Development of the First North American Colony of Manx Shearwaters

ANNE E. STOREY[1] AND JON LIEN[1,2]
[1]Department of Psychology and [2]Newfoundland Institute for Cold Ocean Science,
Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9, Canada

The initiation and progress of a Newfoundland colony of Manx Shearwaters (*Puffinus puffinus*) was studied from 1977 to 1981. Band records, egg dimensions, behavior on the breeding grounds, and the low number of eggs and chicks all suggested that most of the birds were prebreeders or young breeders. Shearwaters initially selected rock crevices as burrow sites, but as these became scarce they dug earth burrows. Burrow length appeared to be an important determinant of whether the burrow remained active from year to year. Band recoveries suggested that birds remained in the same subcolony on the island for one or more breeding seasons before the first egg was laid. Availability of suitable burrow sites was an important factor in limiting the expansion and breeding success of this colony.

A report of a pair of Manx Shearwaters incubating in a burrow on Penikese Island, Massachusetts (Finch 1973, Bierregaard et al. 1975) was the first known breeding in North America for this species. Manx Shearwaters may have nested on Bermuda until 1905 (Bourne 1957), but the existence of this colony has been questioned (Bannerman 1959). The Massachusetts report plus increased sightings of this species in east-coast waters (Post 1967) suggest that the breeding range of the Manx Shearwater may be extending to North America. In 1974 Manx Shearwaters were occasionally seen and nocturnal calls heard on Middle Lawn Island, Newfoundland. A survey of the island revealed no signs of shearwater breeding activity. By 1976 nocturnal vocalization had increased and flocks of several hundred birds were seen frequently near the island (Lien and Grimmer 1978). Breeding activity may have started in 1976 since birds were found ashore, but examination of potential burrow sites yielded no signs of breeding.

Manx Shearwater burrows were first found on Middle Lawn Island in 1977. From 1977 to 1981 the number of burrows increased from 76 to 221, and the population was estimated to have grown from about 200 to more than 350 birds. We document the development of this colony of Manx Shearwaters from 1977 to 1981, describing (1) their origin and reproductive status, (2) the characteristics of burrow sites selected by first and later colonizing birds, and (3) movements of nonbreeding shearwaters within the colony.

Middle Lawn Island (46°55'N, 55°36'W; see Fig. 1), 2 km south of the Burin Peninsula in southern Newfoundland, is about 300 m in diameter with a maximum height of 60 m. About 26,000 pairs of Leach's Storm-Petrels (*Oceanodroma leucorhoa*) nest in the peat towards the top of the island (Lien and Grimmer 1978,

Grimmer 1981), whereas Manx Shearwaters burrowed in the lower slopes, at the junction between vegetation and rock (see Fig. 1).

Each year from 1977 to 1981 the island was surveyed to determine the status of old burrows and the location of new ones. All potential burrows were marked with numbered stakes, and signs of shearwater activity were recorded. Burrow contents were examined during incubation; any adults found were banded, and the length and width of eggs were measured. Burrow length was measured and the distal end of the burrow was prodded with a metal probe to determine whether the substrate was soft enough for further excavation by the shearwaters. Banding of individuals found in the colony at night was done in all years between 1977 and 1981, with most banding done in 1977 and 1978. Only one or two complete island surveys were made in 1979–1981 to minimize disturbance. Birds removed from burrows for banding were returned to their burrows, and birds caught on the ground were released after banding. Thus, except for one loose band that was recovered, all recapture records on the island were from live birds. Birds were sexed on the basis of their distinctive calls (Brooke 1978, Storey 1984).

Burrows were assigned to four categories depending on the level of activity. The presence of an egg or chick indicated a fully active breeding burrow (group 1, breeding burrows). Vocalization in the burrow at night or digging, defecation, or feathers at the burrow entrance were signs that a cavity was becoming a breeding burrow (group 2, potential breeding burrow). Whether Manx Shearwaters used a burrow was determined by placing a grass lattice across the entrance of the burrow. If the grass had been disrupted the next day, then a bird presumably had visited the burrow. Due to the larger size of the shearwater, lattice disruptions indicating shearwater visits usually could be easily distinguished from activity of petrels. Assessment of the activity of latticed burrows was based on the burrow being active on more than 50% of occasions latticed (group 3, visited burrows). Burrows were latticed at least 20 times/season in 1978 and 1979, and all burrows were latticed at least 4 times in 1980 and 1981. Another group of burrows that had been active and then became inactive in subsequent years (group 4, active-to-nonactive burrows) also was monitored. Possible reasons for these burrows becoming inactive, such as flooding or being in substrate too rocky for adequate digging, were recorded.

During the 1980 breeding season thermometers were placed in artificial burrows on the east and west
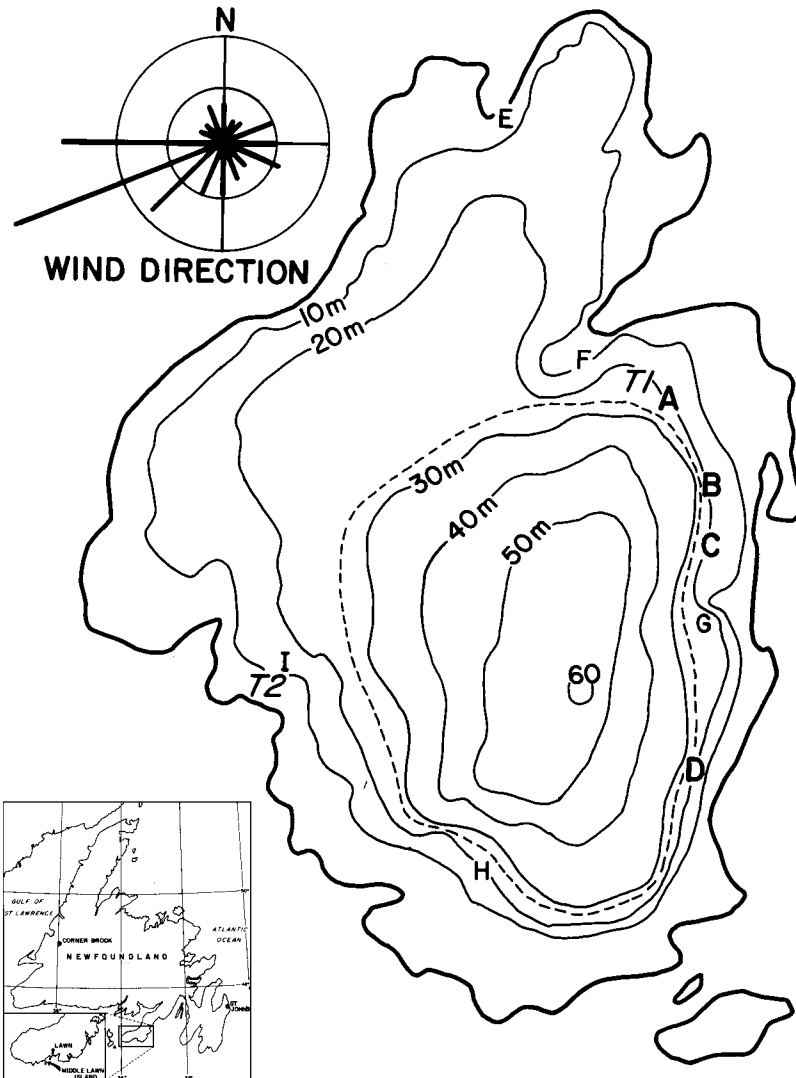
Fig. 1. The distribution of the Manx Shearwater colony on Middle Lawn Island (island length is approximately 300 m). A–D are the major subcolonies and E–I indicate the smaller burrow clusters. The area within the dotted line indicates the location of the highest density of petrel burrows. T1 and T2 are the locations of the temperature records. Wind direction line length indicates the proportion of hourly readings that wind came from each direction; concentric circles mark off 5% intervals. The inset map of Newfoundland shows the location of the Burin Peninsula and Middle Lawn Island.

sides of the island (T1 and T2 in Fig. 1). Burrow temperature and wind speeds and direction were recorded 3 times daily at these sites: between 1200 and 1300, between 1500 and 1600, and between 1900 and 2000.

Origin and reproductive status.—Recaptured birds and bands recovered from Middle Lawn and other parts of Newfoundland suggest that at least some of the Manx Shearwaters on Middle Lawn Island are young birds that originated from populations breeding on

Skokholm and Skomer islands, Wales (Table 1). All 10 band recoveries were from birds aged 6 yr or younger. Nine of the shearwaters were banded on Skokholm and the tenth on Skomer. A 5-yr-old Skokholm bird, found on the ground on Middle Lawn Island in 1977, was recaptured the same year but not since. Band recoveries of 2 other young birds were made within 10 km of Middle Lawn, 1 in 1970 and the other in 1976.

TABLE 1. Band recoveries from area near Newfoundland, 1954–1981.

	Recapture data[a]		
Date found	Recapture location	Age (yr)	Banding location
30 June 1954	Bonavista Bay (48°55′N, 53°10′W)	2	Skokholm, Wales[b]
9 July 1958	Cape Spear (47°32′N, 52°34′W)	1	Skokholm
10 Aug. 1966	Bonavista Bay (48°47′N, 53°30′W)	1	Skokholm
20 Sept. 1967	Fogo Island (49°47′N, 54°00′W)	1	Skokholm
22 Aug. 1969	Belleoram (47°15′N, 55°50′W)	1	Skokholm
2 July 1970	Lord's Cove (46°55′N, 55°36′W)	6	Skokholm[c]
13 Nov. 1970	Twillingate (49°38′N, 54°45′W)	5	Skokholm
20 Aug. 1976	Lawn (46°56′N, 55°32′W)	5	Skomer, Wales[b,c]
20 Aug. 1976	Lumsden (49°18′N, 53°39′W)	1	Skokholm
7 July 1977	Middle Lawn (46°55′N, 55°36′W)	5	Skokholm[c]
10 July 1978	Catalina (40°31′N, 53°05′W)	—	Middle Lawn, 1977[d]
12 Aug. 1981	Lawn (46°56′N, 55°32′W)	—	Middle Lawn, 1977[d]
12 Apr. 1981	Lawn (46°56′N, 55°32′W)	—	Middle Lawn, 1977[d]

[a] From Tuck 1971 and L. M. Tuck pers. comm.
[b] Skokholm, 51°42′N, 5°16′W; Skomer, 51°45′N, 5°18′W.
[c] Birds recaptured within 10 km of Middle Lawn Island.
[d] Year banded, age unknown.

Although many burrows were excavated and occupied by the birds, only a few pairs laid eggs (maximum 6% of burrows contained eggs in 1981), and very few chicks were produced (Table 2). Due to the complex architecture and depth of some burrows, some eggs and chicks may have been overlooked during the survey, but even with the inclusion of suspected eggs, the total number of eggs would have increased by less than 5%. Sixty-eight percent of all eggs or 70% of first eggs in a particular burrow had length-to-width ratios indicative of birds younger than 9 yr (Table 3).

The proportion of chicks hatched relative to the number of eggs laid was also low (see Table 2). For example, in 1980 only 4 out of 12 eggs hatched, and 6 were not incubated, were broken, or were submerged in water in a flooded burrow. Presumably, the availability of dry burrow pouches without sharp rocks affected reproductive success. Burrows with

chicks ($n = 9$) had been established 1.7 yr, significantly longer than burrows in which eggs did not hatch (0.7 yr, $n = 15$, $t = 2.04$, df $= 22$, $P < 0.05$). This suggests that inexperience was a factor contributing to low hatching success. This low hatching success was probably not due to intervention because observers checked burrows only once during incubation, at a time when incubation should have been well under way. Previous studies (Harris 1966, Brooke 1978) found that most breeding shearwaters were not disrupted by more frequent interventions than occurred in this study. Egg mortality usually was easy to detect because the birds pushed the egg out of the burrow.

Prebreeding activities usually were initiated at least one breeding season before the first egg was laid. All but one of the burrows where an egg was found had been visited (group 3 burrows) the previous season, and most had calling birds (11 out of 19), digging (10

TABLE 2. Number of active burrows, eggs, and chicks on Middle Lawn, 1977–1981.

	Number of active burrows[a]			
Year	Initiated each year	Cumulative total	Eggs	Chicks
1977	76	76	3	1
1978	40	116	3	1
1979	40	156	7	3
1980	35	191	12	4
1981	30	221	13	7

[a] Groups 1, 2, and 3. See text for explanation.

TABLE 3. Length/width ratios of eggs on Middle Lawn as an indicator of adult age.

	Age	
	5–9 yr	>9 yr
Number of eggs (%)	19 (68%)	9 (32%)
Number of eggs for first egg laid in a burrow (%)	14 (70%)	6 (30%)
Ratio from Brooke's 1978 study	1.51 ± 0.011 SE	1.45 ± 0.012

out of 13 nonrock burrows), or both during the season prior to laying. Prebreeding activities include the male prospecting for and digging in the burrow, and then calling from in or near the burrow to attract a female (Storey 1984). Once the female approached the male, a duet began that continued after the pair entered the burrow. Pairs frequently engaged in duetting for several nights the year before the first egg was laid in the burrow. Duetting restarted if a pair lost an egg or chick.

Activities of nonbreeders fluctuated throughout the breeding season. Digging and vocalization were most frequent in June and July and decreased in August. The proportion of burrows used for courting or visited by shearwaters also showed significant monthly changes ($F = 3.76$, df = 2,49, $P < 0.05$). There was a significantly lower proportion of active burrows in August (62%) than there were in either June (72%, Newman-Keuls test, $P < 0.05$) or July (74%, $P < 0.05$). Some burrows without eggs were visited in September, but the proportion was much lower than earlier in the season.

Characteristics of breeding burrows.—The number of burrows initiated each year on Middle Lawn (Table 2) is a conservative estimate because only burrows that continued to be active in subsequent years were included. To be considered active the burrow must have contained an egg or chick (group 1), had courting birds (group 2), or have been entered on at least 50% of times latticed (group 3) in more than one season. Burrows were grouped into 4 discrete subcolonies (with more than 20 burrows) and 5 smaller clusters. The interburrow distance decreased from year to year since burrows were found in all areas in 1977 and more recent arrivals selected burrow sites between burrows established previously.

All of the subcolonies and two of the other clusters face northeast to southeast (Fig. 1). One cluster with northern exposure and another with a southwest exposure were in protective caverns. Wind direction helps to explain this distribution. In the months of May–August for the years 1978–1981, 49% of hourly wind-direction readings were between south-southwest and west (data from the Canadian Atmospheric and Environmental Service, St. Lawrence station). In all 16 months the prevailing wind direction for the month was either west-southwest (13 out of 16 times) or west (3 out of 16 times). The average percentage of hours that wind came from each direction confirms that wind most frequently came from west-southwest to west (Fig. 1). Nesting away from the prevailing winds resulted in a warmer temperature in the burrow cavity. For the two artificial burrows, the temperature at T1 on the northeast side of the island was significantly warmer than T2 on the west side (average difference 0.45°C, $t = 2.42$, df = 124, $P < 0.01$).

Burrows are usually used for many years, as pairs tend to be faithful to each other and the nest site

(Harris 1966, Brooke 1978). The types and locations of burrows chosen when the birds first came to the colony were compared with the burrows started later. Shearwaters selected burrow sites along the outer slopes of the island in the rocky outcroppings, possibly because much of the top of the island was already occupied by the petrel colony (Fig. 1). Alternatively, the shearwater sites on slopes of 24–30° (Lien and Grimmer 1978) may provide easier access to and from the sea. Although there was vegetation around shearwater burrows, there was a much higher proportion of rock present than in the petrel areas.

A high proportion of the first burrows were in rock crevices, and only when all of those were taken did birds dig new burrows (Table 4). A significantly higher proportion of burrows initiated by shearwaters in 1977 were in rock crevices than in 1981 ($\chi^2 = 20.7$, df = 1, $P < 0.01$) or 1980 ($\chi^2 = 6.19$, df = 1, $P < 0.01$). The proportion of rock burrows initiated in 1977 did not differ significantly from the proportion initiated in either 1978 or 1979. Rock burrows may be easier to prepare with less digging required, provide more protection from digging predators, and reduce the risk of burrow collapse or burrow flooding. Flooding is less frequent at rocky burrows because they are often elevated from the hillside and water draining down the island usually does not seep into the burrow. For dug burrows, shearwaters selected sites where the burrow had been started either by erosion or by digging of petrels, gulls, humans, or sheep. This suggests that burrow sites may be limited by the availability of rock burrows and of places where the vegetation was disrupted.

The use of existing burrows by shearwaters extended to their rapid use of the artificial burrows. The artificial burrows consisted of a square wooden box (40 cm/side) with a 45-cm stovepipe tunnel perpendicular to one side. They were rapidly taken over by shearwaters (3 had eggs and another had courting birds within 2 yr). Many of the shearwaters that used the artificial burrows (5 of 8 birds in 4 burrows) had been banded in earlier years at a location near the artificial burrow. A sixth bird found in an artificial burrow was banded 4 yr earlier in an adjacent area of the colony. The remaining 2 birds did not have bands. This suggests that birds may prospect in an area of the colony for more than one season and is consistent with the idea that a shortage of burrow sites limits the rate of colony expansion. Three of the burrows initially were placed on the low-density south and southwest sides of the island, but these showed no signs of shearwater visitation. Presumably, the shearwaters preferred the east side.

Location of appropriate substrate may have been responsible for most burrows being on the east side of the island. Because of the prevailing west wind, the east side is less eroded and contains many more large rocks for burrows and outcroppings for protection. Of the 49 rock burrows, only 9 were on the west

TABLE 4. Number of burrows initiated in rock or earth substrate (% of total) for each year.

Year	Mostly or all rock	Partial	Mostly or all dug	Total
1977	31 (41)	26 (34)	19 (25)	76
1978	15 (38)	9 (22)	16 (41)	40
1979	14 (35)	11 (28)	15 (38)	40
1980	8 (23)	8 (23)	19 (54)	35
1981	1 (3)	5 (16)	24 (81)	30

or southwest side, and 6 of those were in a protected cavern.

Burrow length or potential length seems to be an important factor in determining its use by a mature breeding pair. The four burrow types (groups 1, 2, 3, and 4) differed significantly in length ($F = 31.6$, df = 3,244, $P < 0.001$; see Fig. 2). Burrows with eggs (group 1) were significantly longer (Newman-Keuls test, $P < 0.01$) than other burrow types. Group 2 burrows were significantly longer than burrows in either group 3 or 4 ($P < 0.05$). Many of the burrows where digging occurred (group 2) were only initiated in 1981 and thus were not yet excavated to the average length of egg burrows. Because group 2 burrows initiated in 1981 were significantly shorter than those started in previous years ($F = 9.81$, df = 1,91, $P < 0.01$), the burrow length analysis was repeated without the 1981 group 2 burrows. The results were essentially the same as the first analysis.

Many burrows used early in the colonization were deserted later (group 4). Of the 61 group 4 burrows, 25 were short burrows (31.6 cm) that could not be dug further because of the rockiness of the substrate. In contrast, group 2 burrows that could not be dug further were significantly longer (49 cm, $t = 3.20$, df = 54, $P < 0.01$) than the group 4 burrows, suggesting that the potential for further digging affects burrow retention more when the burrow is short. Collapsing walls ($n = 10$) and flooding ($n = 7$) were other possible causes of burrow abandonment. In 4 cases where a petrel nest was found in a burrow used previously by a shearwater, petrels had probably taken over an abandoned shearwater burrow.

Population estimate and movement of birds within the colony.—Mark-recapture analysis suggested that the initial population in 1977 was about 220. The total had increased to about 360 birds by 1981 [estimated from Schnabel's repeated marking technique (*in* Seber 1982)]. Because most of these birds were non-breeders, mark-recapture data can be used to estimate population size. In a mixed population of nonbreeders and breeders, the relative ease of catching nonbreeding birds may inflate population estimates (Orians 1958).

The 90 recaptures of 271 banded birds showed a high degree of area fidelity (74% across years) among
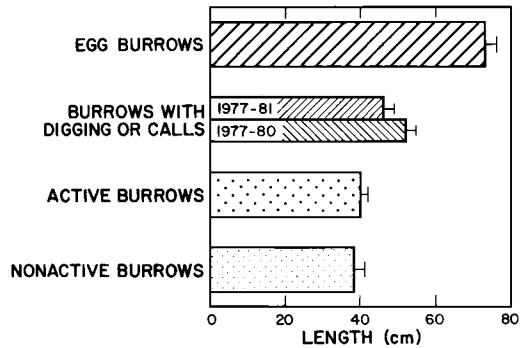

Fig. 2. Burrow length ($\pm$SE) for each of the four groups of burrows.

the nonbreeding birds (Table 5). About 42% of the 67 birds recaptured in the area of banding were recaptured one or more years after banding, indicating that many nonbreeders stay in one area or subcolony for several years. Frequently when burrows first active in 1977 had eggs for the first time or when artificial burrows were taken over, the inhabitants were individuals banded nearby several years before (21 out of 23 previously banded birds). These data support the idea that shearwaters may stay in an area and prospect or attempt to attract a mate for several years before breeding.

Birds recaptured more than once also showed a high level of area fidelity. All birds (35 second or subsequent recaptures for 24 birds) were found in the same area or an area adjacent to their original banding location, and 95% (36 out of 38 third or subsequent recaptures for 27 birds) were found in the same location as on their most recent previous recapture. There are fewer birds in the recapture-banding location comparison (24) than in the comparison of the two most recent recaptures (27) because in the former group precise banding locations were not known for 3 birds. One chick banded on the island in 1977 was found 4 yr later in a burrow in another area of the colony.

Many of these colonizing Manx Shearwaters appear to be either younger than 5–6 yr, the normal age of first breeding (Harris 1966), or young breeders. In the most recent year (1981) only 6% of the Middle Lawn burrows contained eggs, as compared to 75% on Skokholm (Orians 1958). Egg measurements showed that more than twice as many breeding birds were 9 yr or younger than in Brooke's (1978) sample of known-age birds from the Skokholm colony. Burrows with chicks had been established for longer than burrows in which eggs failed to hatch, again suggesting that these are relatively young birds. Other studies also have shown that young and inexperienced seabirds have low reproductive success (Ryder 1980). Finally, the extensive courtship activity

TABLE 5. Number of band recoveries in same, adjacent, or distant areas of the colony.

	Area or subcolony		
	Same	Adja-cent	Dif-ferent
First recaptures			
Definite locations[a]	62	9	11
Probable location[b]	5	3	0
Total (%)	67 (74%)	12 (13%)	11 (12%)

[a] Both banding and recapture location were precisely known.

[b] Original banding occurred before all burrows were marked.

on the island also suggests many of these birds are prebreeders looking for mates or nest sites. That so many of the colonizers are younger birds is consistent with data in Perrins et al. (1973) that showed that 1-yr-olds accounted for half of the birds banded in Wales and recaptured in North America.

Shearwaters preferred burrow sites among rocks but also excavated burrows. Digging in substrate too rocky for excavation of a long burrow was frequently associated with an active burrow becoming inactive. Most of the burrows faced northeast to southeast, which may be due to the lack of rock burrows on the west side or to the warmer air temperatures and lower winds on the east side. Surface air currents may reach the pouch of burrows much deeper than these shearwater burrows (White et al. 1978), so nesting in a burrow does not entirely eliminate the effects of surface weather. Banded breeding and nonbreeding birds showed high fidelity to subcolonies. The rate of recapture away from the original subcolony was similar to that reported by Perrins et al. (1973).

The Manx Shearwater colony on Middle Lawn Island appears to be growing gradually, with many of the same birds, including the one chick banded on the island, returning in subsequent years. It is not clear why the colony is growing so slowly, although the lack of good burrow sites and the youth of the birds may be factors. It is possible that normal colony initiation is a gradual process during the first years, and the Middle Lawn colony may not be unusually slow. Slow colony growth occurred for the related Northern Fulmar (*Fulmarus glacialis*), suggesting that growth may typically be slow until a critical number of breeding birds are present (Montevecchi and Tuck MS). In the Middle Lawn colony, breeding shearwaters are distributed in all the subcolonies rather than being in a cohesive group that might stimulate breeding activities in other birds.

Surveys of adjacent islands in 1977 and 1978 revealed no signs of shearwater breeding activity. Of all the surrounding islands, Middle Lawn is the only one without a significant breeding population of either Great Black-backed Gulls (*Larus marinus*) or Herring Gulls (*Larus argentatus*), species that kill shearwaters (Harris 1965). Perhaps the low gull population on Middle Lawn is the reason for the success of the shearwater colonization (Lien and Grimmer 1978). Breeding range expansion in Manx Shearwaters is substantiated by the initiation of this Newfoundland colony and the report of the breeding pair in Massachusetts. Expansions of seabird ranges from Europe to North America have been documented previously (e.g. Northern Fulmars in Newfoundland, Nettleship and Montgomerie 1974, Montevecchi et al. 1978). Other Newfoundland islands may have been colonized by these species but are visited so infrequently as to be unrecorded.

LITERATURE CITED

BANNERMAN, D. A. 1959. Manx Shearwater. Pp. 86–100 *in* Birds of the British Isles, vol. 8 (D. A. Bannerman, Ed.). London, Oliver & Boyd.

BIERREGAARD, R. O., A. BEN DAVID, T. D. BAIRD, & R. E. WOODRUFF. 1975. First northwestern Atlantic breeding record of the Manx Shearwater. Auk 92: 145–147.

BOURNE, W. R. P. 1957. The breeding birds of Bermuda. Ibis 99: 94–105.

BROOKE, M. DE L. 1978. Some factors affecting the laying date, incubation and breeding success of the Manx Shearwater, *Puffinus puffinus*. J. Anim. Ecol. 47: 477–495.

FINCH, D. W. 1973. The nesting season: northeastern Maritime region June 1–July 31. Amer. Birds 27: 1020–1025.

GRIMMER, B. L. 1981. Habitat selection of Leach's Storm-Petrel (*Oceanodroma leucorhoa*). Unpublished M.Sc. thesis, St. John's, Newfoundland, Memorial Univ. Newfoundland.

HARRIS, M. P. 1965. The food of some *Larus* gulls. Ibis 107: 43–53.

———. 1966. Age of return to the colony, age of breeding and adult survival of Manx Shearwaters. Bird Study 13: 84–95.

LIEN, O. J., & L. GRIMMER. 1978. Manx Shearwater nesting in Newfoundland. Osprey 9: 50–54.

MONTEVECCHI, W. A., E. BLUNDEN, G. COOMBES, J. PORTER, & P. RICE. 1978. Northern Fulmar breeding range extended to Baccalieu Island, Newfoundland. Can. Field-Naturalist 92: 80–82.

————, & L. Tuck. MS. Newfoundland birds: roots of North American ornithology.

Nettleship, D. N., & R. D. Montgomerie. 1974. The Northern Fulmar, *Fulmarus glacialis*, breeding in Newfoundland. Amer. Birds 28: 16.

Perrins, C. M., M. P. Harris, & C. K. Britton. 1973. Survival of Manx Shearwaters (*Puffinus puffinus*). Ibis 115: 535–548.

Post, P. W. 1967. Manx, Audubon's, and Little shearwaters in the northwestern North Atlantic. Bird-Banding 38: 278–305.

Orians, G. H. 1958. A capture-recapture analysis of a shearwater population. J. Anim. Ecol. 27: 71–84.

Ryder, J. P. 1980. The influence of age on the breeding biology of colonial nesting seabirds. Pp. 153–

168 *in* Behavior of marine animals. Vol. 4, Marine birds (J. Burger, B. Olla, and H. Winn, Eds.). New York, Plenum Press.

Seber, G. A. F. 1982. The estimation of animal abundance. New York, Macmillan.

Storey, A. E. 1984. Function of Manx Shearwater calls in mate attraction. Behaviour 89: 73–89.

Tuck, L. M. 1971. The occurrence of Greenland and European birds in Newfoundland. Bird-Banding 42: 184–209.

White, F. N., G. A. Bartholomew, & J. L. Kinney. 1978. Physiological and ecological correlates of tunnel nesting in the European Bee-eater, *Merops apiaster*. Physiol. Zool. 51: 140–154.

Long Laying Intervals: A Possible Mechanism and its Implications

Lee B. Astheimer[1]
Department of Avian Sciences, University of California, Davis, California 95616 USA

The time interval between oviposition of consecutive eggs within a clutch is longer than 24 h in many species. This phenomenon has a broad phylogenetic occurrence and does not appear to be restricted to ecologically or developmentally defined assemblages (see Appendix). Laying intervals longer than one day seem the rule among the Sphenisciformes, Pelecaniformes, Psittaciformes, Falconiformes, Strigiformes, and many tropical suboscine passerine families, but are conspicuously rare in the Galliformes, Anseriformes, and the oscine Passeriformes. The laying interval is of fixed length in most species, although exceptions include the Harpy Eagle (*Harpia harpyja*, 4–9 days), the Australian Mallee Fowl (*Leipoa ocellata*, 2–17 days), and members of the Cuculiformes that have irregular laying frequencies (see Appendix). Lack (1968) implied that these patterns may reflect underlying differences in the abilities of these animals to obtain energy for egg synthesis. However, the relatively fixed nature of laying intervals for many species suggests that such phenomena may reflect evolutionary selection and thus increases the difficulty in demonstrating proximate causes. I describe here a general mechanism, staggered yolk initiation, by which long laying intervals may develop, and explore some of the energetic consequences implied. Before considering these relations, I will address an alternative interpretation of the factors underlying long laying intervals proposed by Williams (1981).

Williams suggests that "the time required for mo-

bilization and deposition of . . . calcium [and] possibly phosphorus for the formation of the relatively heavy shell [of penguin eggs] is the main cause of the long laying interval [3–4 days] in the penguins." This statement is supported by the fact that penguin eggshells comprise a larger percentage of total fresh egg mass (13–15%) than shells of other species [precocial birds: 10% ($n = 55$), altricial birds: 7.7% ($n = 51$); Ar and Yom-Tov 1978], with the implication that this represents a proportionate demand for calcium that cannot be met in a single day. The rationale for considering phosphorus as a factor restricting shell formation is that penguin eggshells contain 2–6% more phosphorus/g than shells of other seabird species (Siegfried et al. 1978). However, that avian shell mass increases disproportionately relative to total egg mass is demonstrated by the relation (Paganelli et al. 1974):

$$S_m = 0.0485 \, E_m^{1.132},$$

where S_m is shell mass and E_m is total egg mass. This relation is derived from data for 368 species [after Schonwetter (see Paganelli et al. 1974)] with egg masses varying by over 5 orders of magnitude. The relative shell masses range from 6% of total egg mass in hummingbird (*Chlorostilbon canivetii*) to 17% of eggs of the extinct elephant bird (*Aepyornis*). Although the estimates of penguin shell mass predicted from this equation are lower than measured values (Williams et al. 1982), the latter fall within the 95% confidence limits provided by Paganelli et al. (1974). Table 1 presents the allometric relations of shell mass as a function of total egg mass for eggs from various avian taxa. It is apparent that the slope of these regressions (*b*) changes little, while their intercept value