COMPARISON OF ECOLOGICAL ASPECTS OF RHINOCEROS AUKLETS AND TUFTED PUFFINS ON TRIANGLE ISLAND, BRITISH COLUMBIA.

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Triangle Island was chosen for investigations on the breeding of Rhinoceros Auklets (Cerrorhinca monocerata) and Tufted Puffins (Lunda cirrhata) as large numbers are known to be there. The objectives of this investigation were to document the breeding populations and compare the time of breeding, nesting, habitat, reproductive rates, and growth of the two species. A comparison of the breeding of Rhinoceros Auklets and Tufted Puffins makes sense as both species are members of the family Alcidae and are closer related within that group than their names suggest. Storer (1945) classified the Rhinoceros Auklet as a puffin based on its morphology. The two species occupy ecologicially closely related niches in their requirement of marine islands, free from mammalian predation, for nesting purposes and their dependence on small marine fish for food. Both nest in burrows, possess a clutch of one egg each, breed at similar times of the year at the same latitudes and commonly on the same islands.

DESCRIPTION AND METHODS

Field studies on Rhinoceros Auklets and Tufted Puffins were conducted from 23 June to 14 September, 1975 and from 1 June to 11 September, 1976 on Triangle Island. Triangle Island (50° 52' N; 129° 05' W), the outermost of the Scott Islands, is situated 46 Km northwest of Cape Scott, at the northern end of Vancouver Island, British Columbia (Fig. 1).

Its greatest distance from point to point is approximately 1.5 km. As its name implies the island is roughly triangular in shape. Its highest point, 205-210 m above sea level, was the site of an active light station from 1909 to 1919. Now only the concrete shell of the lighthouse, foundations of dwellings and rusted rails of a railway remain. A general description of the climate, flora and fauna of Triangle Island has been given by Carl et al (1951) while its bird source has been described in more detail by Vermeer et al. (1976).

Breeding populations of Rhinoceros Auklets and Tufted Puffins were determined by measurement of their nesting habitat in quadrats, a count of all nesting burrows in those quadrats and by determining the occupancy rate of the burrows. Burrow occupancy was determined by investigating the reproductive success of the birds in a sample of burrows during the nesting season. Where nesting habitat was inaccessible for direct measurement, we resorted to photography of the nesting area.

The chronology of fledging of Rhinoceros Auklets and Tufted Puffins were recorded in 1975. In 1976, the hatching and fledging of Rhinoceros Auklets were observed. Hatching and fledging of Tufted Puffins were not recorded in 1976 because of extensive reproduction failure for that species in that year. Egg-laying and hatching periods were calculated by back dating from the time of fledging with the aid of known fledging and incubation periods. Observations were also made on the arrival and departure of Rhinoceros Auklets to and from the island.

Nest burrows were marked with numbered wooden stakes to determine the reproductive success of the two species in 1975 and 1976. The hatching success of Rhinoceros Auklets in 1975 was estimated by planting toothpicks in burrow entrances prior and at the time of hatching to determine

burrow occupancy. Occupied burrows were checked weekly in late July and begin August and on alternate days at the time of fledging in August and September for chick survival. In 1976, Rhinoceros Auklets were checked daily from the time of incubation until fledging. However, about 50 percent of those burrows became deserted, presumably because of frequent disturbance during checking. After desertion, an equivalent number of burrows were added into the study in order to determine the fledging success. It was found that a weekly check on the burrows of Tufted Puffins during periods of late incubation, hatching and early chick stage and an alternate daily check at the late chick and fledging stage caused little or no desertion. In 1976, extensive desertion of Tufted Puffins all over Triangle Island during incubation left few burrows for further investigation.

In 1975, body weights and wing lengths of banded Rhinoceros Auklet and Tufted Puffin chicks were measured every few days in the weeks prior to fledging. In 1976, Rhinoceros Auklet chicks were weighed daily from birth to fledging. Wing lengths were measured from the wrists to the tips of the wings and by straightening that portion along a metric ruler. Chicks and adults were weighed with 500 gram Pesola scales.

Fish brought by Rhinoceros Auklets to their chicks were caught by placing a mist net over the nest burrows. The fish were dropped by the birds and scattered below the net. The weight, length and species of fish and the number of individuals carried per load were recorded in 1976. Information on the same parameters were unobtainable that year for the Tufted Puffins.

Nest burrows were marked with numbered wooden stakes to determine the reproductive success of the two species in 1975 and 1976. The hatching success of Rhinoceros Auklets in 1975 was estimated by planting toothpicks in borrow entrances prior and at the time of hatching to determine burrow occupancy. Occupied burrows were checked weekly in late July and begin August and on alternate days at the time of fledging in August and September for chick survival. In 1976, Rhinoceros Auklets were checked daily from the time of incubation until fledging. However, about 50 per cent of those burrows became deserted, presumably because of frequent disturbance during checking. After desertion, another number of burrows were included for investigation, to add up to the initial number, to determine the fledging success. It was found that by checking the burrows of Tufted Puffins weekly at late incubation, hatching and during the early chick stage and on alternate days at the late chick and fledging stage in 1975, little or no desertion occurred. In 1976, extensive desertion of Tufted Puffins all over Triangle Island during incubation left few burrows for further investigation.

RESULTS AND DISCUSSION

Breeding Populations of Rhinoceros Auklets and Tufted Puffins

Major known breeding concentrations of Rhinoceros Auklets and Tufted Puffins are found in the northern region of Vancouver Island (Fig. 2). The largest known Tufted Puffin colony in British Columbia, as well as in the areas to the south in the United States, is located on Triangle

Triangle Island also contains ~~the second largest known~~ a large Rhinoceros Auklet colony ~~in that province.~~ The largest breeding concentration of Rhinoceros Auklets in British Columbia as well as in North America, with approximately 40,000 pairs of birds, is situated on Pine Island (Fig. 2).

The breeding population of Tufted Puffins in 1975 on Triangle Island was estimated by several methods. On the southwest peninsula of the island, where most puffins nested, the total nesting habitat of puffins was measured to be 25600 M^2 l.e. Six plots, 9 by 9 M each and totalling 486 M^2 l.e., were set out in different parts of this habitat (Fig. 3). Of 321 burrows counted in those six plots, 95% were actively occupied. The total number of nesting puffins on the southwest peninsula was therefore estimated to be $\frac{26500}{486} \times (321 \times 95\%) = 16628$ pairs.

Another large number of nesting puffins was found on the southern portion of the east slope of Triangle Island (Fig. 3). This was a somewhat inaccessible area for direct measurements of the total nesting habitat. One plot, 30 by 30 M was set out there and its corners were marked with tall poles painted bright yellow. By photographing the whole southeast nesting habitat from a boat in the water and by dividing the marked area in the total breeding habitat, it was calculated that the puffins nested there on approximately 9000 M^2 l.e. Forth-three nests were counted within a 7.6 by 7.6 M area of the marked plot. From the above figures and allowing for a 95 percent occupancy rate of the burrows, it was calculated that the breeding population of puffins on this slope consisted of approximately 6500 pairs.

Puffins nested also in much smaller numbers in several other locations of Triangle Island (Fig. 3). The breeding population in those

locations was estimated to be between 1500 to 2000 breeding pairs. The total breeding population of puffins on Triangle Island in 1975 is therefore estimated to consist of approximately 25,000 pairs on the basis of the above figures.

Rhinoceros Auklets were only found in large numbers on the eastern part of the south slope (Fig. 3). The total nesting habitat of Rhinoceros Auklets was measured to be 74,457 m^2. A total of 38 plots 5 by 5 m each, totalling 950 m^2, were set out systematically through the nesting habitat in 1976 (Fig. 3). A total of 397 burrows were counted in those 38 plots. The occupancy rate of burrows was determined from investigating 109 burrows for eggs and chicks during the breeding season. Only 43 percent of the 109 burrows was occupied. The total number of breeding Rhinoceros Auklets was estimated to be $\frac{74457}{950} \times (397 \times 43\%) = 13,380$ pairs.

NESTING HABITAT

Most of Triangle island is covered by salmonberry (Rubus spectabilis) which is pruned by strong winds where exposed. Lady ferns (Athyrium filix-femina) constitute large patches within the salmonberries. Normally growing under forest cover these ferns are found in the open, indicating the island's prevailing humid environment. Tufted hairgrass (Deschampsia caespitosa) covers most wind-exposed ridges and hill slopes. Salal (Gaultheria shallon) is abundant near rocky promontories, perhaps as its roots can penetrate deeply along rock faces. The slope substrate was high in rock contents, much more so than on the less steeply undulating top of the island (Table 1). Most of rock material in the substrate

consisted of pieces less than 3 cm long. Besides rock the substrate contained soil, peat and vegetative material such as roots or dead grass in tufted hairgrass areas. Much of the dead grass may have been worked into the substrate by the burrowing alcids. No correlation was observed between the dominant vegetation types and their substrate. Microclimatic conditions such as wind exposure, may therefore chiefly determine the distribution of dominant vegetation types. Perhaps hairgrass chiefly grows on wind exposed ridges and slopes as no other major cover plant can resist strong aeolian exposure (winds known to be up to 130 km/hour). Tufted Puffins nested predominantly in hairgrass, but not all slopes covered with this vegetation were occupied by puffins. Mostly the steepest slopes or the relatively flat perimeter just above a cliff face, covered with this grass appeared to be preferred nesting habitat of the puffins. The nesting patterns of puffins suggest that they need steep slopes for taking off from their burrows. When departing from their nest sites puffins dropped in their initial flight almost parallel along the nesting slopes. Perhaps their high wing loading compared to that of Rhinoceros Auklets limits the puffins chiefly to steep slopes (Table 9).

Rhinoceros Auklets, contrary to puffins, nested in all major vegetation types and at slope angles ranging from 0 to 60 degrees. Since it was not obvious from the Rhinoceros Auklets' nesting distribution if they preferred nesting in certain vegetative cover or on gradual or steep slopes, burrow density in 38 plots was regressed on the three major vegetation types, absence of vegetation, slope angle and altitude (Appendix 1). Cassin's Auklets (Ptychoramphus aleuticus) nested with

Rhinoceros Auklets. Therefore the burrow entrance density of Rhinoceros Auklets was also regressed on that of Cassin's Auklets. Each variable in the stepwise multiple regression analysis was transformed into a natural logarithmic form. The estimated regression line was:

$$D = -1.45 + 0.55 \text{ Log GRA} + 0.32 \text{ Log SB} - 0.13 \text{ Log ABS} - 0.12 \text{ Log C}$$

($F = 21.2$; $P < 0.01$) ($F = 10.2$: $P < 0.01$) ($F = 1.2$) ($F = 0.28$)

$$+0.36 \text{ Log SLO} \quad (F = 0.32) \qquad - 0.05 \text{ Log SAL} \quad (F = 0.15) \qquad - 0.04 \text{ Log ALT} \quad (F = 0.016)$$

where

D = number of Rhinoceros Auklet burrow entrances

GRA = % Tufted hairgrass cover

SB = % Salmonberry cover

ABS = % Absence of vegetation

C = Number of Cassin's Auklet burrow entrances

SLO = Slope angle

ALT = Altitude

SAL = % Salal cover

Of the independent variables, only the tufted hairgrass and salmonberry covers were significant explanatory variables. The addition of Log GRA gives a greater increase in the regression sum of squares than the addition of Log SB, indicating that the Rhinoceros Auklets have a greater preference for tufted hairgrass than salmonberry. However Rhinoceros Auklets prefer salmonberry to salal or absence of vegetation. From the above findings it appears that Rhinoceros Auklets are similar to Tufted Puffins in that theyprefer nesting in open hairgrass habitat. Rhinoceros

Auklets differ from puffins in their nesting at a wide range of slope gradients and in vegetation other than hairgrass. Tall salmonberry did not prevent Rhinoceros Auklets from landing as evidenced from seeing and hearing them crashing in this vegetation before reaching the ground. Rhinoceros Auklets also differed in that their nesting density and burrow occupancy were also considerably less than that of puffins (Table 2). The reason for these differences is unknown. Perhaps more Rhinoceros Auklets bred on Triangle Island in the past. Comparison of nest burrow parameters in Table 3 show that nest bowl dimensities for Tufted Puffins were larger than for Rhinoceros Auklets. This is to be expected as Tufted Puffins are larger than Rhinoceros Auklets. The species also differed in that the nest bowl of the Rhinoceros Auklet usually was located at the very end of the burrow, while that of the Tufted Puffin terminated some distance before the tunnel end. The burrow entrance parameters for the species were surprisingly similar. Perhaps it is advantageous for the larger puffins not to have a correspondingly large entrance as a narrow opening may prevent burrow corrosion, deter avian predation and provide a more constant ambient burrow temperature for a successful hatching of eggs and production of young.

ACTIVITY PATTERNS

The arrival and departure of Rhinoceros Auklets to and from the colony are mostly restricted to dusk or dawn respectively while puffins enter and leave the nesting grounds any time during the day. The first few Rhinoceros Auklets arrive at the colony around 20:00 beginning July and at about 20:30 by late August (Fig. 4). This difference in arrival

time coincides with the earlier onset of darkness as the season progresses. Most birds land within one hour after the first individual landing. Their crashing in the salmonberry bushes can then be heard frequently and everywhere over the nesting slope. Their approaching behavior varies. On misty or cloudy evenings the birds arrive 15 to 20 minutes earlier and make many more passes or circles along the nesting slope than on sunny days. Their circling becomes also less extensive as the season progresses. During fledging, from mid-August on, most birds fly straight to their nesting burrows. While raising chicks, adult birds would gather on the water in large rafts about 0.5 to 1. kilometers from the shore, approximately one to two hours before sunset and wait there until dusk before flying to their burrows. Similarly to the synchronized arrival, almost all Rhinoceros Auklets were observed to depart from the colony in July between 0350 and 0450 in the morning (Table 4). Rhinoceros Auklets are also restricted to nocturnal activities during egg-laying (Richardson, 1961; Leschner, 1976) as compared to the more diurnal pattern of Tufted Puffins (Wehle, 1976). Cody (1973) suggested that nocturnality in Cassin's and Rhinoceros Auklets may be a mechanism to counter piracy and predation by gulls, which have diurnal activity patterns. Manuwal (1974) and Bédard (1976) pointed out that Cody's suggestion was inconsistent with observed predation pressure on Arctic alcid colonies exposed to continuous daylight during the summer. However, it is conceivable that Rhinoceros Auklets are sufficiently flexible to develop this mechanism where advantageous and possible at lower latitudes. Approximately 200 pairs of Glaucous-winged gulls (larus glaucescens) and two pairs of Peregrine Falcons (Falco peregrinus) nest on Triangle Island. No piracy by gulls on Rhinoceros Auklets was observed. Peregrine

Falcons, known predators on alcids, were seen to be active during dawn, daytime and dusk. Although there were signs of falcon predation on alcids, no falcons were seen pursuing Cassin's Auklets or Rhinoceros Auklets, perhaps because of the large size of the island and the observers' occupation with alcid investigations. R. W. Campbell (pers. comm.) however, observed Peregrine Falcons preying upon adult Rhinoceros Auklets in British Columbia. Synchronized arrival and departure of Rhinoceros Auklets at the colony may diffuse a predator's concentration on one individual auklet. Rhinoceros Auklets were observed to fly faster than puffins in their approach to and departure from the colony. Perhaps the Rhinoceros Auklets' faster flight is enhanced by the more favourable wing loading than that of puffins (Table 10). Because of their fast flight, the Rhinoceros Auklets' projected course is predictable to a falcon which may aid this predator in apprehending its prey. Rhinoceros auklets are not synchronized in their arrival at all breeding colonies. They fly into Sea Lion Caves, Oregon, during the day and are diurnal at South Farallon Island, California (Scott et al. 1974). Perhaps predation pressure is much less on Rhinoceros Auklets at locations where they are diurnal and their activity patterns are less synchronous.

Favourable wing loading, fast flight and daytime absence from the colony allows the Rhinoceros Auklets to travel greater distances at sea than the puffins. Although Tufted Puffins may range far out at sea, they appear to forage close to the colony at the time of feeding the chicks (Wehle, 1976). Many Tufted Puffins were usually seen on the waters near Triangle Island during the chick stage, while comparatively few Rhinoceros Auklets were seen near the island at that time (Table 5).

Cody (1973) reported Rhinoceros Auklets to range farther at sea from the breeding colony than Tufted Puffins at Washington State. Cody theorized that interspecific differences in foraging range of alcids is a competition-reducing mechanism for food. Bédard (1976) criticized Cody's theory on ecological isolation of alcids predominantly by linear selection of feeding areas from the colony as somewhat naive. Bédard pointed out that many other factors, such as coastline and slope configuration, general water circulation, oceanographic conditions and seasonal and local events all exert a powerful influence upon the birds' selection of feeding area. Concurring with Bédard's criticism but considering Cody's hypothesis with certain modifications that ecological isolation in alcids is not a strict linear relation, it is suggested that Rhinoceros Auklets on the basis of wing-loading and activity patterns alone may feed farther from the colony than puffins while raising chicks. Rhinoceros Auklets like puffins feed extensively during the day. It would be conceivable that Rhinoceros Auklets could reverse their activity patterns at the colony, i.e. arrive at dawn and leave at dusk to counter predation, but such a pattern would be incompatible with diurnal feeding.

BREEDING CHRONOLOGY

The mean fledging periods for Rhinoceros Auklets and Tufted Puffins, which are the times between the hatching of a chick and its departure by first flight from its nesting burrow, were 54.4 and 55.2 days respectively (Table 6). Since there are indications that the fledging of Rhinoceros

Auklets on Trinagle Island in 1976 may have been somewhat delayed by food shortage, the fledging period of 50 days for this species at Cleland Island (Table 6) has been used for back dating the chronology of hatching of this species at Triangle Island in 1975. Mean incubation periods of 42 and 45 days reported for Rhinoceros Auklets and Tufted Puffins by Summers (in prep.) and Sealy (1972) respectively have been used for calculating the chronology of egg-laying for the two species on Triangle Island. Some recorded but incomplete data on hatching of Tufted Puffin eggs in 1975 supported the derived chronology of hatching for this species in 1975 by the process of back dating (Table 7). The composite picture of observed and calculated chronology of egg-laying, hatching and fledging of Rhinoceros Auklets and Tufted Puffins shows that Rhinoceros Auklets started to breed one week later in 1976 than in 1975 (Fig. 5). Puffins started laying slightly later but fledged a good week later than Rhinoceros Auklets in 1975. It can be concluded, that the overall length and time of the nesting season for the two species is remarkably similar. The onset of the chronology of egg-laying, hatching and fledging of the Rhinoceros Auklets, however, appears to be distinctly different from that of the puffins. The onset of observed fledging in 1975 is much more abrupt for Rhinceros Auklets than Tufted Puffins. This sudden initiation is not evident for the fledging of Rhinoceros Auklets in 1976 because of the extensive chick mortality which resulted in a small number of fledglings in that year. But the observed hatching of Rhinoceros Auklets in 1976 also demonstrates the abrupt chronology of breeding for this species. Comparison of the weekly percentage distribution of

fledging for the two species in 1975 in Figure 6 shows that the fledging of Rhinoceros Auklets is more abrupt; takes place over a briefer period; and follows a less normal distribution than that of the puffins. The cumulative percentage distribution shows that it takes 3 weeks for Rhinoceros Auklets but 5 weeks for Tufted Puffins before more than 90% of the chicks fledged. Most of the synchronized fledging of the Rhinoceros Auklets can be attributed to the synchronized hatching which in turn may result from synchronized egg-laying at Triangle Island. It was calculated from Leschner (1976) that Rhinoceros Auklets on Destruction Island, Washington lay about 90% of their eggs within the first three weeks of clutch commencement. The breeding synchrony of Rhinoceros Auklets at Triangle and Destruction Islands therefore appears similar.

The initiation of egg-laying in birds may be determined by the amount of food required for the female to form eggs (Lack, 1966, 1968, Harris, 1969, Perrins, 1966, 1970). The variation in breeding synchrony between Rhinoceros Auklets and Tufted Puffins may be brought about by a difference in appearance of large quantities of prey to the birds. If prey becomes suddenly available, birds feeding upon this prey may respond with abrupt or synchronized egg-laying.

The differences in breeding synchrony between the two species may also result from interspecific differences in activity patterns. Restricted nocturnal activities may stimulate synchronized breeding in Rhinoceros Auklets. Leschner (1976) reported Rhinoceros Auklets to be less synchronous breeders at Smith and Protection Islands than at Destruction Island in Washington. Perhaps Rhinoceros Auklet activities are less synchronous

and/or the appearance of prey to the birds is more gradual at the former than at Destruction and Triangle Islands.

GROWTH

Mean body weights of Rhinoceros Auklets and Tufted Puffin chicks from 4 weeks before to the time of fledging are compared in Table 8. The mean body weight of Tufted Puffin chicks and fledglings was significantly above those of Rhinoceros Auklets. The mean weekly growth rate was on the average (1975 and 1976 combined) twice that of the Rhinoceros Auklets during the last four weeks before fledging. The slower growth rate of Rhinoceros Auklets than that for Tufted Puffins may be related to reduced feeding activity for adults. Diurnal puffins feed their young several times a day while Rhinoceros Auklets make only one trip a day per sex (Leschner, 1976).

Rhinoceros Auklets were somewhat lighter at fledging in 1976 than in 1975 at Triangle Island. The weights of fledglings were significantly below those of Cleland Island and generally below those of Destruction Island, while adult weights were similar at all three locations (Table 9). It can be seen from Figure 7 that Rhinoceros Auklet chicks at Triangle Island in 1976 weighed considerably less after their first two weeks of life than those at Cleland Island. The lower chick weights may reflect a shortage in certain prey fish and/or prey size available to the Rhinoceros Auklet chicks at Triangle Island as compared to those at Cleland and Destruction Islands. It is evident from Table 9 and Figure 7 that Rhinoceros Auklets can adjust to a slower growth rate. Such an adjustment allows for chick survival under adverse feeding conditions.

Average wing lengths of Rhinoceros Auklets and Tufted Puffin chicks from 10 days before until the time of fledging in 1975 are compared in Figure 8. Because of little fluctuation in wing growth in the last 10 days before fledging, these measurements proved to be better indicators of the approaching time of fledging than those of body weights. The mean wing lengths of the fledglings of the two species overlapped but that of the adults differed significantly (Table 10). Body weight/wing length ratios also differed significantly between adult and between fledglings of the two species. The relatively low ratios for Rhinoceros Auklet fledglings may indicate favourable wing loading. Young Rhinoceros Auklets attained 83% of the wing length of adults compared to young Tufted Puffins which attained 76% of that of adults at fledging. Long wings and favourable wing loading may enhance the survival of young Rhinoceros Auklets at fledging as it allows them to follow the adults far out at sea when departing from the colony.

REPRODUCTIVE SUCCESS

The Rhinoceros Auklets and Tufted Puffins have a clutch of one egg each, that of the puffins being on the average larger than that of the Rhinoceros Auklet (Table 11). Since Rhinoceros Auklets and Tufted Puffins raise only one brood per breeding season and have a one-egg clutch, they cannot produce more than one young annually. As much can go wrong during breeding, their productivity is generally much less than one young per pair of birds. The overall reproductive success for the two species was very similar in 1975 (Table 12). Perhaps 1975 represents normal reproduction for Rhinoceros Auklets and Tufted Puffins. In 1976, the Rhinoceros Auklet production of young was only half that of the preceding year, while Tufted Puffins produced very few young compared to 1975.

There are indications that the poor reproduction of Rhinoceros Auklets in 1976 is related to food availability. Four species of fish, Pacific Sauries (Cololabis saira), Sockeye Salmon fingerlings (Oncorhynchus neeka), Sand lance (Ammodytes hexapterus), and Blue Lantern fish (Tarleton beania crenularis) were brought by the adult birds to their chicks in 1976 of which Pacific Sauries were most numerous (Table 13). Sauries were also the heaviest, sturdiest and largest of the prey (Table 14). In July, sauries were on the average smaller than in August (Table 15). Many sauries brought to the chicks were not eaten, resulting in a large number of sauries being left in the burrows (Table 16). No other fish than sauries were found there. Many more sauries were left in August than in July. In August, 1976 a large number of chicks were observed to have died of starvation and a disease (Table 17) of which the symptoms were loss of balance and co-ordination. The disease may have been related to starvation or other causes. Not only were dead birds found in the burrows but many were encountered on the nesting slope outside the burrows. The peak of the dead and dying chicks on the slope came after that in the burrows (Table 18). The chicks probably wandered from the burrows after initial starvation. Saurie tails were often observed protruding from the mouths of chicks in the burrows (Figure 10). In a few cases, dead chicks were also found with a fish protruding from their mouth on the ~~western~~ nesting slope (Fig. 11). It appeared that they had choked on the fish. In 1975, no fish were observed protruding from the chicks and no fish were observed in the burrows. No chicks were encountered that year in the burrows or on the nesting slope who obviously died of starvation or disease. The extensive chick mortality in 1976 may be partly or wholly related to an unsuitable

diet. Sauries may have been too large and sturdy a prey, causing digesting difficulties. The pelagic Pacific sauries may not constitute the usual diet for Rhinoceros Auklet chicks. Rhinoceros Auklets feed mostly on Sandlance (~~Ammodytes hexapterus~~), anchovies (Engraulis mordax), smelt (Hypomesus pretiosus and Spirinchus starksi) and herring (Clupea Hárengus) in Washington (Richardson, 1961; Cody, 1973 and Leschner, 1976) and chiefly on sandlance in Alaska (Heath, 1915). They feed offshore as well as in bays and coastal inlets. The first author observed Rhinoceros Auklets feeding extensively in bays and inlets along the west coast of the Queen Charlottes in the summer of 1976 in association with Glaucous-winged Gulls, Pigeon Guillemots (Cepphus Columba), Marbled Murrelets (Brachyramphus marmoratus), Common Murres (Uria aalge) and Pelagic Cormorants (Phalacrocorax auritus).

The cause of the reproductive failure of Tufted Puffins on Triangle Island in 1976 is more obscure than that for Rhinoceros Auklets. Most Tufted Puffins deserted Triangle Island during incubation. Different factors may have caused the reproductive failure. A helicopter landed for half an hour in the midst of a high density of nesting puffins on the southwest peninsula of the island on June 24, 1976. The purpose of the landing was to establish a reference point for the surveying and mapping of the area by the Government of Canada. One of the observers rushed to the helicopter to inform the surveyor of the disturbance to nesting seabirds. The helicopter left immediately but 300 pairs of Common Murres and 80 pairs of Pelagic Cormorants, nesting approximately 50 - 100 meters from the landing site, did not return to their nests with eggs and young. Puffins also deserted their burrows in the vicinity of the landing as evidenced by numerous cold eggs and empty burrows observed and puffin eggs

found preyed upon by gulls and crows after the incident. Burrows of puffins were observed to be deserted on a large scale at other nesting localities on Triangle Island, not previously investigated, in the beginning of July. Therefore, it is unlikely that the helicopter was responsible for the desertion of Puffins all over the island. Most of the desertion may have been caused by other factors, such as food shortage near the island or weather interference with the attainment of prey. Rough water conditions occurred frequently at Triangle Island in the summer of 1976. The summer of 1976 was noted for its excessive rainfall along the British Columbia coast. Since precipitation was measured at nearby Cape Scott in 1966, the rainfall for May - July, 1976 was approximately twice the average of that for May - July in the preceding ten years (Table 19).

Reproductive failure in oceanic birds resulting from adverse weather conditions has been reported elsewhere. Nettleship (1972) reported that the reproductive success of Common Puffins (Fratercula arctica) at Great Island, Newfoundland during an extremely wet summer was about half that of a normal season. Litvinenko (1976) found that nestlings of Japanese Shearwaters (Puffinus leucomelas), Karamzin Island, Pacific U.S.S.R. starved in adverse weather conditions. Birkhead (1976) observed that feeding rates of Common Murres (Uria aalge) declined during rough seas. He suggested that this may be due to fish moving into deeper waters under those conditions.

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TABLE 1. Comparison of the 25 cm top layer composition of substrate between hilltops and slopes of Triangle Island.

Location of Sample	No. of Samples	% Mean Composition of Substrate (range in parentheses)		
		rock	soil	vegetation
Hill tops	10	3.0 (0-18.8)	59.7 (9.4-92.2)	37.4 (6.2-87.5)
Hill slopes	16	43.6 (9.4-81.2)	33.2 (9.4-65.6)	23.2 (3.1-68.7)

TABLE 2. Comparison of nesting densities and occupancy rates of burrows of Rhinoceros Auklets and Tufted Puffins, Triangle Island.

Nesting density and occupancy	Rhinoceros Auklet	Tufted Puffin
No. nesting burrows	393	321
Nesting area investigated (No. sample plots in parentheses)	950 m^2 (38)	486 m^2 (6)
Burrow density	1 burrow/2.4 m^2	1 burrow/1.6 m^2
No. nests occupied	169	306
Occupancy rate	43%	95%

TABLE 3 Comparison of burrow dimensions (in cm) of Rhinoceros Auklets and Tufted Puffins, Triangle Island.

Burrow parameters	Rhinoceros Auklet n	$\bar{x}$	Range	Tufted Puffin n	$\bar{x}$	Range
Burrow entrance height	30	21	13-32	36	22	13-38
Burrow entrance width	15	12	9-20	19	12	6-23
Nest bowl height	30	25	17-36	31	32	25-41
Nest bowl width	13	15	10-22	15	18	13-33
Length of burrow	30	97	46-183	28	99	56-155

TABLE 4. Number of Rhinoceros Auklets observed departing from 41,240 m^2 area on July 21 and 29, 1976.

Observation time (standard time)	July 21, 16,025 m^2 area	July 29, 25,215 m^2 area	Total 41,240 m^2 area
0340 - 0350	0	0	0
0350 - 0400	85	222	307
0400 - 0410	5400	1395	6795
0410 - 0420	2176	8000	10176
0420 - 0430	116	5175	5291
0430 - 0440	26	1116	1142
0440 - 0450	4	145	149
0450 - 0500	0	0	0
Total number of birds observed	7807	16053	23860

Table 5. Comparison of alcids observed on the sea during a boat voyage near Triangle Island, British Columbia, August 1, 1975.

Distance from Triangle Island in Km	Tufted Puffin	Rhinoceros Auklet	Common Murre	Cassin's Auklet
0 - 4	126	10	5	0
4 - 8	127	18	5	2
8 - 12	20	4	8	2

Table 6. Mean incubation and fledging periods of Rhinoceros Auklets and Tufted Puffins in days.

Species	Location	Incubation period	Range and sample no.	Fledging period	Range and sample no.	Source
Rhinoceros Auklet	Destruction Island	45.5	42-50; n=10	54.3(1974) 51.0(1975)	50-60; n=19 42-62; n=37	Leschner, 1976
Rhinoceros Auklet	Smith Island	-	-	48.3	42-57	Manuwal, in prep.
Rhinoceros Auklet	Cleland Island	42.0	-	50.0	- ; n=12	Summers, in prep.
Rhinoceros Auklet	Triangle Island	-	-	54.4	48-60; n=5	This study
Tufted Puffin	-	45.0 (estimated)		-	-	Sealy, 1972
Tufted Puffin	Triangle Island	-	-	55.2	54-56; n=5	This study

TABLE 7 Hatching chronology of Tufted Puffin eggs in 77 nesting burrows July 7 - 17, 1975, Triangle Island

Date of Observation	No. eggs	No. eggs not hatched	No. eggs failed to hatch	% eggs hatched
July 7	53	22	2	29
July 11	30	40	7	52
July 17	9	59	9	77

Table 8. Body weights in grams of Rhinoceros Auklet and Tufted Puffin chicks at four weekly intervals before fledging, Triangle Island

Weeks before fledging	Rhinoceros Auklet → 1975 n	1975 $\bar{x}$	1975 Range	1976 n	1976 $\bar{x}$	1976 Range	Tufted Puffins n	Tufted Puffins 1975 $\bar{x}$	Tufted Puffins 1975 Range
0	11	294	210-330	15	266	217-336	13	482	415-545
1	18	276	220-355	15	280	237-332	10	435	360-535
2	9	245	185-285	10	264	231-294	6	401	330-480
3	11	243	165-295	8	251	209-318	4	335	265-385
4	5	221	180-240	7	221	162-254	5	279	210-320
Mean weekly growth Rate in grams		18.2			11.2			50.8	
Percentage weekly growth*		~~6.5~~ 6.2			4.2			10.5	

* Mean weekly growth rate / Fledging weight

Table 9. Comparison of body weights of adults and fledglings of Rhinoceros Auklets and Tufted Puffins at different locations (Destruction Island - Leschner, 1976; Cleland Island - Summers, in press)

Species	Location, year	No. of Adults	Mean weight of adults (A) in grams	No. of fledglings	Mean weight of fledglings (F) ± 95% Conf. int. in grams	F/A in %
Rhinoceros Auklet	Triangle Island, 1975	41	521*	11	294 ± 27	56.4
Rhinoceros Auklet	Triangle Island, 1976	41	521*	15	266 ± 20	51.1
Rhinoceros Auklet	Destruction Island, 1974	51	521*	19	308	59.1
Rhinoceros Auklet	Destruction Island, 1975	51	521*	51	339	65.1
Rhinoceros Auklet	Cleland Island	10	518	14	359 ± 19	69.3
Tufted Puffin	Triangle Island	7	756	13	482 ± 28	63.8

* Combined adult weights, for 1975 and 1976 at Triangle Island and for 1974 and 1975 at Destruction Island.

Table 10 Comparison of wing length and body weight/wing length ratios of adult and fledgling Rhinoceros Auklets and Tufted Puffins, Triangle Island, 1975

Species	Age	n	Mean wing length ± 95% Conf. Int. in mm.	Body weight/wing length Ratio ± 95% Conf. Int. in grams/mm
Rhinoceros Auklet	Adult	31	177.5 ± 2.7	2.9 ± 0.1
Rhinoceros Auklet	Fledgling	11	148.0 ± 3.2	2.0 ± 0.2
Tufted Puffin	Adult	7	199.1 ± 6.6	3.8 ± 0.2
Tufted Puffin	Fledgling	13	150.8 ± 2.2	3.12 ± 0.1

TABLE 11 Comparison of egg dimensions (in ~~cm~~ mm) of Rhinoceros Auklets and Tufted Puffins, Triangle Island.

Egg parameters	Rhinoceros Auklet			Tufted Puffin		
	n	$\bar{x}$	~~SE~~ se	n	$\bar{x}$	~~SE~~ se
Length	40	68.0	0.39	52	70.5	0.34
~~Length~~ Width	40	45.9	0.18	52	48.7	0.15

TABLE 12 Reproductive success of Rhinoceros Auklets and Tufted Puffins at Triangle Island, 1975 and 1976

Species	Year of study	Hatching success			Fledging success			Overall reproductive success		
		No. eggs	No. hatched	% hatched	No. chicks	No. fledged	% fledged	No. eggs	No. fledged	% fledged
Rhinoceros Auklet	1975	50	35	70.0*	35	31	88.6	50	31	62.0
Rhinoceros Auklet	1976	47	44	93.6*	44	15	34.3	47	15	31.9
Tufted Puffin	1975	77	62	80.5	62	51	82.3	77	51	66.2
Tufted Puffin	1976	70	3	4.3	3	1	33.3	70	1	1.4

* Approximate

Table 13. Species composition of fish brought by Rhinoceros Auklet adults to their chicks Triangle Island, 1976

Time of Sampling	No. Rhinoceros Auklets sampled	Species of fish				Total No. of fish
		Pacific Saury	Sockeye Salmon	Sand-lance	Blue Lantern Fish	
July 16-25	12	27	0	0	5	32
August 7-16	15	19	4	2	0	25
August 17-31	15	24	0	9	0	33
July 16 - August 31	42	70	4	11	5	90

Table 14. Weight and length of fish brought by Rhinoceros Auklets to their chicks, Triangle Island, 1976

Species	Number of fish	Weight in grams $\bar{x}$	Weight in grams Range	Length in mm $\bar{x}$	Length in mm Range
Pacific Saury	70	20.5	3-42	186	114-238
Sockeye salmon	4	15.0	9-21	141	115-182
Sandlance	11	4.9	3-11	116	104-152
Blue Lantern Fish	5	0.8	-	48	45-50

Table 15 Variation in number, weight and length of Pacific Sauries brought by adult Rhinoceros Auklets to their chicks, Triangle Island, 1976

Time of sampling	Total No. of loads*	No. of fish	No. fish per load	Mean weight per load in grams	Mean weight per fish in grams	Mean length per fish in mm
July 16-25	11	26	2.36	35.4	15	168
August 7-16	12	16	1.33	33.2	25	203
August 17-25	14	24	1.73	38.1	22	195

* 100% Pacific Saurie loads.

Table 17 Causes of mortality among Rhinoceros Auklet chicks, Triangle Island, 1976

Causes	No. of chicks found dead or dying	
	In burrows	On slope*
Starvation	14	9
Disease	12	15
Choked on fish	1	1
Burrow flooded	1	0
Undetermined	9	14
Disappeared	2	0

* Only 39 chicks weighed and examined

Table 18 Chronology of mortality of Rhinoceros Auklet chicks in nesting burrows and on nesting slope, Triangle Island, 1976

Time of death	No. of chicks found dead or dying	
	In burrows	On slope
July 11 - 17	2	0
July 18 - 24	1	0
July 25 - 31	0	0
August 1 - 7	3	0
August 8 - 14	9	0
August 15 - 21	8	7
August 22 - 28	6	30
August 29 - September 4	3	39
September 5 - 11	0	5
Total no. of chicks	32	81

TABLE 19. Comparison of monthly precipitation between May - July, 1976 and 1966 - 1975 at Cape Scott, British Columbia

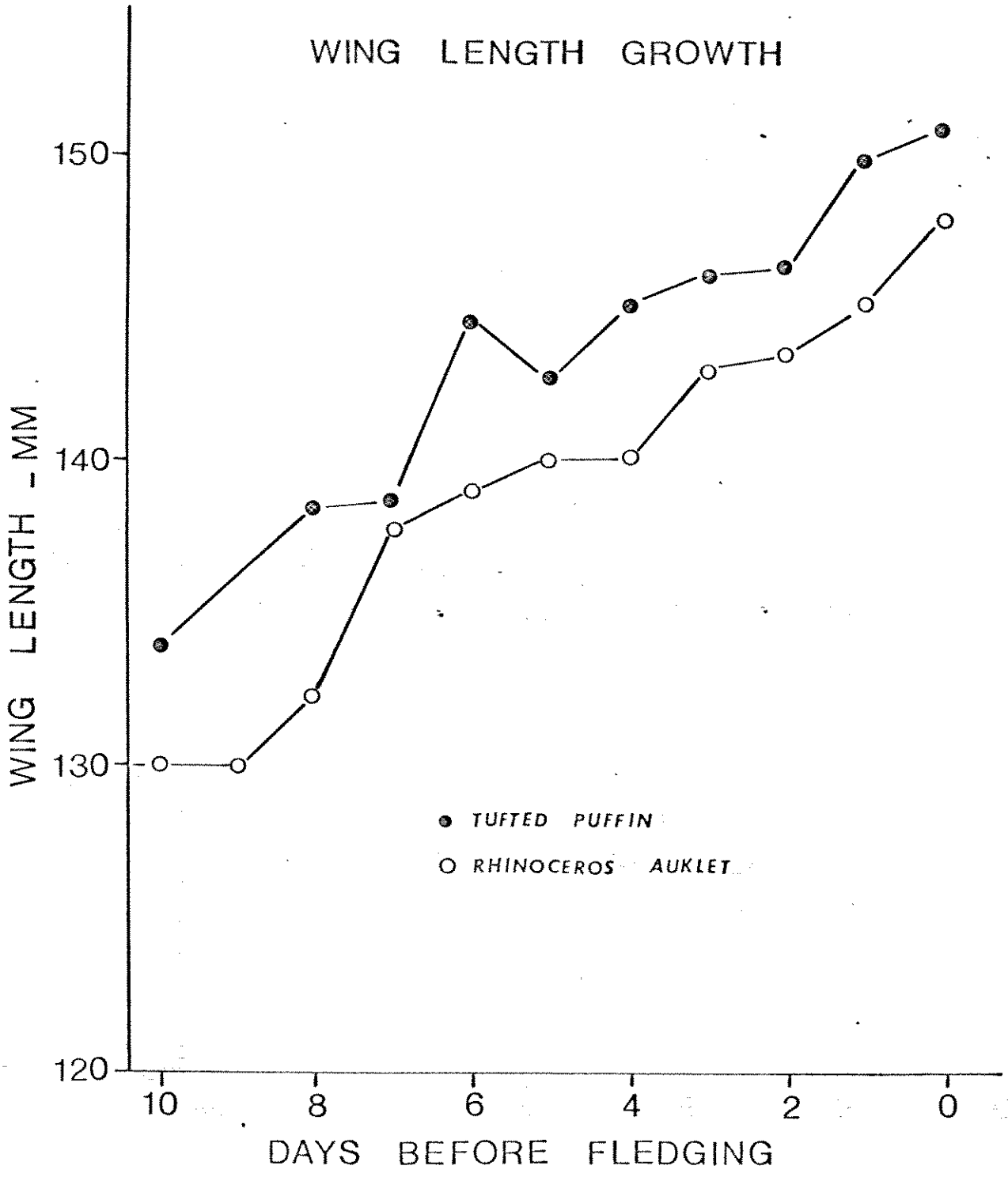
Month	Amount of monthly precipitation in cm.		
	1976	Average 1966-1975	Maximal 1966-1975
May	32.4	15.9	23.3
June	18.8	10.8	21.2
July	19.5	7.8	12.2

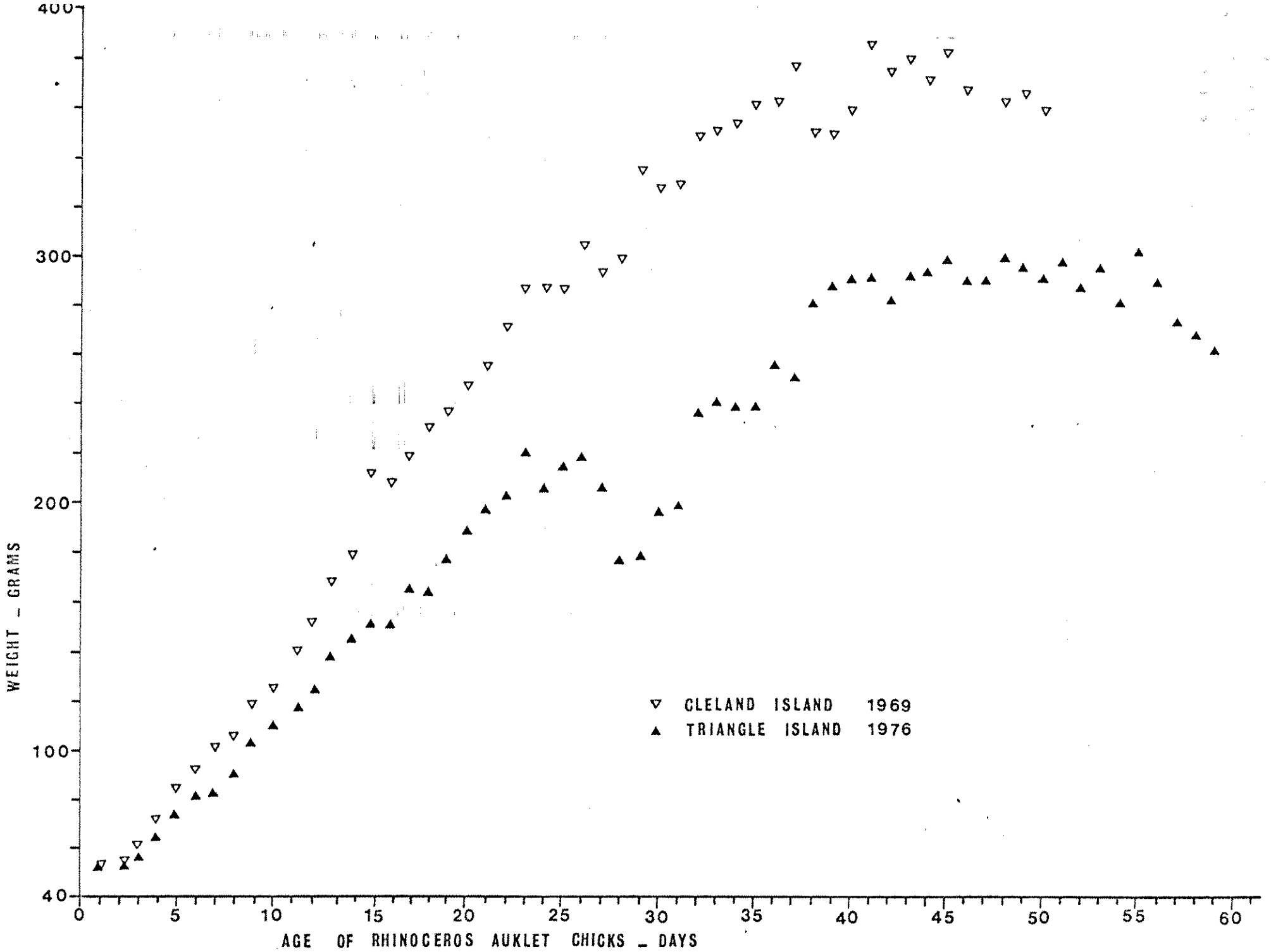
Appendix 1. Comparison of density of Rhinoceros Auklet burrow entrances with those of Cassin's Auklets in 25 m^2 quadrats and with slope angle, altitude and vegetation types of quadrats, Triangle Island, 1976

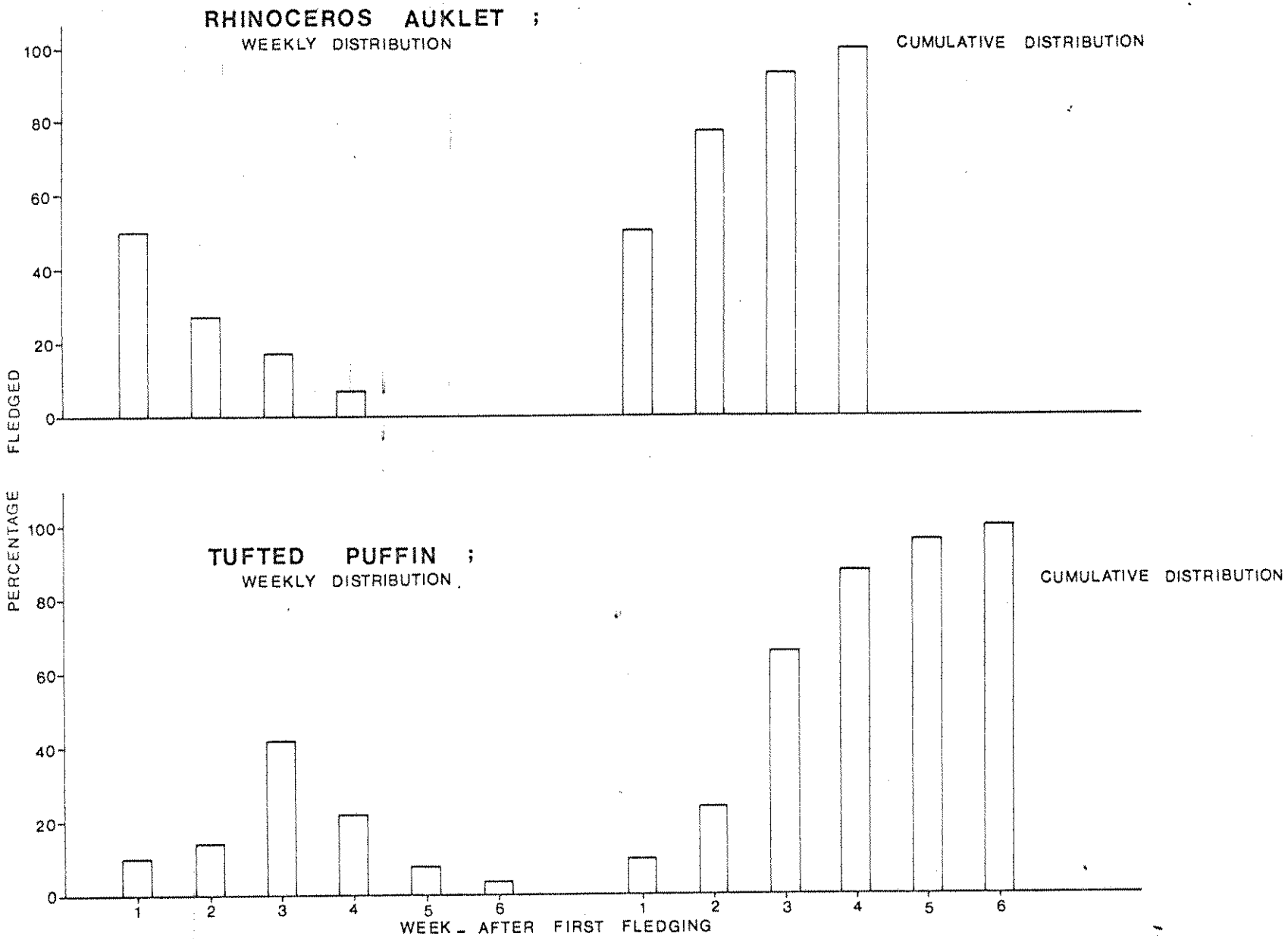
Quadrat No.	No. of burrow entrances		Slope angle in degrees	Altitude in Meters m	% Estimated Vegetation Cover			
	Rhinoceros Auklets	Cassin's Auklets			Salmonberry	Salal	Tufted hairgrass	Absence of Vegetation
1	6	17	40	23	46	0	40	10
2	12	10	47	42	10	0	80	10
3	14	3	36	52	11	20	60	5
4	12	5	42	67	35	4	45	10
5	13	6	41	88	30	4	65	1
6	0	0	19	9	95	0	0	0
7	18	2	40	27	65	0	35	0
8	13	5	46	51	20	15	65	0
9	18	33	26	77	50	0	40	10
10*	0	0	41	9	2*	0	0	0
11	12	8	41	34	100	0	0	0
12	1	26	36	69	0	0	23	75
13	2	40	14	84	80	0	10	10
14	1	1	47	35	95	5	0	0
15	0	0	50	58	30	30	0	30
16	0	71	15	77	0	0	80	20
17	7	0	42	27	100	0	0	0
18	0	0	50	65	0	95	0	0
19	11	25	45	75	2	15	95	2
20	24	14	36	92	0	2	100	0
21	12	25	30	111	15	5	80	0
22	18	60	28	92	10	0	100	0
23	0	40	32	94	0	15	90	0
24	32	0	40	16	50	10	45	5
25	35	0	39	42	60	10	30	5

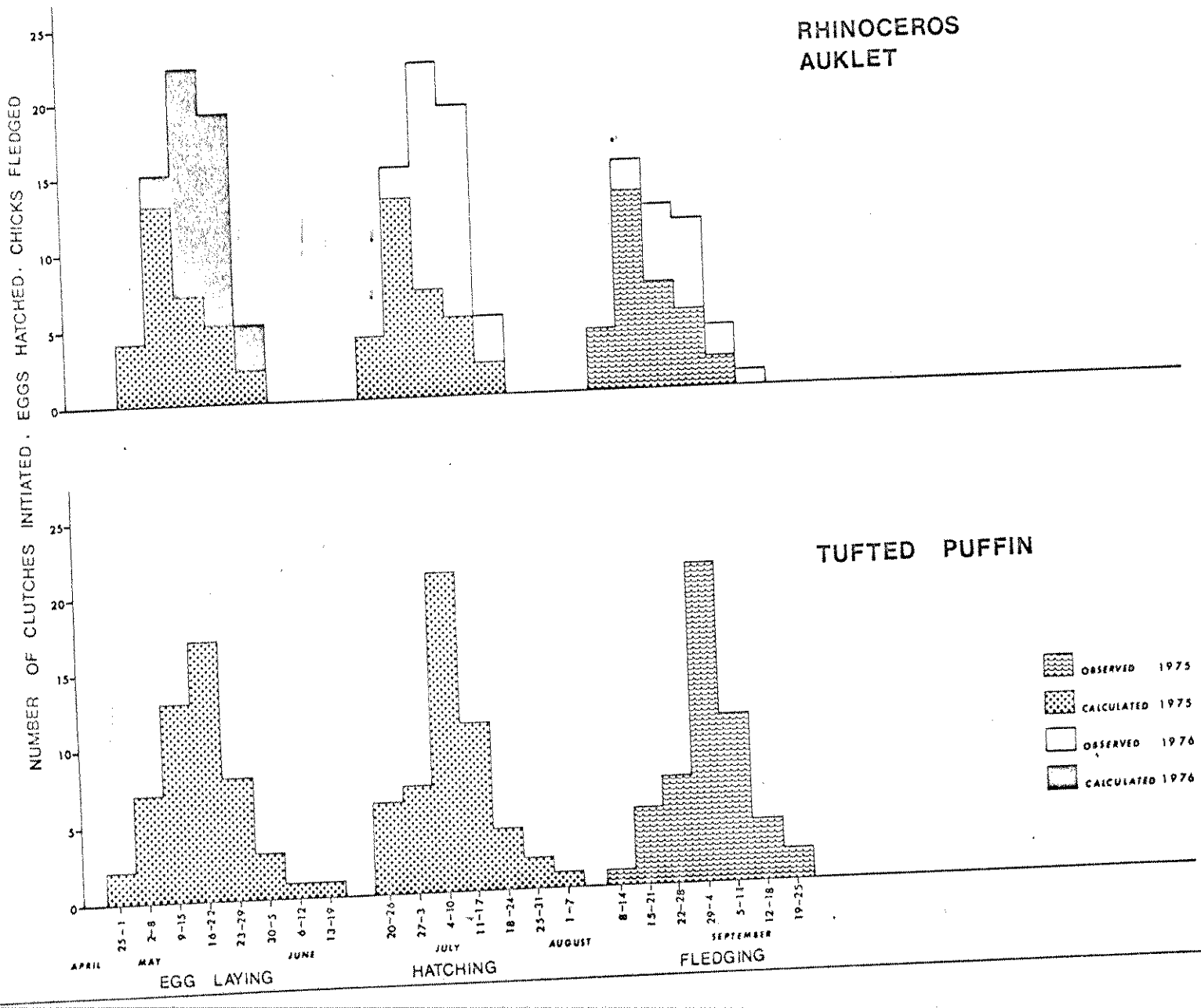
Quadrat	No. of burrow entrances		Slope angle in degrees	Altitude in Meters	Salmon-berry	Salal	Tufted hair-grass	Absence of Vegeta-tion
	Rhinoceros Auklets	Cassin's Auklets						
26	1	2	58	74	15	50	20	0
27	11	2	51	103	80	0	30	0
28	16	3	33	21	40	0	50	5
29	6	3	47	48	0	70	15	23
30	9	5	43	71	60	25	20	0
31	24	3	40	14	50	0	45	0
32	10	4	45	47	75	10	15	0
33	2	1	39	76	95	5	0	10
34*	1	0	46	20	0	0	0	0
35	4	6	60	37	30	0	60	0
36	24	4	35	59	80	1	20	3
37	0	0	50	25	0	20	20	60
38	24	10	35	56	15	30	65	0

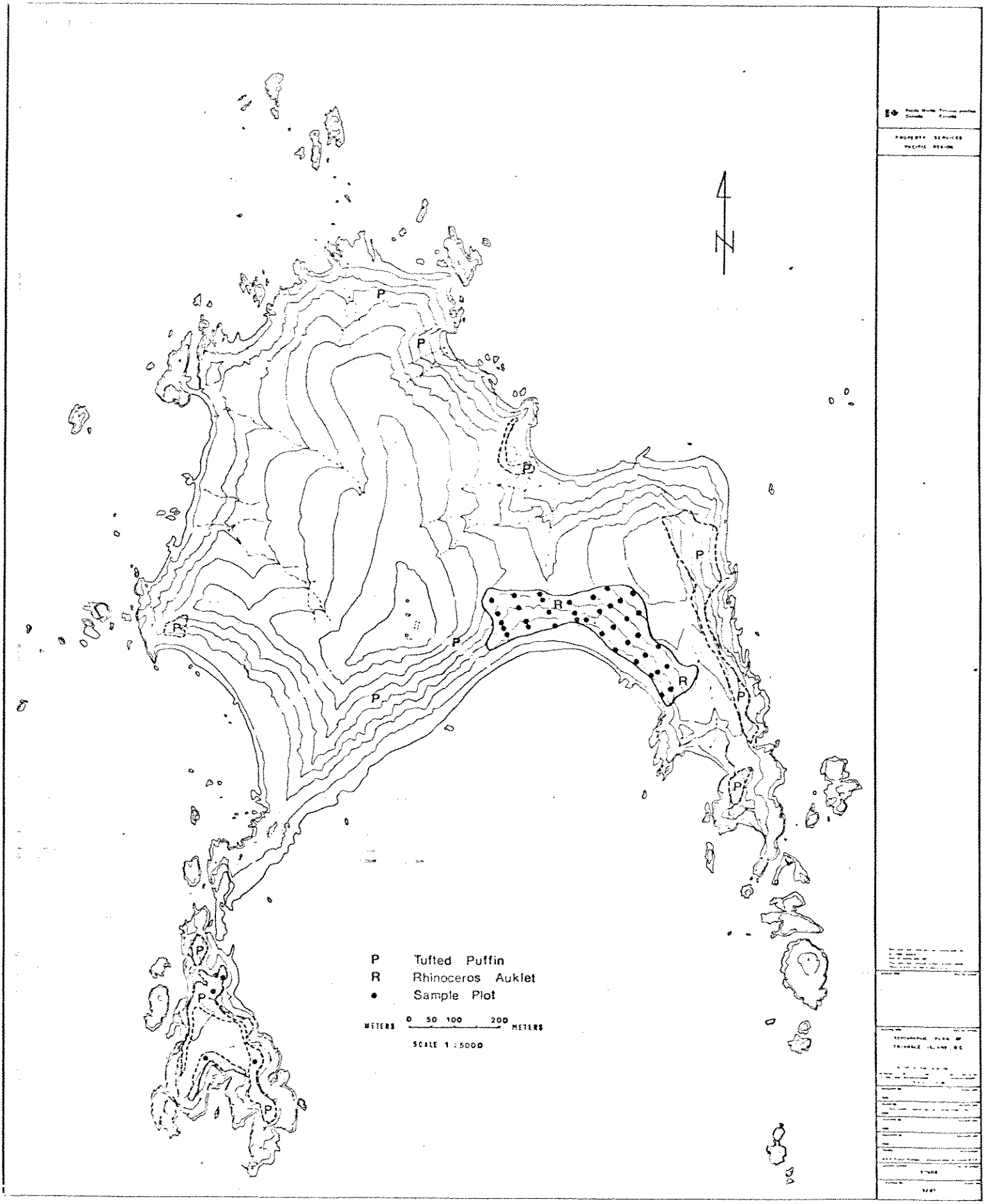
* Other vegetative cover dominant.


WING LENGTH GROWTH
150
140
130
120
WING LENGTH - MM
10
8
6
4
2
0
DAYS BEFORE FLEDGING
TUFTED PUFFIN
RHINOCEROS AUKLET


400
300
200
100
40
WEIGHT - GRAMS
0
5
10
15
20
25
30
35
40
45
50
55
60
AGE OF RHINOCEROS AUKLET CHICKS - DAYS
CLELAND ISLAND 1969
TRIANGLE ISLAND 1976


RHINOCEROS AUKLET ;
WEEKLY DISTRIBUTION
CUMULATIVE DISTRIBUTION
PERCENTAGE FLEDGED
100
80
60
40
20
0
TUFTED PUFFIN ;
WEEKLY DISTRIBUTION
CUMULATIVE DISTRIBUTION
1 2 3 4 5 6 1 2 3 4 5 6
WEEK - AFTER FIRST FLEDGING


RHINOCEROS AUKLET
TUFTED PUFFIN
NUMBER OF CLUTCHES INITIATED. EGGS HATCHED. CHICKS FLEDGED
0
5
10
15
20
25
OBSERVED 1975
CALCULATED 1975
OBSERVED 1976
CALCULATED 1976
25-1
2-8
9-15
16-22
23-29
30-5
6-12
13-19
20-26
27-3
4-10
11-17
18-24
25-31
1-7
8-14
15-21
22-28
29-4
5-11
12-18
19-25
APRIL
MAY
JUNE
JULY
AUGUST
SEPTEMBER
EGG LAYING
HATCHING
FLEDGING


P Tufted Puffin
R Rhinoceros Auklet
Sample Plot
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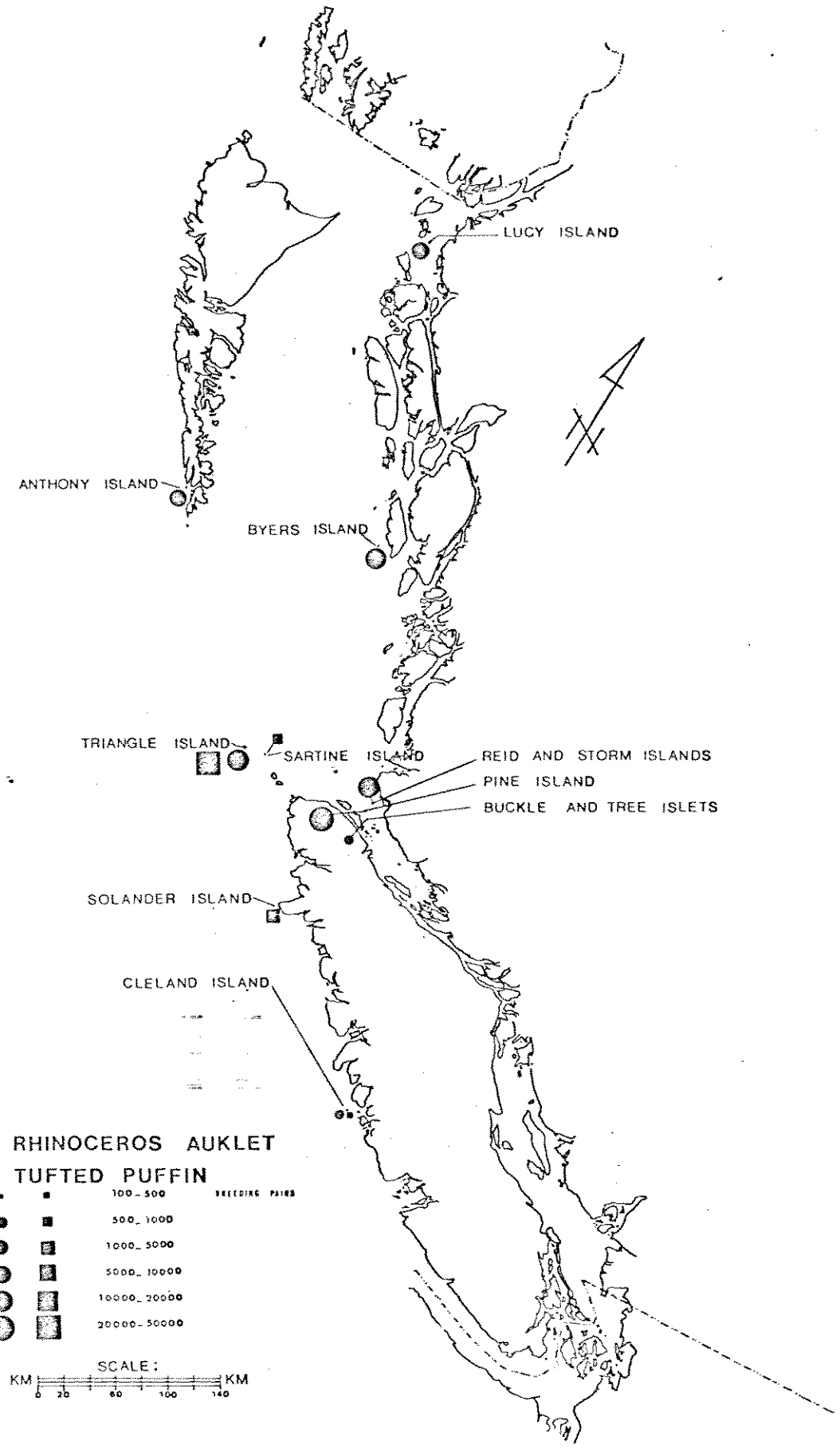
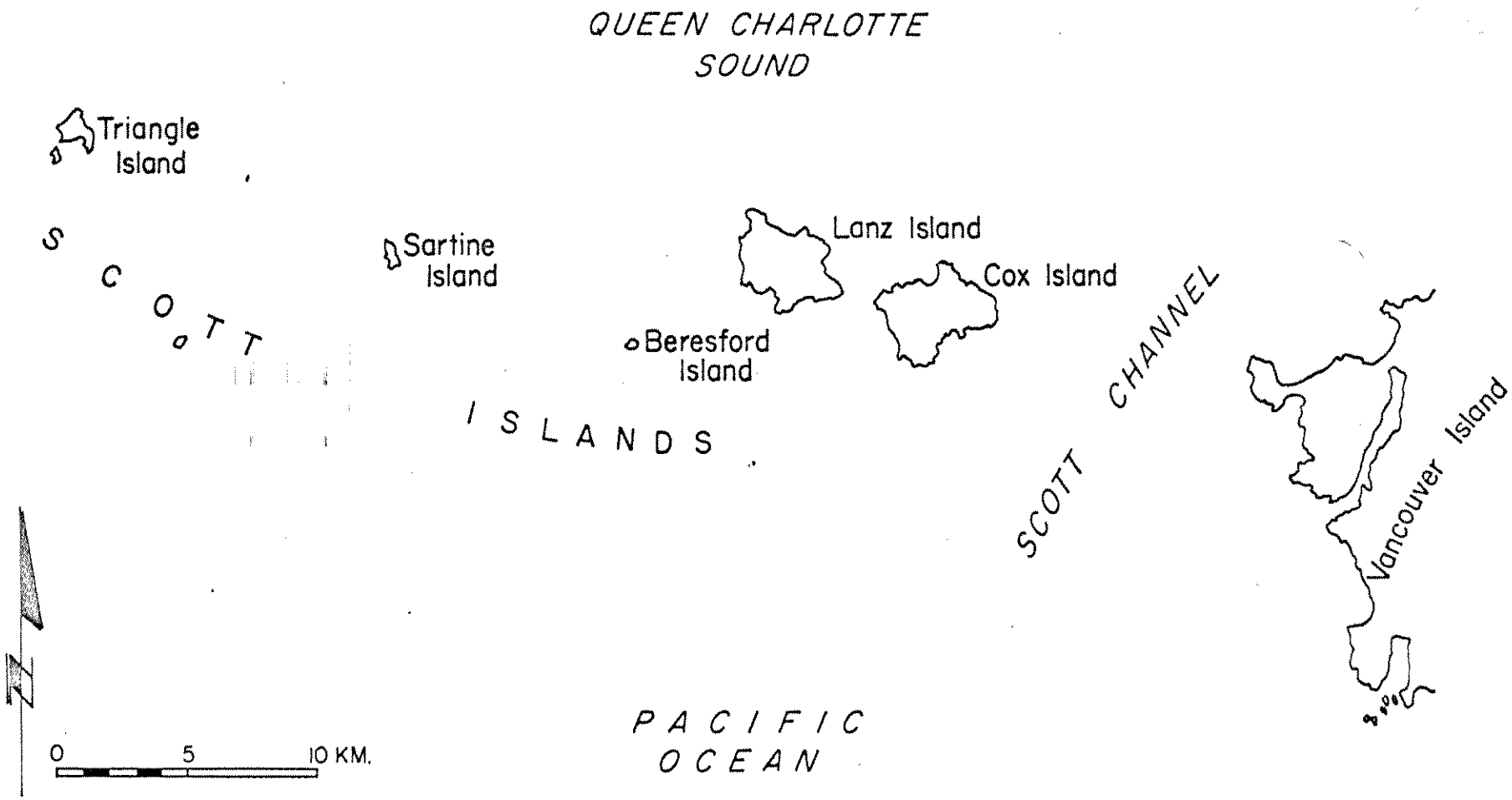
SCALE 1 : 5000


LUCY ISLAND
ANTHONY ISLAND
BYERS ISLAND
TRIANGLE ISLAND
SARTINE ISLAND
REID AND STORM ISLANDS
PINE ISLAND
BUCKLE AND TREE ISLETS
SOLANDER ISLAND
CLELAND ISLAND
RHINOCEROS AUKLET
TUFTED PUFFIN
100 - 500
500 - 1000
1000 - 5000
5000 - 10000
10000 - 20000
20000 - 50000
BREEDING PAIRS
SCALE :
KM
0 20 60 100 140
KM


QUEEN CHARLOTTE
SOUND
Triangle
Island
SCOTT
ISLANDS
Sartine
Island
Beresford
Island
Lanz Island
Cox Island
SCOTT CHANNEL
Vancouver Island
PACIFIC
OCEAN
0
5
10 KM.

Appendix 2. Weight of Rhinoceros Auklet chicks, Triangle Island, 1976.

Age in days	No. birds weighed	Weight in grams	
		Mean	Range
0	12	56.8	47 - 63
1	14	52.8	41 - 59
2	21	54.2	41 - 63
3	21	57.1	46 - 69
4	20	64.2	52 - 85
5	19	72.9	56 - 82
6	21	80.5	61 - 85
7	21	81.5	65 - 97
8	19	90.1	76 - 111
9	20	102.6	77 - 132
10	23	109.4	81 - 133
11	19	116.8	95 - 142
12	15	124.3	96 - 140
13	16	137.9	107 - 168
14	16	144.9	117 - 172
15	14	151.1	113 - 193
16	13	151.1	129 - 176
17	12	165.1	142 - 186
18	10	163.6	121 - 215
19	11	176.3	136 - 215
20	12	188.7	124 - 216
21	9	196.6	128 - 226
22	9	202.7	133 - 247
23	10	220.6	183 - 253
24	7	205.6	222 - 238
25	6	214.0	159 - 246
26	4	218.0	143 - 257
27	5	204.8	158 - 255
28	3	176.7	171 - 286
29	3	178.3	153 - 204
30	4	195.8	178 - 220
31	4	197.8	187 - 234
32	4	236.3	179 - 308
33	3	290.0	157 - 318
34	6	238.2	171 - 299
35	6	238.7	175 - 325
36	5	255.0	174 - 332
37	5	250.0	187 - 319
38	4	281.3	251 - 325
39	2	287.5	274 - 301
40	2	291.0	288 - 294

Age in days	No. birds	Weight in grams	
		Mean	Range
41	4	291.5	283 - 296
42	3	282.3	271 - 290
43	3	292.0	282 - 298
44	2	293.0	276 - 310
45	3	298.7	287 - 295
46	3	290.3	286 - 296
47	4	290.5	285 - 302
48	3	299.3	286 - 308
49	4	295.3	279 - 324
50	3	290.7	266 - 305
51	3	297.7	282 - 308
52	4	287.0	267 - 321
53	2	295.0	282 - 308
54	3	281.0	233 - 319