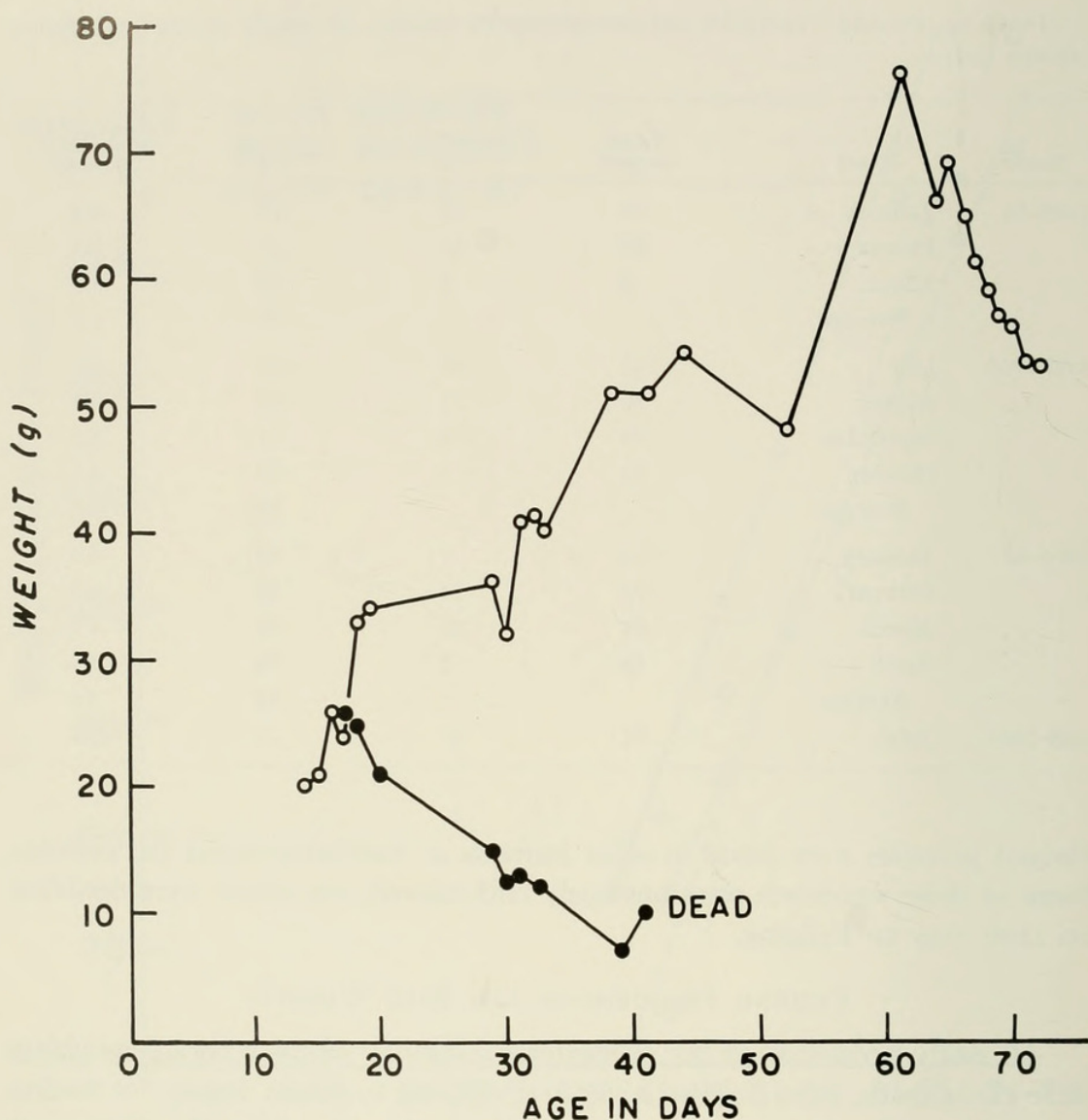


FIGURE 12. Growth curve of *Oceanodroma castro* young in an artificial set of twins in the 1965-66 season.

EXPERIMENTS WITH TWINS

Several small-scale experiments were carried out on the ability of this species to raise two young instead of the normal one.

In the 1965-66 season a single pair were given an extra chick and, although it was fed at first, the introduced young did not grow normally and died after 41 days. The other young had a normal growth curve (fig. 12) and fledged at about 72 days.

In the mid-1966 season, seven sets of twins were established and the results are set out below:

1. One young did not develop and died at 35 days; the other developed normally

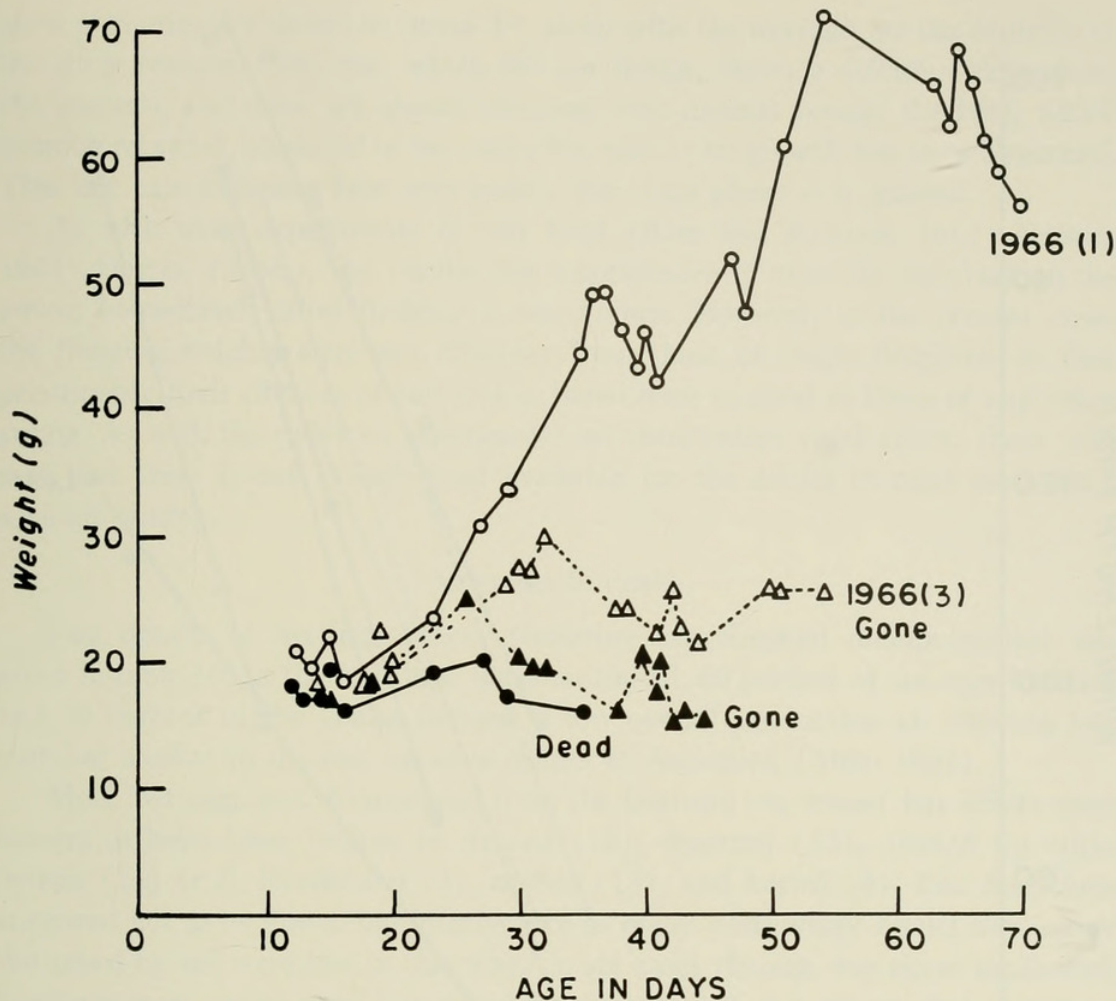


FIGURE 13. Growth curves of individual young of *Oceanodroma castro* in two sets of artificial twins in the mid-1966 season. Circles and solid lines refer to set 1 (see text) and triangles and dotted lines to set 3.

(fig. 13) and fledged at 69 days; 2. One did not develop and died after 52 days; the other did not grow normally, in that it never reached the normal peak weight, but fledged above average weight at 87 days; 3. Neither developed very well and both died, at about 44 and 54 days (fig. 13); 4. One was lost at 45 days when weighing more than its foster sibling; remaining bird fledged; 5. One died after 12 days; the other was lost at 90 days when near fledging; 6. Both were lost within 10 days; 7. One was lost within 6 days; the other developed normally but did not fledge.

In the 1966-67 season four more attempts were made but with similar results: 1. One did not develop and died after 30 days; the other fledged at 74 days; 2. Neither developed and both died at 45 and 51 days; 3. One died after 26 days; the other developed normally but was lost, probably to an iguana, after 45 days; 4. One died after 38 days; the other fledged at about 76 days.

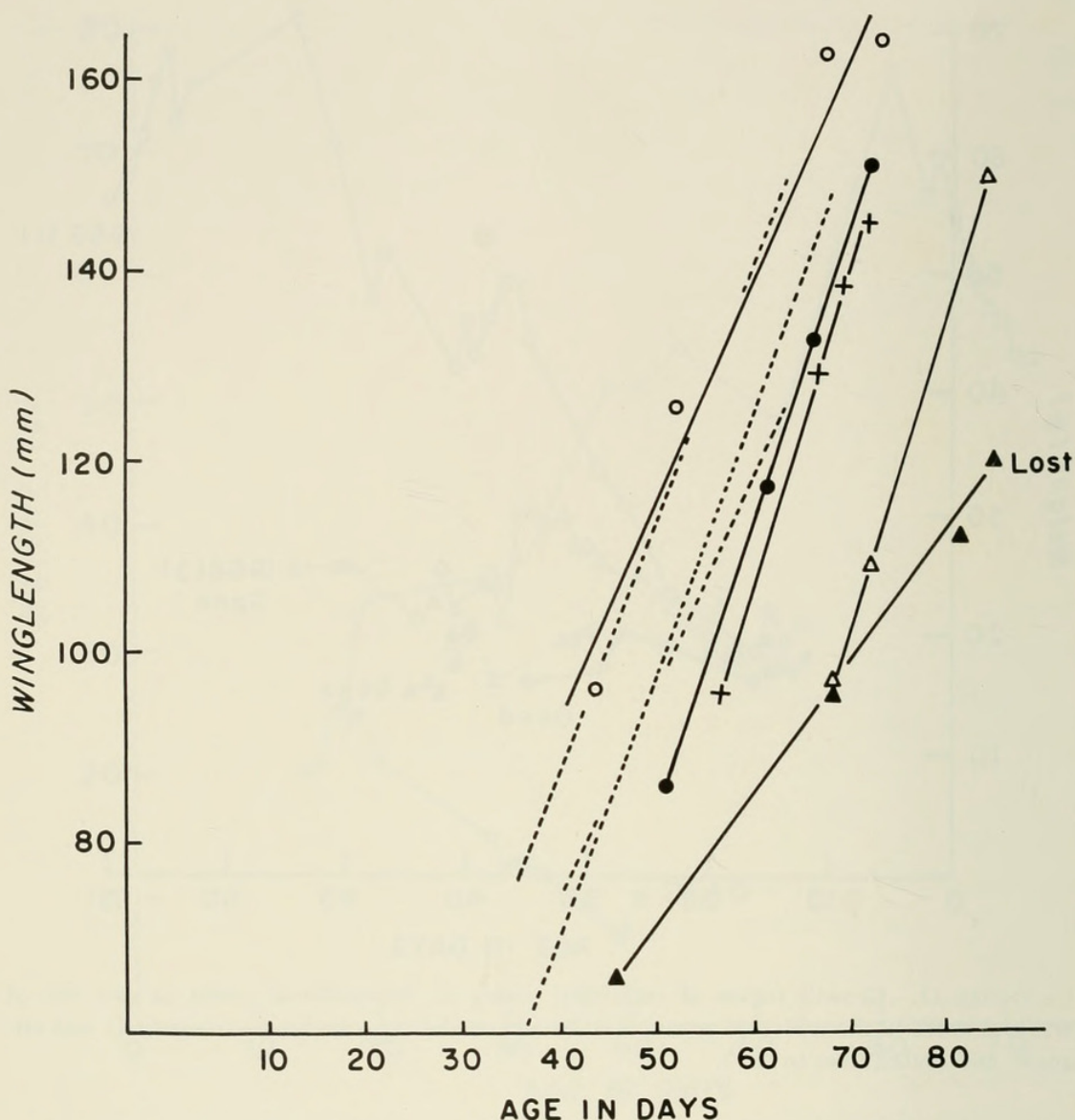


FIGURE 14. Increase in wing lengths with age in four successful and one unsuccessful *Oceanodroma castro* young from five sets of artificial twins. Also shown (dotted) are the average curves for normal young in the three seasons.

The 12 pairs with 24 young succeeded in rearing 6 young, the same success per pair as with normal pairs. Of the young which did not fledge, four were lost (perhaps to predators) when developing normally, and the remainder died of starvation. This starvation was not due to the parents rejecting the chicks, but to one of the young becoming dominant and taking the majority of the food. It is significant that in the pairs where this did not occur, both young died. In only two instances were both young fed on the same night, possibly when the two adults returned together.

The wing-growth curves of five of the twins which developed far enough to

grow primaries are shown in figure 14, along with the average for the controls in the three seasons. Only one, which did not fledge, shows a different slope from the controls, and three are almost identical with normal young; the fifth, which is much retarded, belonged to the mid-1966 pair 2; its growth was very abnormal. This last case indicates how very plastic the chick phase is in petrels.

As with most experiments of this kind (Rice and Kenyon, 1962; Nelson, 1964; Harris, 1966b), the results are inconclusive in that the survival of the young immediately after fledging is not known. However, in the present cases the fledging weights were not different from those of single fledglings so that presumably their chances of survival to breed were as good as those of any other young. As with the previous experiments on shearwaters cited above, these suggest that there is not enough food available for the adults to raise more than a single young.

NESTING SUCCESS

Full details of nesting success (omitting experimental manipulations) are given in table 10. In the full three seasons studied, 60 percent of the eggs hatched and 50 percent of the young fledged, a low overall production of .3 young per pair but similar to the one season's results at Ascension (Allan 1962).

Most lost eggs just disappeared from the burrows (63 cases) but others were known to have been broken or dented (16), deserted (23), ejected by other petrels (13) or *P. lherminieri* (3), addled (13), and buried (4). The desertions appeared not to be due to my interference as many nests where adults were never disturbed by me were lost in this way; in six cases the egg was never incubated. Similarly most young were just noted as missing (31), but others died of starvation (6), were eaten by *Asio galapagoensis* (3) or *Grapsus grapsus* (3) or *Ardea herodias* (1), died due to sea spray (5), ejected by other storm petrels (1) or *P. lherminieri* (1), or just wandered from the nest site (1). Egg losses were evenly spread over the whole incubation period but about 40 percent of chick losses occurred within 10 days of hatching owing to a variety of causes, among which predation by crabs and accidental crushing by iguanas were probably important.

POSSIBLE FACTORS INFLUENCING BREEDING SUCCESS

1. SEASON OF LAYING. There was no advantage in birds laying in either the hot or the cold season as far as fledging success was concerned.

2. DATE OF LAYING WITHIN A SEASON. This was important (table 10) as the proportion of eggs which gave rise to fledged young was highest early in the course of each breeding season studied. The decline was most marked in the survival of young from hatching to fledging.

The losses of eggs due to possible predation of the adults or failure to hatch because of being addled, did not increase as each season progressed.

The causes of chick losses were mainly unknown, but starvation (as mea-

TABLE 10. *Breeding success of Oceanodroma castro in relation to season and date of laying. Note that in the 1965-66 season the November egg success is too high as many nests were not found until December. Of ten other eggs laid before mid-January, one hatched but the young did not fledge. The mid-1967 figures show the range of nesting success after known losses are removed.*

Season	Month	Third-month period	Eggs laid	Young hatched	Per-cent	Young hatched	Young fledged	Per-cent	Percent overall success
1965-66	November	2	1	1	(100)	1	1	(78)	(78)
		3	8	8		8	6		
	December	1	7	5	61	4	0	13	8
		2	14	7		7	1		
		3	5	4		4	1		
	January	1	2	2	67	2	0	0	0
		2	1	0		0			
mid-1966	April	2	1	0	67	0		50	34
		3	2	2		2	1		
	May	1	11	6	64	3	1	58	37
		2	34	22		15	8		
		3	33	22		18	12		
	June	1	12	6	41	6	2	33	14
		2	7	3		3	1		
		3	3	0		0			
	July	1	6	3	50	3	0	0	0
1966-67	November	2	2	0	50			66	33
		3	6	4		3	2		
	December	1	17	15	68	12	7	64	43
		2	15	8		6	5		
		3	8	4		4	2		
	January	1	9	5	50	5	2	33	16
		2	1	0		0			
		3	2	1		1	0		
	February	1	1	0	0				
		2	1	0					
mid-1967	April	3	1	0	0				
	May	1	7	4	49-71				
		2	20	14-18					
		3	32	11-20					
	June	1	17	5-14	19-79				
		2	9	1-7					
		3	7	0-5					
	July	1	4	0-2					

sured by weights of young) was unimportant and, to judge from the growth rates of the young, food was apparently uniformly available throughout the year. Predation was observed in only seven nests, but it might have been the reason for some other losses; however there was no correlation between the extent of possible predation and the date of hatching within any season. The very latest young may be evicted by the new pair returning to take over the nest, and some very small young may be lost through intruders, but the main causes of the decline of fledging success and its date are not apparent. It is possible, but unlikely, that purely social factors are important in that the birds breed more efficiently when other birds are also breeding. Against this however, Allan (1962) found that some out of season nesting produced at least third-grown young.

3. FOOD SHORTAGE. This is hardly likely to affect hatching success unless severe enough to drive the birds from the colonies. Eggs were often found without an incubating bird, and usually it appeared that the bird due to take an incubation spell was late returning, which certainly suggests it was hungry. Some eggs hatched after being left at least 6 days within the normal incubation period. However, the chances of an egg hatching decreased if left unattended; 116 of 163 eggs which were never seen without a bird (but on the average only checked 1 day in 3) hatched, the corresponding figures for eggs left on only 1 day were 24 out of 46 and for eggs left between 2 and 8 days the figures were 15 out of 51. Eggs laid in the hot seasons were more frequently left (11 percent of possible days for all birds) than those in the cold seasons (5 percent). There are three possible reasons: (a), the birds might be more willing to leave eggs during the warm season as there would be less chilling; (b), a food shortage might exist at this time of year; (c), more isolated birds may be more prone to leave the colonies, for some reason or other, during a time when there is less breeding activity. The reduced chances of eggs hatching due to being left unattended are probably the result of interference by nonbreeders or low enthusiasm in those parents.

Associated with leaving eggs unincubated is the resistance to chilling of petrel embryos (Matthews, 1954). Some observations, made on eggs which came to hand, of several Galápagos sea birds, showed that resistance to chilling (table 11) was most pronounced in the storm petrels. One embryo of *O. castro* remained alive for 23 days without incubation, and a chick inside a chipping *O. tethys* egg continued to call for 16 days. Surprisingly two embryos of *P. lherminieri* were dead when first examined 10 days after the egg had been last incubated. Other species showed survival for up to 6 days, even in species such as *F. minor*, where there is little chance of an egg surviving predation if left uncovered for even a few minutes.

Food shortage is doubtless important in determining the rate of growth of the young, and the twinning experiments suggest that there is not a superabundance of food. However, it was extremely rare to find starving young, and

TABLE 11. *Some observations on the ability of sea bird eggs to withstand chilling. "Less than 3" indicates that the embryo was dead when the egg was first opened 3 days after incubation ceased.*

Species	Days after last incubation embryo still showing movement	State of development of embryo
<i>Oceanodroma castro</i>	6+	half developed
	9-16	half developed
	23	half developed
<i>Oceanodroma tethys</i>	9-10	half developed
	16	chipping egg
<i>Puffinus lherminieri</i>	less than 10	near hatching
	less than 10	third developed
<i>Phaethon aethereus</i>	less than 3	quarter developed
	less than 3	half developed
	less than 6	quarter developed
	less than 8	quarter developed
	5-6	quarter developed
<i>Creagrus furcatus</i>	3-5	three-quarters developed
	less than 3	quarter developed
	less than 3	half developed
	less than 4	third developed
	less than 5	quarter developed
<i>Fregata minor</i>	5+	near hatching
	3+	three-quarters developed
	less than 3	three-quarters developed
	less than 3	three-quarters developed
	less than 3	three-quarters developed
<i>Sula sula</i>	less than 6	just started development
	less than 7	half developed

those few could be due to one of the adults having died. Of the six young which died of starvation, one was very small, two were in holes where one of the adults did not reappear the next year so may have died during the first season, and two had both adults alive the next year. The parents of the other were not known.

During my stay in the Galápagos, I saw evidence of severe food shortage in *P. lherminieri*, *Phaethon aethereus*, and *S. nebouxii*, but never in *O. castro*. It appears therefore that food shortage is not a common cause of chick losses.

4. PREDATION. Several large young were known to have been eaten by owls or herons and there were a few other cases in which this was suspected. Some few breeding adults may also have been killed by owls (see later).

An indirect measure of the effect of predation can be obtained by comparing nesting success one year with the numbers of adults returning a full year later. The proportion of birds returning was much higher in those which had previously raised a chick (56 of 67 birds) than in those which had failed to hatch an egg (41 of 65) or raise a hatched chick (69 of 111). It is difficult here to determine

cause and effect, but the faithfulness of adults to nest sites suggests that at least some observed differences were due to predation of adults at the colonies and not just to successful birds being more likely to retain the same nest sites.

5. COMPETITION. Although some eggs (22 out of 72 known causes of failure) were lost due to competition for burrows, the numbers of birds caught in a burrow during a season apparently had no effect on nesting success; of 183 eggs in burrows where no intruder was caught, 56 percent hatched and 25 percent of the young fledged; of 75 burrows where up to four intruders were found, 53 percent of eggs hatched and 21 percent of young fledged. As two eggs were found in a burrow very infrequently, it seems that once a pair has established itself, there is little chance of another pair laying in the hole the same season, although losses might still be caused by intruders and prospecting birds.

6. NEST SITES. The nest sites were extremely varied but, apart from two very open and marginal sites where the adults may well have been killed by owls, it is difficult to see why the nest site should affect the nesting success. There was, however, a markedly high-nesting success in the most frequently used burrows. Of the 57 burrows where observations were carried out in all four seasons, 24 (42 percent) were used all four seasons and had an overall success rate of 40 percent as against 13 percent for all other layings. This difference was due almost entirely to the varying fledging success (65 percent to 23 percent) and not to any factor which might prevent the eggs from rolling out or being dented. There were different pairs involved in at least two of the three seasons, and also a few other changes due to mortality. There was no tendency for birds in these burrows to nest earlier than average. Indeed in all burrows there was no correlation between laying date and the success or fledging date from the immediately prior season. One is forced to the conclusion that these nest sites were in some way more attractive to the more efficient, perhaps older or more experienced, adults, and not to the actual physical potentialities of the burrows.

7. SOCIAL FACTORS. Allan (1962) concluded that on Ascension in the year he studied that "no factor other than the behavior of the petrels during the breeding season was obviously a major cause of loss of eggs or young." My more detailed study has explained many more of the losses, but there is still a substantial number unaccounted for, especially of eggs and small young. Some losses were directly attributable to other birds, and I must agree with Allan in that disturbance due to intraspecific competition is an important source of loss. In *O. tethys* (later) intraspecific competition was responsible for almost all the observed egg losses.

8. INTERSPECIFIC COMPETITION. There is some little conflict with *P. lherminieri* but this is not severe enough to be important. On Tower, Nelson (1966) thought that interspecific competition with *O. tethys* was an important source of egg loss of these two species. He was however mistaken as the species do not nest in the same area.

On Isla Pitt however interspecific competition is important as there the large colony of *O. tethys* apparently prevents *O. castro* from breeding during the cold season by occupying all the available nest sites. At this time *O. castro* does visit the island, but no nests were found even in sites used for breeding during the hot season.

MOLT

Primary molt in sea-bird populations has, with a few important exceptions, been little studied, but it is known that it is extremely variable with regards to its timing in relation to the breeding season.

Within the procellariiformes, some shearwaters, including *P. tenuirostris* (Marshall and Serventy, 1956) and *P. gravis* (Bourne in Palmer, 1962), delay their wing molt until they have migrated the long distance to the nonbreeding grounds. The same applies to some storm petrels including *Oceanites oceanicus* (Murphy, 1918) and *Pelagodroma marina* (Bourne in Palmer, 1962). *Puffinus puffinus* is an interesting species as the British race *P. p. puffinus* does not molt at the breeding grounds (personal observations) and presumably must molt in its winter quarters off South America, as the birds migrate immediately after the breeding season. The Mediterranean race *P. p. mauretanicus*, which has no extensive migration, molts immediately after it has finished breeding (Mayaud, 1931). Other species of the order may start the primary molt when feeding young, that is, *H. pelagicus* (personal observations) and the giant petrel (*Macronectes giganteus*) (Warham, 1962).

The four species of oceanic terns breeding on Ascension and studied by Ashmole (1962 and 1963), Dorward (1963), and Dorward and Ashmole (1963), show interesting variations in the primary molt. *Sterna fuscata* and *Anous tenuirostris* both usually finished their molt before returning to breed but some may then start the next cycle before the young are fully grown. The fairy tern (*Gygis alba*) was never found molting primaries when incubating or feeding young chicks and must therefore have completed the molt between breeding cycles. In this species, the wing molt is irregular with primaries in different parts of the wing being replaced at the same time. *Anous stolidus* molted during the breeding cycle as it also does in Galápagos (personal observations).

MOLTING

As far as possible all nonincubating birds were examined for primary molt, and scattered observations were also made on body and tail feathers. In the following account the primaries are numbered in the standard way from the inside (shown on the left of the diagrammatic formulae) outwards, and the stages of molt are represented as 1 = empty socket or pin feather, 2 = vane up to one-third its final length, 3 = vane between one- and two-thirds grown, 4 = vane

two-thirds to full grown, N = new feather without any blood in calamus, O = old feather (Ashmole, 1962). The outermost, minute primary is ignored.

The start of the primary molt of the breeding adults which is from the innermost primary outwards is extremely variable, but appears never to occur before the young is well grown and some birds do not start until their young have fledged. One adult with an almost-fledged young had the two inner primaries on each wing a third grown on 5 April. On the same date, when only adults feeding young would be expected to be visiting the colonies, netting produced two molting adults —

2	2	0	0	0	0	0	0	0	0
N	1	1	0	0	0	0	0	0	0

and four with exceptionally worn plumage but with only body molt.

Two males out of 10 birds netted at Tower on 16 February had one and two primaries respectively just starting regrowing in each wing. Both these birds were carrying food and so presumably were feeding young.

Non- and failed breeders may undergo a body molt when at the colony but not a wing molt. The only possible exception was a bird caught on 13 February in a hole where it had not bred, which had its inner primary in pin.

Almost all the primary molt occurs when the birds are away from the colonies, 6 to 7 months for successful breeders, but some newly arrived birds returning at the start of a breeding season have the outermost primary still growing. One bird had the fourth secondary half grown, the fifth old, and the remainder new, two growing rectrices and feather replacement of the upper parts. This bird laid exactly a month after this examination.

It seems, therefore, that the primary molt of the population and certainly of some individuals, takes the whole time between breeding attempts and it might be, as suggested for *S. fuscata* (Ashmole, 1963), that the birds are prevented from breeding more frequently by the necessity of the whole population fitting in this molt, that is, the molt governs the intervals between breeding. However some individuals of *Puffinus lherminieri*, with more wing feathers to replace, are able to undergo a complete molt and breed again in 5 months after the end of a previous breeding attempt. Even allowing for the differences in feeding habits, this suggests that a storm petrel just might be able to complete its molt in a similar time. Possibly this elongated molt is adapted so as to spread any inefficiency it brings about over the longest possible time; and there is some other factor responsible for the timing of the breeding cycle. A third possibility is that this molt pattern was primarily evolved in an annual breeding, oceanic species (as *O. castro* on Ascension), as it is reasonable to suppose that a nonannual cycle has come from an annual, where the birds had to roam widely for food and could not hope regularly to find a rich feeding ground where rapid molt could be safely undertaken. In this case again it would be the molt preventing more frequent

breeding. In Galápagos, with two populations breeding 6 months out of phase, there is probably little advantage in the molt being shortened even if this were possible.

Birds with body and/or tail molt were found throughout the breeding season. There was no orderly replacement of tail feathers and it was often difficult to classify individual rectrices as old or new.

Unfortunately few specimens of *O. castro* have been collected away from the breeding colonies and only two from near the Galápagos show any primary molt. They are

11 April, near Galápagos	N	N	N	N	N	N	N	N	N	4
18 June, off Cocos Island	N	N	N	N	N	N	N	N	N	2

It is not known if *O. castro* breeds on Cocos Island (about 500 miles from Galápagos) but this bird could possibly be an immature from the Galápagos or Hawaiian populations.

This sequence of molt is similar to that of birds on Ascension (Allan, 1962) and the few skins I have examined from other Atlantic colonies which show any primary replacements:

28 June, Cape Verde Islands	N	N	N	N	N	N	N	N	N	4
12 June, Madeira	N	N	N	N	N	N	N	N	N	4
15 June, Madeira	N	N	N	N	N	N	N	N	N	4
12 Sept., Madeira	N	1	0	0	0	0	0	0	0	0

suggest that the molt pattern found in Galápagos is universal in this species. The mallophaga found on *O. castro* included *Halipeurus pelagicus* and *Philoceanus* species. An undescribed flea *Parapsyllus* species was found on both *O. castro* and *O. tethys*, this genus of flea is associated with sea birds in the Southern Hemisphere.

PREDATION

Oceanodroma castro in the Galápagos is heavily preyed on by *Asio galapagoensis* and counts of fresh prey remains on Plaza (table 12) showed that predation was greatest during the cold season. These peaks may be slightly retarded as some remains were 2 to 3 weeks old when found. Unfortunately remains often consisted of a pair of wings so that it was impossible to calculate the proportion of ringed to unringed birds. This was quite small, however as only a single ringed bird (a recently fledged juvenile) was found killed by an owl. Many owl pellets were collected on North and South Plaza during the study and consisted of remains of *O. castro* (547 pellets), *P. lherminieri* (51), *Creagrurus furcatus* or *Phaethon aethereus* (16), *Rattus rattus* (14), finches (4), and insects (three entirely and they were present in five others). Among these a single ring was discovered, that from a breeding member *O. castro*, suggesting that birds regularly frequenting burrows (many ringed), were not so likely to be caught as nonbreed-

TABLE 12. *Monthly incidence of kills of Asio galapagoensis found on Plaza. The figures in brackets are definite juveniles and are included in the main totals. At the start of the study the following older remains were found: O. castro (21), P. lherminieri (25), and during the study an additional 39 remains of O. castro and 74 of P. lherminieri which were too old when found to be classified as to month. One individual of Puffinus lherminieri weighs about the same as 4½ of O. castro.*

Year	Month	Number of remains		
		Oceanodroma castro	Puffinus lherminieri	Others
1965	December	36	15	
1966	January	12	8	
	February	4	2	
	March	0	2	
	April	1	1	
	May	10	0	
	June	23	0	
	July	81	2	
	August	25	6	<i>Creagrus furcatus</i> [2]
	September	31 [5]	16 [3]	Lizard [2], <i>P. pacificus</i> [1]
	October	6 [6]	25 [6]	<i>Heteroscelus incanum</i> [1]
	November	9 [6]	30 [14]	
	December	5 [1]	12 [6]	<i>Squatarola squatarola</i> (1)
1967	January	15	19 [10]	<i>C. furcatus</i> (1), <i>Phaethon</i>
	February	3	3	<i>acthereus</i>
	March	0	5 [1]	
	April	2 [2]	0	
	May	27	1	
	June	21	0	
	July (1st week)	16	0	

ers (few ringed) which spent more time actually on the ground looking for holes. In *P. puffinus* it has been shown (Harris, 1966a) that these nonbreeders are much more likely to be caught on the surface than breeders, which are either in the burrow, and therefore safe from most predators, or actually going into or leaving the burrow.

The owls did not breed, or roost at all frequently, on South Plaza during the study but were always present on North Plaza and were frequently seen at dusk and dawn flying between the islands. Indeed they may well have bred there in 1966, but it is extremely unlikely that they did so in 1967 when regular checks were made. There was no evidence that more than one pair of owls was involved in this predation.

This pattern of kills found need not fit exactly with the predation, for, if the owls had unfledged young, they would take the intact prey back to the nest. When the young had fledged they could well follow the parents to South Plaza and the plucked remains of kills would then be found. It must be stressed that there is no

evidence for this speculation, as no birds were heard to give the typical food-begging calls.

Although the numbers of eaten specimens of *O. castro* found fit very closely the number of eggs and young in the petrel colony, it does not follow the pattern of nonbreeders visiting the holes. The number of nonbreeders was highest just before and during the egg-laying period and then decreased before the majority of the young hatched. Indeed, by July and February there were very few nonbreeders or failed breeders in the holes and probably very few visiting at night. It is therefore difficult to explain the peak of corpses in July, 1966, except that the owls may have been feeding young.

Asio galapagoensis in Galápagos may breed in many months of the year (Lévêque, 1964) so, although predation could obviously shorten the time that nonbreeder petrels spend at the colonies, it could hardly affect the timing of the returning birds unless by coming back at the same time as the breeders, they "swamp" the predators and so reduce the chance of any individual petrel being killed.

When there are few petrels in the colonies, the owls prey on other sea birds, especially *P. lherminieri*, but given the choice they appear to prefer to take storm petrels. The prey spectrum is wide and includes the introduced *Rattus rattus* from the mainland of Santa Cruz and migrant waders so that it is only on rare instances that the species on Plaza can be really short of food.

During the study there were two periods when food may have been short for owls, February and March in both 1966 and 1967, when there were only a few petrels, mainly breeders feeding young frequenting the colonies, therefore unlikely to be caught on the surface; there were also very few shearwaters (Harris, 1969). In 1967 the absence of shearwaters was much longer than in 1966 and could have prevented the owls from breeding. In 1966 it might have delayed breeding so that the owls could lay only in April when the storm petrels and shearwaters returned. Then they would have missed the peak of storm petrels at the colonies and preyed on the nonbreeders which were not frequenting burrows but still prospecting for holes. From other studies on shearwaters (Serventy, 1967; Harris, 1966a) it seems that these might be younger than those which returned with the breeders early in the season.

SURVIVAL OF ADULTS

There has never been a satisfactory direct estimate of the annual mortality of a storm petrel species, and indeed the difficulties of obtaining one may be insurmountable. Richdale (1963) has suggested on the basis, as he admits, of inadequate data, an annual mortality of 45 percent for *Pelagodroma marina* which is obviously impossible for a bird having a single egg clutch, fairly low nesting success, and deferred maturity. For *H. pelagicus*, Davis (1957) had at least 60 out of

74 breeding adults surviving overwinter, an 81 percent survival, which is again too low to allow the species to keep its population steady. Lack (1966) suggested a 7 percent annual mortality for this species but only used the successful breeders, which could be a biased sample as some adults may well have died at the colonies, and the period over which the measurement was made was less than 12 months. However to judge from other birds with a single egg clutch and deferred maturity, for example the royal albatross (*Diomedea epomorpha*) with a 3 percent annual mortality (Lack, 1954) and *P. puffinus* with 6 percent (Harris, 1966a) it should be in this region. In the 1966-67 hot season I retrapped 71 percent of breeding adults ringed in the 1965-66 season, in the mid-1967 season 65 percent of those from the mid-1966 season. These survival rates were too low to allow the population to remain stable. I know that I missed some adults in my study burrows and many more must have moved, perhaps only a few feet, into burrows where I could not find or reach them.

The estimate of .3 young raised a pair means that 100 adults would produce 15 young to fledging every year, and even if all these survived to breed, the adult mortality could not exceed 15 percent, if the population was to remain constant. Unfortunately we have no data on the age of first breeding in this species. Allan (1962) using rather inadequate data calculated that four seasons are passed before maturity is reached. At least one representative of *O. leucorhoa* (Gross, 1947) and one of *H. pelagicus* (a bird ringed by me and recovered by D. Scott) are known to have bred at 3 years, but the average age of first breeding is probably much older. Huntingdon (*personal communication*), working at the same colony as Gross, has found one individual of *O. leucorhoa* breeding at 4 years and four at 5 years. As it seems likely that birds do not breed until their third year or later and probably have a postfledging annual mortality higher than that of the adults, one would suspect that the annual mortality could not be higher than 5 to 7 percent.

The causes of mortality of adults are varied. In the colonies I found five birds dead and jammed in holes (one hole had two dead birds wedged in the entrance), a female apparently egg-bound, two died after getting their wingtips caught in thorny bushes, and one was found badly pecked (? by a frigate). These were in addition to all those killed by owls. A Galápagos hawk (*Buteo galapagoensis*) was also reported (Dr. U. Eliasson) as killing an injured storm petrel (? species). Ritchie (1966) recorded an adult of *Oceanites oceanicus* as taken by a shark as it pattered along the water.

DISCUSSION OF THE BREEDING SEASON

It was shown earlier that there were two entirely separate populations of storm petrels nesting in the same nest holes approximately 6 months out of phase with each other, a situation which has not yet been described in any other bird.

It is also known that the seas around the Galápagos have a well-marked seasonal water temperature fluctuation, though my fortnightly surface-plankton sampling failed to show any associated differences. This latter point is however inconclusive because of the plankton being extremely patchy and the fact that the sampling may have been inadequate to pick up any changes. There is also the possibility that the birds may have been feeding in waters which bear little or no relationship to changes detected in the inshore waters of the Galápagos.

Although there were a few marked differences between the various seasons studied, for instance in growth curves of the young, these may only show how variable are the conditions under which the species breeds. The only differences between the hot and cold seasons were egg diameters (not significant), fledging periods (70 days in the hot as compared to 78 days in the cold) and the fact that approximately half as many birds breed during the hot season as in the cold. The latter points might seem to be irreconcilable in that a longer fledging period suggests less available food, but it is at this time that the majority of birds are choosing to breed. However, this could be due to depletion of the food supply by the greater number of birds breeding, though this is less likely in forms like storm petrels which eat surface food. Nevertheless, any disadvantage to the young might be overcome by the advantage to the adults by reducing the proportion of birds taken by predation. Be this as it may, there was little difference between the hot and cold seasons studied.

In *O. castro* on Ascension (Allan, 1962) and *O. tethys* on Tower (later), a few eggs were laid out of the normal breeding season. If out-of-season eggs were successful, this could quickly give rise to a situation in which birds were breeding throughout the year. Alternately, if there were some factors to separate them from the normal season, they might result in the situation found in *O. castro*. The latter situation assumes that it is advantageous for each individual to be synchronized in its breeding with others, and that it is incapable of breeding less than annually. Perhaps the timing of the molt is crucial, as it might be advantageous for this to be spread over the longest possible time. Even so, it is surprising that the earliest failed breeders should not return to relay until a year after their previous egg.

Bourne (1957) has postulated that in Madeira, *O. castro* and *Pterodroma mollis* might each have twice colonized the island from different areas and the two populations now breed at different times of year. This might be true of *P. mollis* where the two populations are slightly morphologically different, but we have too little information on *O. castro* to make an evaluation. However, this is unlikely to have happened in Galápagos as the two nearest populations breed at similar times.

The difficulty of explaining the two cycles is not so much how they may have come about, but how they remain separate. In every month there were some

birds producing eggs or feeding young, both of which activities require large quantities of food, which implies that food is available in every month of the year. It is conceivable that with the movement north and south of the Humboldt Current, the optimum feeding conditions could occur every 6 months or so, but this is contrary to the available evidence. If food is in fact uniformly available, why is not *O. castro* breeding throughout the year, like some other Galápagos species such as *C. furcatus*, *P. lherminieri*, *Phaethon aethereus*, *S. sula*, and *S. nebowxii*.

The detailed studies on tropic birds on Ascension by Stonehouse (1962) and the observations made in Galápagos by Snow (1965) and myself, show that in these continually breeding hole-nesting species, competition for holes resulted in heavy losses. For a storm petrel, which rarely lays a replacement egg, this would be a wasteful process, and the present situation allows a large number of birds to utilize an apparently limited number of the most suitable nest sites. But how this might be regulated by natural selection, and how it prevents any individual pair from attempting to nest away from the peak times, is not at all clear. Presumably there is some advantage to a pair in nesting when the majority of individuals do so, and that this is so great that it more than compensates for losses due to the additional competition for food and nest sites within each of the two seasons. Predation by *Asio galapagoensis* could well be one of the important factors in bringing about synchronization of breeding, as was predation on *S. fuscata* by cats and frigate birds on Ascension (Ashmole, 1963).

The decline in breeding success within each season appeared not to be due to food shortage and is too marked to be explained by the death of the adults, so provides another puzzle.

The sharp beginning of the breeding season is also difficult to explain, unless most individuals cannot breed much quicker and those which try cannot find mates, or are heavily preyed upon, or suffer heavy losses when the majority of the birds return. Whatever the selection forces involved, they are at present highly obscure. The present situation is probably the most economical for the species in this habitat, because a well-synchronized breeding season, brought about by display flighting and calling, might well help to reduce losses due to predation and conflicts between adjoining seasons, and so increase the chances of the individual producing young.

OCEANODROMA TETHYS

Unlike the previous species, *O. tethys* is normally restricted to the Humboldt Current, though a few birds have been recorded as far north as southern California (Murphy, 1936).

The species has been divided into two subspecies '*kelsalli*' breeding in Peru and '*tethys*' in Galápagos (Lowe, 1925). The Galápagos race is bigger in all di-

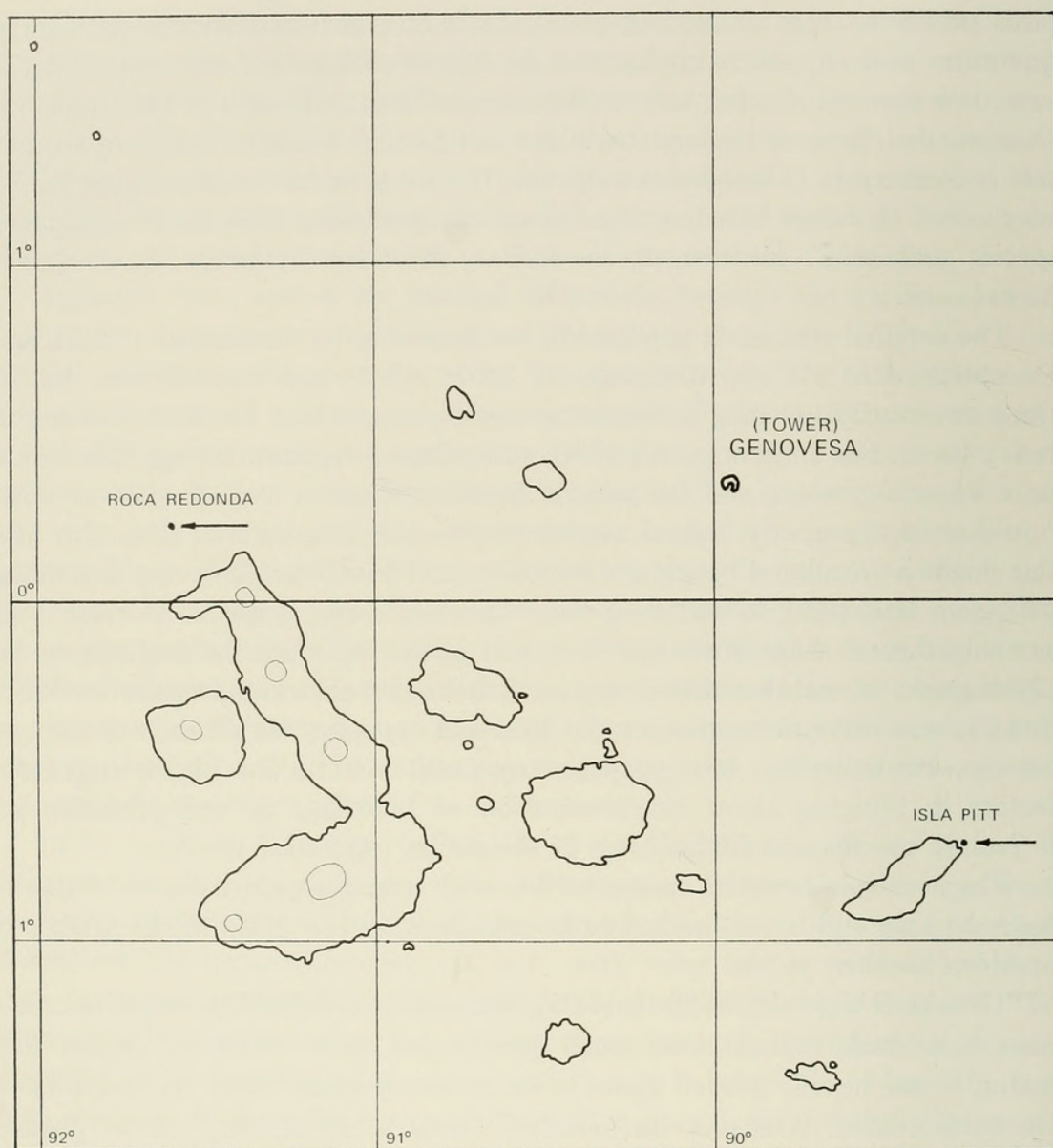


FIGURE 15. Colonies of *Oceanodroma tethys* in the Galápagos. Breeding has not been proved on Roca Redonda.

mensions (100 adults measured had wings averaging 136.1 mm., standard deviation 3.4) than the other race (30 taken off South America averaged 124.6, standard deviation 2.8). The few large individuals collected off the continent (wings 129, 129, 130, and 131 mm.) might in fact have belonged to *O. t. tethys* as it is likely that the two populations mix off Ecuador and Colombia.

The species is very common at sea in Galápagos waters and nests on Tower Island and Isla Pitt, an islet off the eastern tip of San Cristóbal (fig. 15). Sr. Miguel Castro told me that in March, 1966, he saw this species flying around Roca Redonda off the north of Isabela and it could well nest there too.



FIGURE 16. Flying in *Oceanodroma tethys* on Tower Island. Comparatively few of the birds nest in these cliffs but they are the focal point of flying during the nonbreeding season (when this was taken). The extensive white rump patch and the lighter wing coverts can be seen on some of the birds (top left). Also in the photograph is a single individual of *Phaethon aethereus* and some nesting and roosting ones of *Creagrurus furcatus*.

The colony on the southeast coast of Tower has an extremely large population in two very different habitats, cliff and its adjoining lava field. The cliffs here are composed of lava flows a foot or so thick tiered like layers of a cake to a height of 50 feet (fig. 16). Some members of *O. tethys* nest in this area along with large numbers of *Phaethon aethereus*, *Puffinus lherminieri*, *C. furcatus*, and possibly the bulk of the island's population of *O. castro*. Although the cliffs overhang and were frequently soaked in spray, the cracks are so deep that many nest sites are available to the birds.

In spite of the fact that at some times of the year it appeared otherwise, the vast majority of petrels nested in a bare lava field stretching half-a-mile along the cliff top and a hundred yards inland (fig. 17). Inland the colony was bounded by a deep fissure, the other side of which was scrub composed of *Cordia lutea*, *Croton scouleri*, and *Bursera graveolens*, the nesting ground of large numbers of *Sula sula*, *S. dactylatra*, and *Fregata minor*. In the lava plain were a few stunted bushes and the cactus *Brachycereus* species. The lava was fissured and raised in bubbles which gave the birds access to a subterranean maze of passages from a few inches to a foot high; the petrels shared these with about 50 pairs of *Phaethon aethereus*, a few pairs of *Puffinus lherminieri*, and the Galápagos dove (*Neso-*



FIGURE 17. Mist-netting *Oceanodroma tethys* on Tower early in the morning in the non-breeding season before too many birds had arrived at the colony. In the foreground is the edge of the flat lava field under which these storm petrels nest.

pelia galapagoensis). The finches *G. magnirostris* and *G. conirostris*, the mockingbird (*Nesomimus parvulus*), and the owl *Asio galapagoensis* regularly fed here, the last on sea birds.

Nelson (1966) reported that the owls on Tower preyed on both *O. tethys* and *O. castro*, that there were two different calls heard from the burrows, and that there were two species of storm petrels flying together over this colony. He therefore cast doubt on November observations by Castro, who thought that only *O. tethys* was involved, as it was based solely on sight observations. The owls do indeed prey on both species of *Oceanodroma* but catch representatives of *O. castro* when they come ashore at night. The two calls both refer to *O. tethys* (see later). Dr. D. Snow (in his notes at the Charles Darwin Research Station) during a visit to the colony with Nelson, saw only a single species flying, *O. tethys*. There can be no doubt that only a single species is diurnal on Tower, and that this is *O. tethys*.

Isla Pitt is an islet of crumbly lava about 50 yards across and 100 feet high, in part with bushes of *Cryptocarpus*, *Malvastrum*, and *Periloba galapagensis* on which nested *Fregata minor* and *S. sula*. Every *Periloba* bush had a pair of frigates nesting and their guano transformed all but the few topmost twigs into a solid mass, allowing the petrels to nest underneath. Numbers of seabirds also

nested in the cliffs. During the warm season, *O. castro* bred on the island, but when *O. tethys* returned to breed in the cold season it appeared to oust *O. castro* entirely by sheer force of numbers. There was intense competition for nest sites as every available nook and cranny was occupied by several pairs of *O. tethys*.

FOOD

I examined the stomachs of 13 adults and 3 young and the food regurgitated by approximately 50 netted birds. Fish (in thirteen stomachs and 27 regurgitations) was the commonest food followed by cephalopods (seven stomachs and 4 regurgitations), and crustacea (three stomachs and 6 regurgitations). Seventeen fish ranged from 24 to 36 mm. long and averaged 28 mm. Almost all birds regurgitated large quantities of red oil which was probably stained by pigment from red planktonic crustacea.

The species is normally a nocturnal feeder and birds caught early in the morning normally had undigested food. Many of the regurgitated fish had proportionately large eyes, suggesting that they may visit the surface only at night.

Occasionally I have seen these birds feeding by day, when they dip or dart sideways to pick food from the surface of the sea. Once about 30 birds fed under the cliffs at Isla Pitt where a sea lion was killing a fish. Some birds then pattered on the surface of the water like species of *Oceanites* but this was atypical.

This apparently is the only storm petrel which normally flies at its colonies by day and feeds at night. This is not due to the lack of predators so is presumably adapted to allow the birds to exploit a rich nocturnal food resource. Several authors (for instance Murphy, 1936) have suggested that other storm petrels feed by day and night, but there is little direct evidence of this. There appear to be extremely few sea birds known to feed at night, *Sterna fuscata* (Bruyns and Voous, 1965), *P. pacificus* (Gould, 1967), *Sula sula* (Murphy, 1936), and possibly *Fregata* species (personal observation), but this mainly occurs on nights with a full moon. It is therefore surprising that Galápagos should have two species, *O. tethys* and *C. furcatus*, which feed at night, the latter species entirely so. There must be much food available to nocturnal feeders which is unavailable to diurnal species and more intensive observations will doubtless show up more species adapted to this niche.

BREEDING CYCLE ON TOWER

The evidence suggests that there is an annual breeding cycle on Tower, most of the eggs being laid in May and June, but birds visit the colony at other times and rarely lay eggs then.

The colony was first visited 15–17 February 1966, when the numbers of birds present was so great as to be almost unbelievable; although it was impossible

TABLE 13. *Numbers of Oceanodroma tethys storm petrels with brood patches in various stages of development in three samples caught on Tower.*

State of brood patch	16.2.66	17.1.67		8.3.67	
	Netted	In burrows	Netted	In burrows	Netted
Not present	3		33	1	15
Half defeathered	7	1	10		
Unvascularized	33	22	57	2	28
Half vascularized	1	1	5		
Vascularized		1*			
Regrowing feathers	10		1		26
Total birds	54	25	106	3	69

* Female with egg about to be laid.

to get any worthwhile estimate of numbers, several observers agreed that there must have been several hundreds of thousands of birds flighting. The bulk of the birds were concentrated at the cliff edge, where they flew time and again near or actually into the cliffs. A much smaller number flew high over the lava and extremely few dipped low as though prospecting for holes, but none actually landed in this area. Birds which did swoop down only circled once or twice before returning to the cliff edge or to the throng about 20 feet up. Many birds were present in holes in the cliff and in the base boulders, and any observer watching would probably think, as did Lévêque (1964) and myself, that the colony was centered on the cliffs. This impression was strengthened by finding two slightly incubated eggs, one in a small hole in the cliff, the other under a lava slab at the cliff edge. Despite a thorough search, no other evidence for breeding was obtained and of 54 birds caught (table 13), only one had any trace of blood vessels present in the brood patch. Three males and five females had undeveloped gonads. A further visit on 27 February failed to produce any other evidence of breeding. At this time no birds were present in the burrows at night.

On my return to the area 18–20 April, I confidently anticipated that breeding would have begun. However no eggs were found, but the pattern of flighting had altered and was now centered around the more inland flatter areas, where many birds were entering holes and even staying overnight. The numbers of birds present were reduced to perhaps a quarter of those in February, a decrease most marked at the cliff edge. It was not due to many of the birds having by then taken over holes, for whereas in February many hundreds of birds had been under the lava, a thorough search produced but one. By the last week in June there were many small young and eggs present, some of them newly laid. No birds were seen breeding in the cliffs, but some may have done so in the top few ledges, which were difficult of access.

Whereas the number of birds present in June was similar to that in April,

by mid-July there were many fewer and these were going directly into and out of the holes, with little circling. It appeared as though at least some of the non-breeders and some failed breeders may have left the colony. By 17–18 August there were yet fewer inland but as many flighting at the edge.

Unfortunately transport difficulties prevented any more visits during this breeding cycle but it is reasonable to suppose that it was coming to an end, as there was little display or fresh breeding activities. Birds are known to be present at the colony in small numbers in September (Loomis, 1918), October (Lévêque, 1964), and November (Brosset, 1963; M. Castro personal communication).

On 13–14 December 1966 large numbers of birds were again present but only near the cliff edge. A single female examined had an undeveloped ovary and unvascular brood-patch. No birds were seen in wing molt and there was no evidence of breeding.

A similar situation was found 16–19 January 1967, except that a few birds were showing an interest in the inland lava. Of 106 birds netted and 25 taken from burrows, the majority had unvascularized brood patches (table 13). One female was caught with an egg about to be laid and another had recently laid; both these birds had only slightly vascularized brood patches. No birds were in wing molt but many of those without brood patches were regrowing body feathers.

A fresh egg was found on 8 March, in a hole where an egg had been laid in February, 1966, suggesting that the same bird or birds may have been involved in both seasons. Twenty-six out of 69 birds netted were now refeathering brood patches, 11 were in body molt, and two had just started the replacement of the inner primaries. A short visit in July showed many young and some few eggs. One breeding adult had also bred a year previously, showing that at least some individuals have an annual breeding cycle.

These data on out-of-season breeding are tantalizing, as they suggest that a very large number of birds come to the colonies out of the normal breeding season and go through many of the pre-breeding activities, but that only a minute proportion actually breed, and these in places not used in the normal season. It would seem that these birds present in the hot season were nonbreeders, as breeders from the cold season would be molting their primaries. To get into phase with the normal breeders, these hot-season birds would have to adjust or interrupt their molt for breeding (Ashmole, 1965). There is no evidence for an interrupted molt in *O. tethys*.

Another possibility is that, as in *O. castro*, there are two populations breeding at different times of year, but for some reason hardly any of the population present during the hot season bred during January to April, 1966, or December, 1966 to March, 1967. It is at present impossible to give definite evidence to

prove or disprove this. Beck (in Loomis, 1918) found 200–300 petrels present and a single addled egg on 15 September, 1906 and collected a single bird with medium-sized gonads. Beck (1902) had previously seen several thousand birds but not eggs in the hot season of 1902, presumably March (Rothschild & Hartert, 1902). The notes of Lévêque (1964) for his visits in March and October, 1961, suggest that breeding was not taking place during those two hot seasons. Against these observations are those of Brosset (1963) which indicated that 11 birds caught in November, 1962, were physiologically ready for breeding.

In view of the available evidence, I conclude that the species normally has an annual breeding cycle centered on the cold season with only extremely few breeding outside this time, but this needs checking by further observations.

BREEDING CYCLE ON ISLA PITT

This colony was discovered by Lévêque (1964) in June, 1961, when eggs but no young were found. Castro (personal communication) has revisited the colony in June and found a similar state of breeding. I visited the islet four times. On 19–20 December 1965 the colony was completely deserted and on 16 April 1966 laying had not begun, although several thousand birds were present. By 10–11 July the majority of eggs had hatched. The next visit was not until 26–28 May 1967 when most of the birds had recently laid.

These observations indicate that there is an annual breeding cycle with the birds deserting the island during the nonbreeding season, and that the dates of breeding were very similar to those on Tower.

THE DIURNAL CYCLE

The birds coming to land showed a very well-marked diurnal cycle in both colonies and at all visits. The first birds usually reached land just before sunrise and the numbers increased to a peak in mid-morning before gradually decreasing during the afternoon. The last birds flying about left at dusk. One bird was caught in a mist net at 1900 hours but this may have been spending the night in a burrow and been scared out by my activities. Nelson (1966) was mistaken in thinking that there were no marked daily or seasonal peaks in the numbers of birds visiting land.

Considerable variations in the diurnal pattern did occur both with this month and with the varying weather conditions. On 27 February when, unlike most visits, the sky was exceptionally overcast, very few birds were ashore by 0745 hours. However the numbers soon increased and by 0930 hours the cloud of birds was visible a mile away. The morning peak is most marked prior to the breeding season and as the season advances birds spend more time at the colony so that the peak is less obvious. By the time the nonbreeders and failed breeders leave the peak is very small.

BEHAVIOR AT THE COLONY

As so few observations have been made on the behavior of storm petrels, because they are mainly nocturnal, it has seemed desirable to quote my few on this diurnal species in detail. The flight behavior was watched closest on Tower but the open nature of some of the nest sites on Isla Pitt allowed closer observations of some burrow behavior.

FLIGHT BEHAVIOR

Nelson (1966) made three generalizations on the aerial display. (A), individuals took part in the flighting for some time; (B), no two individuals were keeping together as in a courtship display; and (C), a few individuals descended repeatedly to the same piece of lava, pattered over the ground with raised wings, at the same time running their beaks over the lava. My observations agree with these and, like Brosset (1963), I was impressed with the relative lack of noise even though some birds did call "tchzz-te-tchzz" in flight and there were frequent aerial collisions.

The general flight was slightly bouncing and tern-like and many birds spent much time doing nothing else but flying about. The flight at the cliff-edge was slightly different as birds hover, with raised wings and usually with tail spread, in the up-currents, or they prospect the topmost cliff holes, before either dropping away for another circuit or being blown upwards. The birds actually visiting the cliff have the rump patch very conspicuously displayed.

When the birds were visiting the inland areas at the start of the breeding cycle, each bird was acting alone in its flighting. One bird when watched for 10 minutes flew in a circle of approximately 30 yards diameter and landed at six different holes before actually entering one and remaining there. In other instances birds were known to have repeatedly landed at the same hole before entering or flying away. Another common action was for birds to pause in flight as though looking for a hole in the lava. This was sometimes associated with birds calling from underground and at least once a bird called in flight and was answered by a bird from a burrow. Frequently birds landed in a completely holeless area, which however had birds under the lava flow, and these too may have been attracted by calling. Birds on the ground either ran with wings raised high and tail spread, or with wings closed.

A rare procedure was for birds to circle, possibly together, and land in turn at a hole. Once this was watched for 10 minutes before I investigated the hole and found a recently dead storm petrel which had jammed itself trying to come out of a very narrow crack. The bird was removed, some regurgitated oil being left behind, but the birds still continued to land, perhaps smelling the oil, or remembering the bird. A similar display with two birds ended by both trying to land together and rushing to the hole, pecking each other and leap-frogging

over each other. This is similar to an aerial chase in *O. castro* described by Allan (1962) but in my observation it was likely that this was a mere jostling for position and not a display.

Some birds on landing appeared to peck at the lava or possibly were regurgitating oil. The reason or the function for this was not clear, perhaps it might be responsible for the slightly musty smell of the colony.

BEHAVIOR AT THE NEST SITE

The calls heard from underground were of two types. The commonest (here called the harsh call) was a slightly screeching churr split up by two quick squeaks, and resembled the calling of *O. castro* which was described by Allan (1962) as a "guttural purring 'urr-rrr-rrr' interjected with a sharp 'wicka'." The other was a low purring (the soft call) with a quiet "Tchzee," in the middle. This purr was made with the bill either open or closed, in the latter instance it was hardly audible 4 feet away. Rarely a chick-like cheep was heard.

Any bird going underground, or under the bushes on Isla Pitt, elicited much calling from other birds, especially if the intruder was forced to pass close to a bird with a nest site. However, disturbances of any sort would start this harsh calling. Each bird appeared to have a small territory which it would defend by calling and fighting if a strange bird came too close.

One calling bird, without any egg, was sitting in a depression under a bush with another bird apparently trying to displace it. The "intruder" kept approaching to within 3 or 4 inches of the sitting bird which then attacked it and a fight developed with both birds calling, pecking, and holding each others wings as they rolled over and over together. After several such fights the intruder left and the remaining bird sat in its hollow and arranged a few pieces of twigs around it. Twice it went 18 inches away to nibble at small stones and twigs but never brought any of them back when it returned. In some pairs the egg was surrounded by small pieces of lava which must have been collected.

An apparent courtship was watched for an hour at another nest. A bird (A), the assumed male, was threatening another (B), which however kept returning and trying to get underneath (A). After a few minutes (B) was accepted and began to pick up and move around stones and twigs but this lasted only a few minutes before it began to nibble gently at the head and especially the nape of (A). After 10 minutes (B) left and was followed by (A) to the edge of the bush (18 inches away). Bird (A) then returned to the scrape.

A few minutes later (B), (or conceivably another individual), returned and was greeted by many threats and wing pulling. Again (B) was entirely submissive and soon they sat quietly side by side while (B) preened (A) and nibbled nest-material. Bird (B) then tried to incubate a small stone and immediately there was mutual head preening. Whenever (A) appeared to grow restive, (B) resumed

nibbling at its nape, or its back if they happened to head to tail. Throughout these displays (A) usually stood whereas (B) moved on its tarsi, and the only calls heard were the soft call. A third bird arrived and was at first scared away by the harsh call but later, on its return, was forcibly evicted. Later in the day, and throughout the night, only a single bird was present. These observations suggest that there is much aggression between birds, perhaps due to intense competition for nest sites, and that the female has to be submissive to be accepted.

INCUBATION BEHAVIOR

Notes were taken at a single nest under a *Periloba* bush. The incubating bird was extremely restless, constantly preened, pecked at various objects around the nest, moved the egg, and even walked up to a foot away for no apparent reason. When settling down on the egg, it either pushed it under with the bill or placed its foot on the egg so that it slid off one side or the other. If it was the wrong side the bird tried again.

The bird threatened any intruder with the harsh call, which was often enough to drive it away; if not, the bird would leave the egg and advance with slightly raised and expanded wings and spread tail. No other call was heard from the incubating bird, but it does not seem that the harsh call is restricted to territorial defense as two birds visited the hole after hearing this note.

The evidence above and some additional observations on the very densely crowded burrows on Tower, suggests that although this species nests in very large, and to our minds overcrowded colonies, there is some division into territories. This is perhaps essential with such competition for nest sites. In the densest areas the size of the territories appears to be governed by the pecking range of the birds. In these very dense colonies adults are very loath to leave their nest sites for any reason.

The very conspicuous white rump patch appears to be important in both aerial and terrestrial displays and it would be desirable to compare the behavior of this species with that of an all black storm petrel. As well as being used as a signal to other birds of the same species, it might conceivably serve as a deflection mark to attract a predator's attention to a nonvital part of the body. Associated with this is the relative ease with which the white upper-tail coverts are pulled out.

FEEDING OF THE YOUNG

Observations were made on an adult brooding a very small young which had an additional young placed alongside it. The adult moved away 2 inches and sat for 40 minutes while both young called the usual 'tweep-tweep-tweep—' and pecked and nibbled at each other. The adults returned and fed the *strange* young for just over 6 minutes during which time the young gained 7.8 grams.

The feeding was by regurgitation at the back of the adult's throat. The chick had its head sideways with the bill tip towards the adult's throat. During the whole feed the young called continuously at a rate of about one call a second. This method of feeding was different from that described for *O. castro* (Allan, 1962) where the young was fed by six successive but separate rations of food, perhaps due to the larger prey taken by *O. castro*.

The above case of an adult feeding a strange young may be unusual, in that in four sets of artificial twins, adults ejected the strange young, suggesting that they can recognize their own young. This is perhaps to be expected with dense crowding, especially as the chick is unusually mobile for a petrel, but is contrary to my results for *P. puffinus*, *P. lherminieri*, and *O. castro*.

SIZE OF THE TOWER COLONY

The immense numbers of birds flighting, which must have included an unknown proportion of nonbreeders, made a direct estimate of the population impossible. The only feasible, and probably the most accurate, method was to determine the density of nests in the colony and then calculate the total nesting area.

The sample area measured 450 square yards (distances paced out on the flat lava) and was probably in the densest part of the colony. The 34 holes examined had a subterranean area of 37 square feet and held 105 eggs and young so that at least this many pairs were breeding. It was thought that approximately half the surface would cover open area suitable for the petrels which meant a density of about 13 pairs per square yard.

The density of nests varied greatly throughout the colony, so that estimates were made in many places of the numbers of birds landing, and to a lesser degree circling, in comparison with the sample area. The areas were then paced out. Burrows were opened up in various parts to check that the scored densities were of the right order of magnitude.

The colony was composed of:

3,000 square yards at the density of the examined sample (or 13 pairs per square yard)

18,200 square yards at $1/2$ this density

10,800 square yards at $1/3$ this density

700 square yards at $1/4$ this density

1,200 square yards at $1/5$ this density

On this reckoning the total population was about 200,000 pairs. The cliff area was ignored as its investigation was impractical.

BREEDING BIOLOGY

The scattered visits made a detailed study impossible but a few data were collected. Adults were weighed on several dates and the results are summarized in

TABLE 14. *Weights in grams of full grown individuals of Oceanodroma tethys in relation to a) date and b) state of brood patch.*

Date	Colony	Number	Average	Range	Standard deviation
a)					
17.1.67	Tower	59	23.4	20.5–30.0	1.9
8.3.67	Tower	53	21.8	19.0–27.0	1.6
18–20.4.66	Tower	10	25.3	22.1–26.8	1.6
26.6.–3.7.66	Tower	6	28.5	26.0–32.5	3.1
27.5.67	Isla Pitt	7	23.5	20.5–29.0	2.6
11.7.66	Isla Pitt	19	26.0	22.0–35.0	2.8
b)					
Birds with eggs		18	25.8	20.5–35.0	3.6
No brood patch		21	23.4	20.0–27.0	2.0
Unvascularized brood patch		57	22.6	19.0–30.0	2.2
Regrowing feathers of brood patch		23	22.2	19.0–27.0	2.0
With body molt		12	22.0	19.0–27.0	2.1

table 14. There were no significant changes in weights with date or breeding condition, except that incubating birds, presumably with stored food, tended to be heavier than nonbreeders.

One hundred and ninety eggs measured (average length 27.8 mm., standard deviation 1.01; breadth 20.6 mm., standard deviation .60) showed no variation between years or colony and were similar to six taken from the Pescadores, Peru (average 27.3×19.7) (Murphy, 1936). Twenty-three newly laid eggs averaged 5.2 grams (range 3.6–6.3, standard deviation .72). The weight of yolk and albumen in seven freshly laid eggs ejected by birds competing for nest sites was approximately equal. Two females, weights 23.0 and 26.0 grams, were caught on fresh eggs weighing 5.0 and 6.0 grams respectively.

Both colonies were extremely crowded. At least two or three pairs were competing for virtually every hole, as shown by the numbers of eggs laid. The greatest density of pairs on Tower was found under a lava bubble of an approximate area 8 square feet (fig. 18). In 1966 at least 21 eggs were laid, seven young hatched and no more than five could have fledged. In July, 1967 this same hole had 22 eggs and five young. This egg loss was typical of the whole colony.

On Tower, nests were checked at 0800 hours, 1700 hours, and in some holes at 1200 hours. Some incubating birds were marked with paint and the average incubation spell was 5.3 days (changeovers in 14 out of 74 daily checks). There was no tendency for birds to change over at hatching but afterwards no adult brooded a chick for more than 2 days. Unlike *O. castro* young, these appeared to be blind at hatching and some did not seem to have full vision until about the tenth day.

The weight increases of chicks are shown in table 15, and indicate that

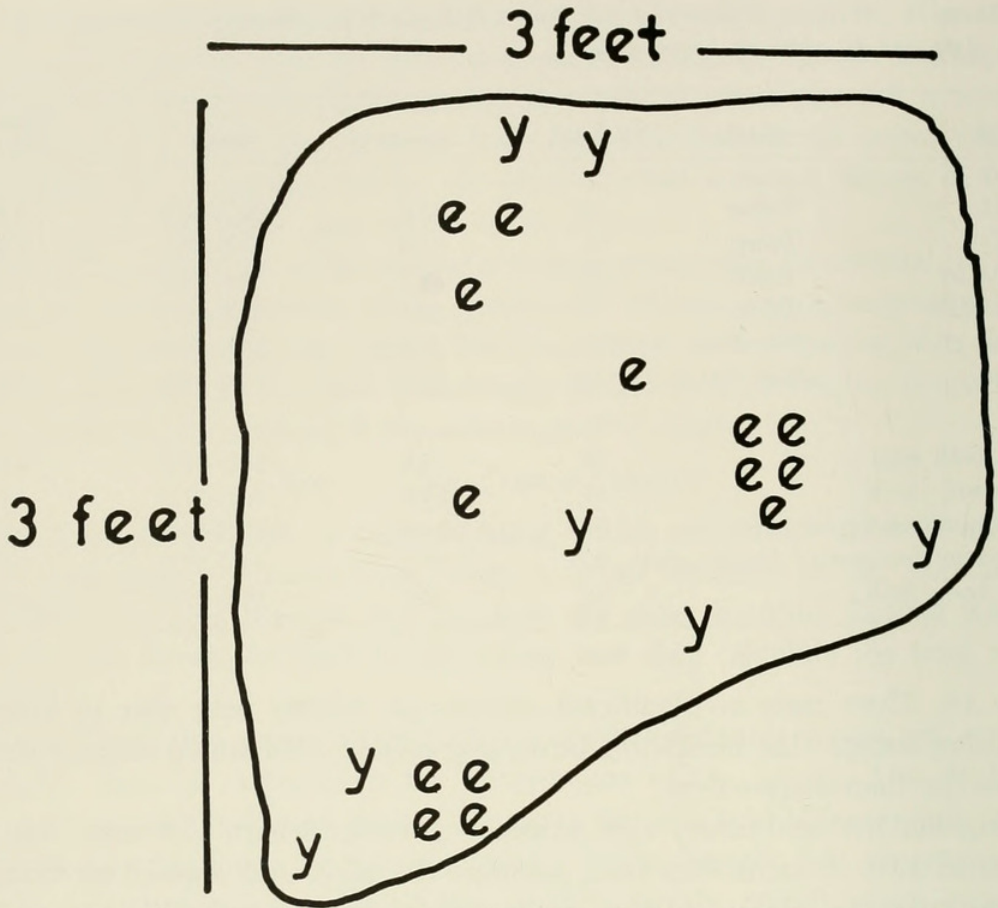


FIGURE 18. Plan of the position of eggs and young in a crowded nesting area of *Oceanodroma tethys* under a lava bubble. No more than five young could have fledged from this hole in 1966. In July, 1967, this hole had 22 eggs and five young.

feeds were most frequent during the day. Many of the overnight feeds were due to adults returning very early in the morning or staying overnight in the burrows. In 91 out of 181 days it was known that a chick was fed at some time in the 24 hours. The maximum recorded increase in the weight of a nestling was

TABLE 15. *Increases in weight of young of Oceanodroma tethys during the day. Tower weighings were made 26 June to 3 July, 1966, and 16 to 18 July, 1966; Isla Pitt weighings, 10 to 11 July, 1966.*

Colony	Time (hours)	Number of young	Number increased in weight	Percent increased	Average increase grams
Tower	0800-1700	246	109	46	3.5
	1700-0800	180	42	23	1.9
	0800-1200	67	12	18	3.8
	1200-1700	67	18	27	3.1
	1700-0800	67	8	12	1.7
Isla Pitt	0830-1630	17	7	41	2.3
	1630-0800	17	2	12	3.3
	0800-1300	17	6	35	2.5

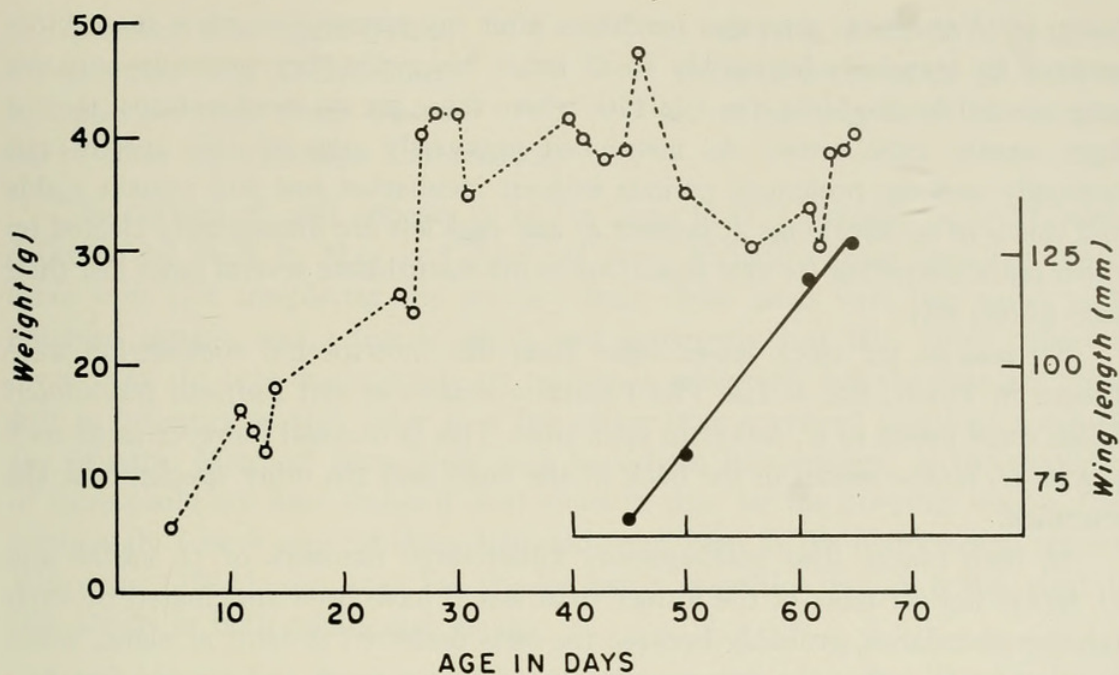


FIGURE 19. Weight and wing length curves for a young of *Oceanodroma tethys* raised by a pair of *Oceanodroma castro*.

12.5 grams, perhaps due to it being fed by both its parents. Additional weighings made on Isla Pitt showed a similar pattern with 13 out of 17 young fed at least once in the 30 hours covered by weighings.

Four young of *O. tethys* were removed to Plaza and fostered under *O. castro* parents. One died soon after introduction but not of starvation as its stomach held food, one disappeared at 72 days but it was unlikely to have fledged, two were successfully reared. These two fledged at 66 and 86 days respectively (both ± 2 days). One of these weighed 32 grams and had a wing length of 137 mm. The growth curve of one young is shown in figure 19.

In the 34 holes on Tower for which I have adequate data, 193 eggs were laid, 63 young hatched and no more than 45 young could have fledged (23 percent of eggs laid). This success rate is not typical, however, as more eggs must have been laid and lost between my visits and the number of young that possibly fledged was a maximum (based on those alive on 17 August and whose remains were not found in December) and many more could have died unrecorded.

CAUSE OF EGG, CHICK, AND ADULT LOSSES

Almost all the nesting losses appeared to be due to the intense intraspecific competition for nest sites. Nelson (1966) was wrong in thinking that the reason for the large numbers of ejected eggs was interspecific competition with *O. castro* for that species did not rest in the same area. Great care had to be taken when replacing stones on the roofs of burrows as eggs in some burrows were

eaten by *Nesomimus parvulus* predators after my inspections when these birds entered by seemingly impossibly small holes. Normally they probably only get eggs ejected by the birds. On Isla Pitt, where there are no mockingbirds, ejected eggs remain until rotten. As mentioned previously eggs of this species can normally undergo prolonged periods without incubation and still remain viable but this is of no advantage at present as any eggs left are immediately ejected by other pairs competing for nest sites. Due to my disturbance several pairs lost their eggs in this way.

No reasons for chick losses other than this interspecific competition were known in Tower, but at Isla Pitt *Phaethon aethereus* and *Puffinus lherminieri* killed some young of *O. tethys* in open sites. This is unusual however as in such places, *O. tethys* nested in the back of the holes and the other species near the entrance.

In both places *Asio galapagoensis* killed large numbers of *O. castro* and *O. tethys* but far more of the former than would have been anticipated by their relative abundance, probably because the owls preferred to hunt at night. When hunting for *O. tethys* the owls usually waited near a crack and jumped feet first at the petrel just as it took off. Once an owl was seen resting itself on bent wings while stretching both feet into a crack to try to get a petrel which it could see but not reach. On Tower the owls also killed prey of *Puffinus lherminieri*, *C. furcatus*, *Phaethon aethereus*, *Anous stolidus*, *Pterodroma phaeopygia*, and *Sterna fuscata*, the latter two species were not otherwise seen here.

Other observed causes of death were: jammed in holes (5), eaten by *Fregata minor* (4) and *Ardea herodias* (3).

WING MOLT

Oceanodroma t. tethys appeared to molt its wing feathers away from the breeding grounds and between breeding seasons, as only two individuals were ever seen in primary molt. Both were from a sample of 80 netted 8 March; they were regrowing the two innermost primaries on each wing. Therefore it follows that the birds flighting in the nonbreeding season cannot be individuals that had bred or were going to breed during the main season. Of 82 skins collected in Galápagos waters, four collected in April (1), May (2), June (1), were just completing the growth of the outermost primaries, presumably just prior to breeding. Other molting birds taken at sea were:

1 August at 13°28' N. 105°52'W. Primaries inner	N	N	N	N	N	N	N	N	N	N	3
1 August 13°28' N. 105°52'W.	N	N	N	N	N	N	N	N	4	1	0
5 August 10°N. 109°W.	N	N	N	N	N	N	N	N	N	2	0
8 August 10°N. 109°W.	N	N	N	N	N	N	N	N	4	2	0
8 August 10°N. 109°W.	N	N	N	N	N	N	N	N	4	2	0
14 August 8°45'N. 106°50'W.	N	N	N	N	N	N	N	3	1	0	0

1 September near Cocos Island	N N N N N N N N N N	4
1 September near Cocos Island	N N N N N N N N	3 0 0
1 September near Cocos Island	N N N N N N N N N N	4 3
All of these were perhaps nonbreeders.		

The pattern of molt appears to be the same in *O. t. kelsalli* for of 37 birds collected by Beck in May and June off Peru, including some breeding birds, three were just completing the primary molt, those birds were two males with enlarged gonads, and a female which had apparently just laid. Birds collected away from the breeding grounds are mainly in wing molt but the data are difficult to interpret as they refer to a few series from scattered positions north of the equator. Many of these birds may have been nonbreeders, as the majority of them could not have finished their molts in time for the breeding season. Unfortunately I have seen no skins collected from Peru in the nonbreeding season. Koepecke (1964) says that the species has a migration but it is not clear if this occurs in both adults and young.

DISCUSSION

The two most impressive aspects of the biology of this species are the dense crowding of nests and the flighting behavior and these are the two most difficult aspects to explain.

On Isla Pitt it was impossible for the colony to expand without emigration to the main island of San Cristóbal, a distance of perhaps a half-mile, as all the good nest sites and many obviously sub-optimal were occupied. This overcrowding on small islands because birds will not leave to start another colony, even a few hundred yards away, is typical of the majority of colonial sea birds. However the Tower colony could expand at either end into apparently identical nesting habitat to that already occupied. Here at least, it is difficult to see what the birds would lose either from protection against predators or from any social factors which might be important by expanding the colony. Any slight losses would be more than offset by the increase in breeding success which might follow from lessening of intraspecific competition.

The advantage to an individual bird of the prolonged display flighting outside the breeding season is again difficult to understand. It might possibly bring all the birds into breeding condition together but other species synchronize their breeding with far less wastage of time and effort and anyway the advantage of synchronized breeding to *O. tethys* remains to be proved. This synchrony of breeding brings about large losses of eggs, but we do not know whether there might be only a short time each year when conditions are suitable for rearing young. Against any advantage must be placed the energy used in flight, the risk of damage from aerial collisions, and the risk of predation.

Another possible explanation which much be considered is that of Wynne-

Edwards' (1962) theory of "epideictic" displays. Nelson (1966) noted several factors which he thought did not fit the flighting to this theory, namely no sharply demarcated daily or seasonal peaks of flighting when the population might be able to gauge its own numbers, and egg losses due to interspecific competition. Even though these conditions are, in fact satisfied, the breeders could hardly get an estimate of the total population as they are not present at the peak of flighting, but away molting. The flighting is therefore unlikely to be an epideictic display but its significance remains obscure.

OCEANITES GRACILIS

The commonest storm petrel seen by most people in Galápagos is *Oceanites gracilis*. As with *Oceanodroma tethys*, this is a species endemic to the Humboldt Current with two separate races, the larger of which "*galapagoensis*" is restricted to the Galápagos (Lowe, 1921).

It is remarkable that despite the searchings of the older scientific expeditions (especially of Beck), Lévêque (1964), and myself, the breeding grounds have yet to be discovered. Similarly no nest of the South American form has been found. Presumably the species is nocturnal in its visits to land and the colonies situated in unusual locations, perhaps cliffs, as in Galápagos almost all the smaller islands have been investigated.

From the examination of gonads it appears that breeding occurs during the cold season (Loomis, 1918). This would fit with the species being restricted to the Humboldt Current. I have seen many birds in wing molt from August onwards, presumably after the breeding season.

I examined a single female in June, 1967, which had an undeveloped ovary and no molt. The bird weighed 17 grams and its stomach contained nine very small fish eye lenses. Loomis (1918) recorded very small fish being taken from a bird shot in Galápagos waters. Flight and feeding habits appear to be similar to the closely related *Oceanites oceanicus*. Food is picked from the surface of the water as birds pattern into the wind — the familiar "walking on the water" of many long-legged storm petrels. Presumably the normal food is small planktonic fish and crustacea, but I have also seen this species eating scraps from the activities of fishermen, sea lions, sharks, and killer whales (*Orcinus orca*).

ECOLOGICAL SEPARATION

Although it is unfortunate that we know nothing of the breeding of *Oceanites gracilis*, which is a member of a group which for the most part breed in the subantarctic zone (Kuroda, 1954), it is ecologically quite distinct from the species of *Oceanodroma*. At least in Galápagos waters, *Oceanites gracilis* is an inshore species, I usually saw it feeding within a mile of the coast and extremely rarely more than 20 miles from land.

Both the Galápagos species of *Oceanodroma* feed well out to sea, but there seems to be a food difference as *O. tethys* eats smaller fish than does *O. castro* and also takes some crustaceans. The basic separation may however, be in the time of feeding; *O. castro* is nocturnal when visiting the colonies so must feed mainly by day, while *O. tethys* must feed mainly at night. The feeding ranges may also be different. *O. tethys*, which is endemic to the Humboldt Current, is common among the islands and between the islands and the Ecuadorian coast. On the other hand, though we have no direct observations, it seems possible that *O. castro* might prefer the bluer, more oceanic waters to the west of Galápagos, as this would fit in with its general distribution in warm waters.

This evidence strongly suggests that the three species of storm petrels resident in Galápagos are ecologically isolated and do not compete with each other for food.

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