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A Comparison of the Breeding and Feeding Ecology
of Pigeon Guillemots at Naked and Jackpot Islands
in Prince William Sound, Alaska

Results of the 1995 field season

APEX Component 95163F

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1011 East Tudor Road
Anchorage, Alaska 99503

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STUDY HISTORY

The field work for Restoration Project 95163F was conducted during the summer of 1995. A similar effort was made in 1994 as Project 94173. Previous related projects have been funded by the Trustee Council. Bird Study Number 9 (Oakley and Kuletz 1994), begun in 1989 immediately after the oil spill, compared various population and reproductive parameters of pigeon guillemots before (Oakley and Kuletz 1979, Kuletz 1981, 1983, Oakley 1981) and after the spill. Also, Project 93034, an extensive survey of pigeon guillemot colonies throughout Prince William Sound, was conducted during the summer of 1993 (Sanger and Cody 1994).

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APPENDIX

A Comparison of the Breeding and Feeding Ecology of Pigeon Guillemots at Naked and Jackpot Islands in Prince William Sound, Alaska

INTRODUCTION

The pigeon guillemot (*Cepphus columba*) is a pursuit-diving seabird that forages mostly in nearshore waters about 10-30 m deep (Storer 1952, Ewins 1993). Adults feed primarily on benthic fish and invertebrates, but also on schooling fish. Chicks are fed mostly fish. Guillemots nest in small scattered colonies or in solitary pairs in natural cavities along rocky shorelines. Unlike most other members of the family Alcidae, the pigeon guillemot typically lays a clutch of two eggs. The chicks are semiprecocial, usually spending about 35 to 45 days in the nest. During the daylight hours, they are fed by both parents, which return to the nest with one fish at a time in their bills.

The population of pigeon guillemots in Prince William Sound (PWS) has decreased from about 15,000 in the 1970's (Dwyer et al. ND) to less than about 5,000 in the 1990's (Agler et al. 1994, Sanger and Cody 1994). There is some evidence suggesting that this population was in decline before the *T/V Exxon Valdez* oil spill in March of 1989 (Oakley and Kuletz 1994). Over 600 guillemot carcasses were recovered after the spill, but this might represent only 10-30% of the actual number killed (Piatt et al. 1990). Based on censuses taken around the Naked Island complex (Naked, Peak, Storey, Smith, and Little Smith Islands), prespill counts (ca. 2,000 guillemots) were roughly twice as high as postspill counts (ca. 1,000 guillemots; Oakley and Kuletz 1994). Also, on Naked I., the relative decline in the numbers of guillemots was greater along oiled shorelines than along unoiled shorelines (Oakley and Kuletz 1994).

King and Sanger (1979) considered the pigeon guillemot to be one of the birds that is most vulnerable to oil spills because of its nearshore foraging habits. Several studies have reported sublethal toxic effects of oil on marine birds (Peakall et al. 1980, Peakall et al. 1982, 1983 as cited in Oakley and Kuletz 1994). Marked declines in populations of the pigeon guillemot or its congener, the black guillemot (*C. grylle*) have been attributed to oil pollution (Ainley and Lewis 1974, Asbirk 1978, Ewins and Tasker 1985).

At Naked I., adult guillemots delivered fewer schooling fish, particularly sand lance (*Ammodytes hexapterus*), to their chicks after the spill than before the spill (Oakley and Kuletz 1994). Numerous studies have shown that changes in the availability of prey species can result in widespread reproductive failure of seabirds (Vermeer et al. 1979, Anderson et al. 1982, Springer et al. 1986, Safina et al. 1988, Uttley et al. 1989, Furness and Barrett 1991; but see Burger and Piatt 1990).

Predation on eggs and chicks, not important previously on Naked I. (Oakley 1981, Kuletz 1983), has been a major factor contributing to the lower reproductive success of guillemots after the spill (Oakley and Kuletz 1994). Studies at other

guillemot colonies have related lowered productivity or emigration to the presence of mammalian predators (Asbirk 1978, Petersen 1979, Cairns 1985, Ewins 1985, 1989).

Thus, because 1) pigeon guillemots constitute an injured resource, 2) their population has been declining for some time, 3) there has been a marked change in their diet, 4) predation at the nest is more prevalent than in the past, and 5) there exist valuable prespill data for this species in PWS, they have been selected for intensive study. We studied the breeding and feeding ecology of pigeon guillemots nesting on two islands in the western part of PWS and found important differences between the two populations relative to the foraging habits of adults, diet of chicks, and the levels of predation occurring during the chick stage.

OBJECTIVES

1. Determine if availability of food is limiting reproductive success of guillemots by collecting the following kinds of data:
 - a. Measuring breeding parameters, including phenology, chick growth rates, fledging weights, and reproductive success at colonies on Naked and Jackpot Islands.
 - b. Measuring foraging parameters, including diet and provisioning rates of chicks, and location of foraging areas.
2. Determine if adult survival and recruitment are affecting the population of guillemots by banding adults and chicks.

METHODS

Study Area

Our field season extended from 1 June through 23 August 1995. Our two principal study sites were located on Naked I. and Jackpot I. in PWS (Fig. 1). Naked I. (ca. 3,862 ha) has a maximum elevation of 400 m and is part of a group of three main islands. The bays of Naked I., and the passages between it and the two neighboring islands, Peak and Storey, form an expanse of water that is less than 100 m deep. Jackpot I. (ca. 1.6 ha) has a maximum elevation of about 15 m and is located near the mouth of Jackpot Bay and the southern entrance to Dangerous Passage. The shoreline of each of these islands is characterized by low cliffs and cobble or boulder beaches; high, steep, exposed cliffs occur along portions of the eastern shores of the Naked Island group. Each is forested to its summit; the principal species of tree are Sitka spruce (*Picea sitchensis*), western hemlock (*Tsuga heterophylla*), and mountain hemlock (*T. mertensiana*). All of these islands are part of the Chugach National Forest.

Naked I., about 30 km southwest of the site where the *T/V Exxon Valdez* ran aground on Bligh Reef, was one of the first areas to be oiled (see Fig. 3, Kuletz 1994:35). Between 27 March and 2 April, 1989, portions of the eastern, northern, and northwestern shorelines were oiled. The prevailing winds moved most of the oil to the south, away from the island, but between 7 and 9 April, southerly winds brought the oil into contact with the southern and western shorelines of Naked I. again. Jackpot Island was not oiled.

Selection of Study Sites

We chose Naked I. in 1994 as one of our principal study sites and as a base of operations. This island has been used as a base camp for several previous guillemot studies (Eldridge and Kuletz 1980, Oakley 1981, Kuletz 1983, Oakley and Kuletz 1994). The two main criteria for determining the potential of a new guillemot colony as a study site were the number of breeding guillemots in that colony and the accessibility of the nest sites. Jackpot I. was the only other island that met our criteria.

Censusing: Population and Colony Attendance

Pigeon guillemot populations at Naked, Peak, Storey, Smith, and Little Smith Islands (the Naked Island complex) were censused by circumnavigating each island in a small boat at a distance of between 50 m and 100 m from the shore when the weather was good and the tides were near high. These censuses were conducted on 3 June during the same time of day (0400-1000 Alaska Daylight Time) and at the same time of year that previous censuses of the this area were made. Guillemots at Jackpot I. were also censused in early June. Also, throughout the breeding season, but mostly during the chick-rearing period, counts of the maximum number of guillemots present at a particular colony were made at 15-minute intervals whenever that colony was being monitored from a boat or a blind.

Nest Sites and Monitoring

At Naked I., we monitored those nests used in 1994 plus several new ones as well. Most were at colonies along the western shoreline. Personnel on Jackpot I. used the 1994 sample plus numerous new ones. Because of their inaccessibility or our inability to determine their contents, some of these nests were monitored only during feeding observations and were not used as part of our productivity sample. Nest sites were classified according to the type of habitat in which they occurred: tree root systems, rock crevices, or talus piles.

We checked nests frequently around hatching to determine hatch dates and then at three-day intervals until near fledging, at which time they were again checked more frequently.

Banding and Morphometrics

Some adults were caught by hand at the nest or with a mist net as they attempted to deliver food to their chicks. Adults were banded on the left foot with a USFWS metal band (bottom) and a color plastic cohort band (top), and on the right foot with a unique combination of two color plastic bands. Chicks were banded on the right foot with a USFWS metal band (bottom) and a color plastic cohort band (top) and on the left foot with a unique combination of two color plastic bands. The 1995 cohort plastic band was orange.

We measured all adults that we handled and all accessible chicks. We measured maximum wing chord and length of the fifth and outer primaries with a rule to the nearest millimeter. We weighed birds with PesolaTM spring scales (0-100 g x 1 g, 0-500 g x 5 g, and 0-1 kg x 10 g) using the scale with the greatest precision possible. Newly hatched chicks were marked on the right foot and on the down of their head with paint markers to distinguish between alpha (first-hatched) and beta (second-hatched) chicks until they were large enough to be banded.

Nesting Chronology

Only nests that were discovered during the egg stage were used to construct the nesting chronology of guillemots at Naked and Jackpot Islands. Laying dates were sometimes back-calculated from hatching dates assuming an incubation period of 32 days for the first egg and 30 days for the second egg.

Productivity

We estimated productivity from those nests found in the egg stage and followed through fledging. During the incubation stage, a nest was considered to be active and included in our sample if it contained at least one egg and if an adult was seen in that nest at least once. If we knew two eggs had been laid in a nest but saw only one chick and no sign of the other egg, we assumed that both eggs hatched and one chick died. It seems unlikely that a predator entering an active nest would take only one egg and leave the other intact. Also, based on other guillemot studies (G. Divoky, personal communication; D.L. Hayes, personal observation), the proportion of two-egg nests in which only one egg hatches is fairly low.

Productivity (chicks fledged/eggs laid) was defined as hatching success (eggs hatched/eggs laid) times fledging success (chicks fledged/eggs hatched). Thirty days is approximately the minimum time spent in the nest by guillemot chicks; the actual time is often much longer. For purposes of estimating fledging, however, any chick surviving in the nest for 30 days was assumed to have fledged. Other measures of productivity used were mean clutch size, number of chicks hatched per nest, and number of chicks fledged per nest.

Predation

Potential nest predators include the river otter (*Lutra canadensis*), mink (*Mustela vison*), northwestern crow (*Corvus caurinus*), common raven (*C. corax*), Steller's jay (*Cyanocitta stelleri*), and black-billed magpie (*Pica pica*). Bald eagles (*Haliaeetus leucocephalus*), peregrine falcons (*Falco peregrinus*), and other raptors might be predatory on adult and fledgling guillemots.

If eggs disappeared from nests between visits, we assumed that predation was the cause. If chicks too young to fledge (i.e., younger than 30 days) disappeared from nests between visits, we assumed predation was the cause only if we were reasonably certain that no chick was still in some hidden corner of the nest. In some instances, where the nest cavity was too long or labyrinthine, it was not possible to make this determination. If after repeated visits to this type of nest, we never saw the chick(s) again, we listed the cause of failure as unknown.

Chick Growth and Fledging Weights

We calculated the growth rates of chicks as the change in weight (g/d) during the linear phase of their growth, which is the period eight to 18 days after hatching (Koelink 1972). Two methods were used to calculate growth rate. In the first (i.e., difference method), the difference between the first and last weights for a given chick during this period was divided by the numbers of days between the two measurements. In the second (i.e., slope method), a linear regression was done on all weights obtained from a given chick within this period to determine the slope (growth rate). Fledging weight was assumed to be the last recorded weight of a chick that was measured within 24 hours of fledging at Naked I. and within 72 hours of fledging at Jackpot I.

Chick Provisioning and Diet

Either from blinds or from boats we observed adult guillemots bringing food items to their chicks throughout the chick-rearing period. Feeding watches ranged from 0.5 h to 18 h; shifts lasted up to 4.5 h. Usually only one observer was in the blind at a time. Binoculars and spotting scopes were used to identify prey items in the bills of guillemots to the lowest possible taxon or "type" of prey. When time and visibility permitted, we also estimated the length of the prey item as a multiple of the guillemot's bill to the nearest half bill length. We recorded the time of each delivery and the number of the nest to which the prey was delivered, as well as how long the adult first remained on the water with the fish before delivering it. We also obtained information about chick diet by retrieving fish found in the nests or by intercepting fish at or near the nest entrance with a mist net.

To test whether deliveries were distributed more or less evenly throughout the daylight hours, the day was divided into three approximately equal periods: early (0600-1100), mid-day (1100-1700), and late (1700-2200). Although a few deliveries occurred very early and very late, when it was too dark to make reliable observations, the period used for analysis was truncated at both ends in accordance with the times listed above. Using a Chi-square goodness-of-fit test, the actual number of deliveries observed during each of the three periods was compared to the expected number of deliveries in those periods if they had been distributed evenly throughout the day.

Provisioning rates were determined for chicks of 15-35 days of age at both one- and two-chick nests. Only deliveries recorded during continuous observations made between 0600 and 2200 were used in determining delivery rates.

2 Sampling of Fish

We occasionally sampled waters (< ca. 15 m) around Naked I. with fish traps set on the bottom or occasionally above it to obtain specimens of fish for analysis of energy content or to aid us in identifying those in the bills of guillemots. Beach seine sets were made at several locations around Naked I. Seines were made at or around high tide at beaches having a substrate that would prevent snagging the net. We measured wet weight and standard length of all fish caught in the traps and from samples taken from the beach seine catches.

2 Data Analysis

Comparisons between Naked and Jackpot Islands or between years were made with two-tailed t-tests, 2 x 2 contingency tables analyzed with a G-test and corrected for continuity, Chi-square tests, and ratio estimation with Z statistics. The level of significance was set at $\alpha = 0.05$. All means are reported as the mean plus or minus one standard deviation.

RESULTS

Censusing

In 1995, 887 pigeon guillemots were counted around the shorelines of the Naked Island complex during the census on 3 June (Table 1). About 80 guillemots were counted around Jackpot I. in early June. Maximum counts of pigeon guillemots usually occurred in the early morning hours, shortly after first light. The birds were first detected in rafts a considerable distance from shore, then gradually moved closer to the colony. The maximum number of guillemots counted at two of the Naked I. colonies was as follows: Nomad (30 on 26 July) and Tuft (38 on 14 July).

Nesting Chronology

Nesting chronology at Naked and Jackpot Islands was similar in 1994. Nesting chronology at Naked I. in 1995 was similar to that of 1994. Dates for Naked I. in 1995 are as follows: median laying (1 June, range 20 May to 24 June); median hatching (1 July, range 21 June to 26 July); and median fledging (10 August, range 23 July to 25 August). The mean number of days that chicks spent in the nest was 39.4 ± 3.3 d ($n = 21$, range = 34 - 45 d) at Naked I. and 38.0 ± 1.9 d ($n = 11$, range = 35 - 40 d); the difference was not significant ($t = 1.264$, $df = 30$, $P > 0.20$).

Productivity

The mean clutch size was 1.77 ± 0.43 ($n = 39$) on Naked I. and 1.79 ± 0.41 ($n = 38$) on Jackpot I.; the difference was not significant ($G = 0.003$, $df = 1$, $P > 0.95$). Of a total of 69 eggs (39 clutches; 30 with 2 eggs, 9 with 1 egg) on Naked I., 55 hatched, 2 were incubated but failed to hatch, 7 were abandoned, and 5 were probably taken by predators. Of a total of 68 eggs (38 clutches; 30 with 2 eggs, 8 with 1 egg) on Jackpot I., 45 hatched, 17 were abandoned, 4 failed to hatch, and 2 were probably taken by predators. Of a total of 55 chicks monitored on Naked I., 30 fledged, 7 were found dead in or near the nest, 1 was killed by a magpie, 9 were probably taken by predators, and the fate of 8 others is unknown. Of a total of 45 chicks monitored on Jackpot I., 25 chicks fledged, 7 were found dead in the nest, 2 were probably taken by predators, and the fate of 11 others is unknown.

Hatching success was 0.80 ($n = 69$) at Naked I. and 0.66 ($n = 68$) at Jackpot I.; it was not significantly different between islands ($Z = 1.38$, $P = 0.0838$), nor between years at each island (Naked I., $Z = 1.15$, $P = 0.1251$; Jackpot I., $Z = 1.27$, $P = 0.1020$). Fledging success was 0.54 ($n = 55$) at Naked I. and 0.56 ($n = 45$) at Jackpot I.; it was not significantly different between islands ($Z = 0.09$, $P = 0.4641$). Fledging success was significantly different between years at Jackpot I. ($Z = 1.89$, $P = 0.0294$), but not at Naked I. ($Z = 0.26$, $P = 0.3974$).

Twenty-one of 39 nests (54%) at Naked I. produced at least one fledgling compared to 20 of 38 nests (53%) at Jackpot I. The difference between the proportion of successful nests was not significant ($G = 0.015$, $df = 1$, $P > 0.90$) between the two islands.

Clutch size, hatching success, and fledging success are compared for nine years at Naked I. and two years at Jackpot I. in Figures 2 - 4. Weighted averages for all years at Naked I. are given inside the box in each figure. Weighted averages from numerous studies in British Columbia, Washington, and Oregon (see Ewins 1993 and references therein) are also given for clutch size and fledging success. It is important to note that the definition of fledging used in these other studies may not be the same as ours (i.e., chicks surviving to 30 days).

Predation

In 1995, there was less direct evidence of predation on Naked I., but the disappearance of chicks too young to fledge strongly suggested that predation was responsible. The same was true for Jackpot I., although the nature of the nests (mostly cavernous tree root systems) made it more difficult to determine with certainty that the chicks were not present.

A magpie was observed flying out of a nest containing the still-warm carcass of a young guillemot chick on Naked I. Magpies and crows were routinely seen following fish-carrying guillemots up to, and occasionally into, the guillemot nests on Naked I. At Jackpot I., a crow forced a guillemot chick out of its nest, over a ledge, and into the water; the chick was not seen again. A crow was seen entering a nest on Jackpot I. containing two chicks, then remained inside for approximately five minutes; one chick was missing the next day. Largely intact, empty eggs with oval-shaped holes (ca. 25 mm long) or egg shell fragments were found outside the entrances of nests on both islands. Piles of feathers were found on Jackpot I. associated with apparent river otter scat. On Naked I. two chicks disappeared from a nest that was just above a river otter latrine site. The same nest was definitely depredated in 1994 (blood feathers and a chewed-off leg from a guillemot were found just outside that nest). The nearly constant alarm calling by guillemots when crows, magpies, or river otters were nearby strongly suggests that guillemots perceived these animals as threats. All three of these potential predators were seen often at both islands.

Chick Growth and Fledging Weights

Using the difference method, the mean growth rate of chicks was 19.5 ± 4.4 g/d ($n = 13$, range = 11.8 - 26.7 g/d) at Naked I. and 17.4 ± 2.7 g/d ($n = 16$, range = 12.44 - 22.6 g/d) at Jackpot I.; this difference was not significant ($t = 1.550$, $df = 27$, $P > 0.10$; see Table A1 for a comparison of growth rates from previous years based on this method). Using the slope method, the mean growth rate of chicks during the linear phase of their growth was 19.5 ± 5.0 g/d ($n = 13$, range = 10.3 - 26.8 g/d) at Naked I. and 16.7 ± 2.8 g/d ($n = 15$, range = 11.9 - 22.2 g/d) at Jackpot I.; this difference was not significant ($t = 1.867$, $df = 26$, $P > 0.05$).

The mean peak weight of chicks was 480 ± 65 g ($n = 22$, range = 350 - 612 g) at Naked I. and 473 ± 45 g ($n = 10$, range = 392 - 521 g) at Jackpot I.; this difference was not significant ($t = 0.321$, $df = 30$, $P > 0.50$). The mean fledging weight of chicks was 455 ± 74 g ($n = 22$, range = 311 - 561 g) at Naked I. and 468 ± 43 g ($n = 10$, range = 392 - 521 g) at Jackpot I.; this difference was not significant ($t = 0.485$, $df = 30$, $P > 0.50$; see Table A2 for a comparison of fledging weights from previous years).

Chick Provisioning and Diet

Collectively, guillemots delivered fish to their chicks throughout the daylight hours at Naked and Jackpot Islands (Fig. 5). Neither distribution was significantly different from a theoretical even distribution of deliveries made throughout the day (Naked I., $\chi^2 = 0.435$, $df = 2$, $P > 0.75$; Jackpot I., $\chi^2 = 0.685$, $df = 2$, $P > 0.50$). Feeding rates varied considerably among nests. At any particular nest, there were periods of several hours in which no deliveries were made. The tidal cycle had no significant effect on the rate of deliveries. The time after sunrise or time before sunset also had little or no effect on the rate of deliveries. Delivery rates to guillemot nests at Naked and Jackpot Islands for 1994 and 1995 are shown in Figure 6.

The diet of pigeon guillemot chicks at the two islands was considerably different (Fig. 7). Schooling fish accounted for about 22% of the chick diet at Naked I. and about 41% at Jackpot I. The fact that three capelin and no herring were among the 26 fish recovered from or intercepted at guillemot nests suggests that the herring/smelt category may have been dominated by capelin at Naked I. At Jackpot I., seven herring and no capelin were among the 22 fish similarly obtained; herring almost certainly dominated the herring/smelt category at this island. The other fish in these two samples are listed in Table 2. At each island there were also marked differences between years. At Naked I., the proportion of sand lance delivered was the same in both years, but that of herring/smelt and gunnells increased, while that of gadids decreased considerably. At Jackpot I., the proportion of sand lance, gunnells, and pricklebacks increased, while that of herring/smelt and gadids decreased.

Foraging

Pigeon guillemots at Naked I. sometimes foraged directly in front of their colony in water less than 15 m deep, but usually foraged in nearby bays or on the broad, shallow-water (< 25 m deep) shelf surrounding Naked I. Guillemots were rarely seen foraging in the immediate vicinity of Jackpot I., but instead flew toward shallower areas near the mouths of Jackpot Bay or Icy Bay or the southern entrance to Dangerous Passage (each ca. 2-4 km distant), presumably foraging there. Guillemots carrying fish were observed returning to the colony at Jackpot I. from the general direction of these areas.

Fish Types Caught in Traps and Seines

Shrimp (mostly *Pandalus danae* and *Eualus gaimardii*) were the most frequently taken animal in the fish traps at Naked I., but were not counted because they were never seen being delivered to guillemot nests in 1994 or 1995. Of 131 fish caught in the traps in 1995, the relative proportions of each type were as follows: 38 arctic shannies (*Stichaeus punctatus*), 30 pricklebacks (*Lumpenus*

fabricii), 20 crescent gunnels (*Pholis laeta*), 25 sculpins (three species), 8 walleye pollock (*Theragra chalcogramma*), 4 Pacific cod (*Gadus macrocephalus*), four greenlings (three species), and two northern ronquils (*Ronquilus jordani*). Of 36 fish caught in traps around Jackpot I. in 1995, the relative proportions of each type were as follows: 12 arctic shannies, 8 northern ronquils, 5 crescent gunnels, 2 Pacific cod, 2 pricklebacks (*Lumpenus* spp.), 2 cockscombs (*Anoplarchus* spp.), and one sculpin.

Few benthic fish were caught with the beach seines. Either herring or sand lance or sometimes both made up the bulk of the beach seine sets at most locations (Table 3; see Figure A1 for locations of beach seine sets).

DISCUSSION

Censusing

Early season counts of pigeon guillemots in the Naked Island complex suggest that their population has decreased considerably from 1978 and 1979. The low counts for Naked I. and the Naked Island complex in 1995 may not reflect the true numbers of guillemots in the area; replicate counts may have resulted in higher numbers. Vermeer et al. (1993a) reported that the optimal time to determine the population of nesting guillemots was at high tide in the morning. Observed colony attendance patterns of guillemots at Naked I. in 1994 indicate that the time of day is extremely important when planning guillemot censuses (Hayes 1995). Replicate counts at the appropriate time of day and tidal cycle would increase our confidence in the actual number guillemots at Naked I.

Productivity

The ideal and most straightforward method of calculating productivity is from a sample of known nests that are followed from before egg-laying through fledging. We did have known nests on both islands that had been found in 1994, but because of when we arrived at the study sites (1 June, when some eggs had already been laid), we had to include nests monitored from incubation through fledging as well. It is important to note that the nests used for measuring productivity do not constitute a "sample" in the true sense of the word. On Naked I., they represent all of the nests that we were able to find and then reach, not a random sample of nests on the island. We can only assume that they are fairly representative of the island as a whole. On Jackpot I., because we believe that we have found most of the nests on the island, they constitute the actual population.

Although the difference was not significant, hatching success was lower at both islands in 1995 than in 1994, especially at Jackpot I. This is likely the result of increased disturbance at the colony; researchers were present on this small island almost every day during the incubation and early hatching period looking

into nests to determine hatch dates or searching for new nests. Several investigators at other guillemot colonies have observed reduced productivity apparently associated with human disturbance (Bergman 1971, Cairns 1980, Vermeer et al. 1993b). Still, the values reported here for productivity of the pigeon guillemots at Naked and Jackpot Islands are well within the range of values reported for this species in other areas of its range (see Ewins 1993 for a review).

Predation

Oakley and Kuletz (1994) noted that the primary difference in productivity of pigeon guillemots on Naked I. that they observed following the oil spill was lowered nesting success, which was the result of nest predation during the **chick stage**. Increased predation pressure relative to that in the past appears to be a continuing problem on Naked I. Its detrimental effects on guillemot productivity should not be underestimated.

Although we have proof only of avian predation, we strongly suspect that mammalian predators are responsible for some of the disappearances of eggs or young guillemot chicks. River otters were seen frequently in the vicinity of our study colonies in both years and are the most likely mammalian predator, but **mink** may also be involved. On Naked I. in 1994, we found carcasses of guillemot chicks with the heads chewed off, suggesting that some kind of mustelid is likely responsible for the predation. Ewins (1985) reported that on the island of Mousa in Shetland, otters (*Lutra lutra*) killed both chicks and incubating adults, and that decapitated carcasses were a sure sign of these predators. Ewins also noted that there were few nests inaccessible to them. Likewise, many of the nests on Naked I., including some of those in rock crevices, and all of the nests on Jackpot I. are probably accessible to otters. Few, if any, nest sites would be inaccessible to the smaller and more agile mink. Crows and magpies are the likeliest avian predators on eggs and chicks. Other studies indicate that crows are a major source of egg predation and sometimes take young chicks as well (Emms and Verbeek 1989, Ewins 1989).

Whatever predators are responsible for taking eggs and chicks on Naked I., the increased predation pressure there might have caused breeding guillemots to move elsewhere. It is possible that guillemots in PWS are emigrating from some colonies on the mainland and large islands like Naked I. to smaller ones like Jackpot I., where ground predators have not become permanently established. Emigration of black guillemots from colonies in Sweden and Iceland have been attributed to predation by mink (Asbirk 1978, Petersen 1979). The principal factor controlling local distributions in Scotland appears to be introduced mammals (M.L. Tasker, personal communication).

River otters and mink typically forage in the intertidal zone. A study that compared the diet of river otters in two areas of PWS before and after the spill showed that there were significant declines in species richness and diversity

(mostly bony fish and mollusks) in otter diets on the oiled area compared to the unoiled area (Bowyer et al. 1994). Another study, also conducted in PWS, clearly indicated that oil contamination was affecting the health of river otters up to two years after the spill (Duffy et al. 1993, 1994). Contamination of the normal intertidal food supply of river otters and mink might have ultimately caused some of these predators to switch to other types of prey, including guillemot chicks.

Adults, and especially fledglings, are probably sometimes taken by large raptors. Bald eagles are known predators of adult guillemots in British Columbia (Vermeer et al. 1989 as cited in Ewins et al. 1993). Beaks of guillemots were found beneath an eagle's nest on Naked I. during a previous study (K. Kuletz, personal communication). We often witnessed a change in the guillemots' behavior when an eagle flew into the area. The guillemots' reactions to the presence of bald eagles (e.g., flushing, moving farther offshore, alarm calling, and diving) suggest that they perceive this potential predator as a real threat.

Chick Growth and Fledging Weights

In 1995, our estimates of growth rates during the linear phase of growth (Naked I., 19.5 g/d; Jackpot I., 17.4 g/d) were similar to those of Oakley and Kuletz (1994) at Naked I. (range = 16.6 - 23.8 g/d), as were our estimates of fledging weights. Growth rates were also similar to those reported by Koelink (1972) for Mandarte Island (15.9 g/d) and Ainley and Boekelheide (1990) for the Farallon Islands (16.5 g/d).

Both methods of estimating chick growth indicated that those on Naked I. grew faster than those on Jackpot I. in 1995. However, in 1994 our data suggested that chicks on Jackpot I. grew faster and fledged at greater weights than those on Naked I. It is important that caution be used when making comparisons based on these data. The sample sizes were small in both years, especially for growth rate in 1994. Also, our estimates of fledging weight in 1995 were far superior to those of 1994 (there was a significant difference between islands in 1994 but not in 1995).

Chick Provisioning

Members of the genus *Cepphus* typically lay two eggs. Most other alcids lay only a single egg, but the near-shore foraging habits of guillemots probably account for their ability to raise two chicks. Mehlum et al. (1993) maintain that long-distance foraging by black guillemots, which typically raise two-chick broods and have a **high wing loading relative** to most other seabirds, is too energetically demanding and might exceed their maximum sustainable working level. Koelink (1972) argues this same point for chick-rearing pigeon guillemots. In his study, although artificial broods of three were successfully raised to fledging, there was a proportional decrease in the amount of food delivered per chick throughout the nestling period. In black guillemots also, artificial triplets have been successfully

raised but with differing results regarding fledging weights. In Denmark, the mean fledging weight of triplets was higher than that of chicks from normal broods (Asbirk 1979 as cited in Harris and Birkhead 1985). In Iceland, triplets fledged at lower mean weights than chicks from normal broods (Petersen 1981 as cited in Harris and Birkhead 1985).

Our measured rates of food deliveries to individual nests (range = 0.31 - 1.38/nest/hr at one-chick nests; range = 0.38 - 1.56/nest/h at two-chick nests) are comparable to those of other studies of *Cepphus* guillemots (Thoresen and Booth 1958, Bergman 1971, Asbirk 1979 as cited in Harris and Birkhead 1985, Cairns 1981, 1987, Kuletz 1983). Without a knowledge of the weight of each prey item delivered, a comparison of provisioning rates (i.e., g/h/chick) is impossible. Furthermore, fish vary considerably in their composition of lipids, proteins, and carbohydrates. Fish higher in lipids have a higher energy content, which can be particularly relevant to the reproductive success of the seabirds feeding upon them. Also, the lipid content even within a single species of fish can vary widely with season, sex, reproductive status, and age class (D. Roby, personal communication). It is almost impossible to accurately estimate the weight of prey items delivered to chicks noninvasively. Measuring the actual energy content of the prey cannot be done by noninvasive means; prey must be intercepted and analyzed in the laboratory. Obviously, this cannot be done repeatedly at the same nest without affecting the food intake of the chicks involved.

Foraging

The maximum diving depth of black guillemots is about 50 m (Piatt and Nettleship 1985). Assuming that the pigeon guillemot has similar diving capabilities, it is restricted to waters no deeper than this when feeding on benthic prey items. The pigeon guillemots breeding on Naked I. generally forage around the island, usually within about 600 m of the shore and in water shallower than 25 m (Kuletz 1983). There is a broad, shallow-water shelf surrounding Naked I. and the neighboring islands (see Fig. 14 in Hayes 1995), which allows guillemots to forage nearby. On Jackpot I., there is very little shallow water immediately around the island (see Fig. 15 in Hayes 1995), and thus guillemots breeding there fly greater distances to obtain food for their chicks. These birds apparently find it necessary to fly several kilometers to Jackpot Bay or Icy Bay or toward Dangerous Passage to find food for their chicks instead of trying to forage around Jackpot I.

Chick Diet

In 1994 and 1995, the most obvious difference in the diet of chicks at Naked and Jackpot Islands was in the proportion of schooling fish, especially herring (Fig. 7). Interestingly, ~~herring or smelt~~ were not noted in the diet of chicks on Naked I. in 1979 or 1980, then accounted for about 16% and 23% of the diet in 1981 and 1989, respectively, and only about two percent in 1990 and 1994 (Fig. 8,

Oakley and Kuletz 1994, Hayes 1995). In the years 1979-1981 Pacific sand lance were the single largest component (42%) of the diet, while in the four years 1989-1990 and 1994-1995, sand lance accounted for a much smaller fraction (12%) of the diet.

The proportion of schooling fish in the diet of chicks might be related to the ephemeral nature of schools of this type of fish and their presence within the foraging range of guillemots. Their capture might occur only coincidentally when behavioral factors (e.g., spawning) or oceanographic factors (e.g., currents, upwelling) bring these prey into shallower nearshore waters. However, the relative increase in the proportion of gadids, presumably caught by the guillemots on or near the bottom, could indicate a pronounced shift in the ecosystem. The fact that gadids did not show up in fish traps in appreciable numbers (Kuletz 1983, Oakley and Kuletz 1994) until 1994 lends support to this hypothesis.

Because of the relatively large proportion of fish that could not be identified, especially at Naked I., the values reported above represent minimum percentage contributions of those types of fish to the total delivered. Those fish listed as unidentified were done so usually because of one of three reasons: 1) the fish was too far away; 2) it was too dark; 3) the observer did not see it for long enough; and 4) the observer got a good look at the fish but it was of a type not recognized. Because the last category was encountered infrequently, there was no distinction made between any of the above four categories when data was being recorded. There is probably a slight bias in the unidentified category in that it probably contains proportionally fewer gunnells (and perhaps pricklybacks); these fish were the easiest to identify, especially under less than optimal conditions.

Fish Types Caught in Traps and Seines

The proportion of pricklybacks caught in the fish traps is perhaps not representative of their distribution; they were rarely caught until we started "fishing" for them by setting the traps in a particular spot among some beds of eelgrass, where these fish seemed particularly abundant. Trap sites were not selected randomly, the traps were not set or checked systematically, and baits may have differed in their relative attractiveness to the different types of fish. Although arctic shannies were the most common fish caught in the traps, they were infrequently seen being delivered to guillemot chicks and were not among the samples obtained at the nests..

Beach seine sets were made at high tide and at beaches having substrates not likely to snag the net as it was pulled in. The operation was not always smooth because of snagging or other problems and some schools may have escaped before we closed the net. Few benthic fish were caught in the nets, either because they could escape under the net, or because the beaches we selected were not the appropriate habitat. Therefore, results of beach seines should not be considered quantitative.

CONCLUSIONS

There have been marked changes in the diet of guillemot chicks on Naked I. Sand lance were the single most important species in the diet of pigeon guillemot chicks on Naked I. in the late 1970's, but accounted for only about ten percent of the chick diet in 1994 and 1995. Likewise, gadids are now more prevalent in the diet than they were. The overall population of pigeon guillemots at Naked I. has decreased from about 2,200 in 1979 to about 1,300 today. The percent of breeding birds among these also appears to have decreased. However, Jackpot I. currently supports a dense, thriving colony of guillemots; over 40% of the chick diet is schooling fish, mostly herring. The decline in many guillemot populations in PWS and their failure to recover may be related to the apparent decline in the abundance of sand lance. The marked shift in the diet of guillemots from predominantly schooling to benthic fish may be linked to some key change in the ecosystem that is affecting other marine birds and mammals in PWS.

Pigeon guillemots appear to be opportunistic foragers and seem to prefer schooling fish when available. When these fish are abundant, foraging at dense schools close to shore is probably more efficient than searching for solitary demersal fish over large areas of the bottom. Because their foraging range is limited by their nearshore habits, the presence of schooling fish, especially sand lance or herring, may be essential for maintaining productive colonies of guillemots in Alaska.

?
singh
white p. on
foraging
flocks?

Predation on eggs and chicks is still an important factor that is affecting the reproductive success of pigeon guillemots on both islands, but especially on Naked I. Its effects, and those of observer disturbance, should be considered when making comparisons of productivity between these two islands.

Future work on pigeon guillemots in PWS should focus on 1) determining what animals are responsible for the increased levels of predation at the nest site on Naked I., 2) marking chicks and breeding adults for estimating recruitment and adult survival, 3) censusing designated colonies on a regular basis using standardized methods, 4) diet composition and energy content of prey items as they relate to growth and productivity, and 5) proportion of schooling fish in the chick diet relative to the size of colonies.

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Table 1. Counts of pigeon guillemots during June censuses at Naked, Peak, Storey, Smith, and Little Smith Islands, Prince William Sound, Alaska, before and after the T/V Exxon Valdez oil spill. Censuses conducted between 3 and 6 June unless otherwise noted. Dashes indicate no surveys were conducted.

Year	Naked Island	Storey Island	Peak Island	Smith Island	Little Smith Island	Total
1978	1115	392	94	175	72	1965
1979	1226	495	150	301	58	2230
1980	891	--	--	--	--	--
1989 ^a	615	193	73	--	--	--
1990	729	293	102	124	31	1279
1991	755	293	102	76	35	1261
1992	586	230	87	100	23	1025
1993 ^b	385	242	94	75	32	828
1994	739	298	81	121	23	1262
1995 ^c	550	165	38	111	23	887

^aCensus conducted on 13-14 June.

^bFrom Sanger and Cody 1994 (censuses in May or June 1993)

^cIn 1994 Naked Island census was done on 30 May, Storey and Peak Islands on 31 May, and Smith and Little Smith Islands on June 1.

Note: Data from all years except 1993 and 1994 from Table 1 (Oakley and Kuletz 1994).

Table 2. Types of fish and numbers (in parentheses) recovered from or intercepted at guillemot nests on Naked and Jackpot Islands in 1995.

Naked Island (n = 26)	Jackpot Island (n = 22)
Sand lance (2) Capelin (3) Crescent Gunnel (7) Daubed shanny (1) Snake prickleback (1) Black prickleback (1) High cockscomb (1) Ribbed sculpin (1) Roughspined sculpin (1) Armorhead sculpin (1) Red Irish lord (1) Walleye pollock (1) Pacific cod (2) Northern ronquil (1) Dover sole (1) Lingcod (1)	Pacific herring (7) Crescent gunnel (2) Ribbed sculpin (1) Crested sculpin (2) Walleye pollock (6) Pacific tomcod (1) Northern ronquil (3)

BEACH SEINE CATCH NAKED ISLAND -- 1995 [seine95]

DATE	GAD	SALMON	GRN	SAN	GUN	SCU	FLA	HERRING	UNK	TOTAL (EST.)	SETS	LOCATION	
07/16/95	30	0	2	200	0	0	0	7	5	244	3	-H2	1
07/23/95	7	0	1	0	0	0	0	0	0	8	2	R-TH	2
07/23/95	0	0	10	1110	0	3	0	181	0	1304	2	MACPHER.	3
07/28/95	5	5	3	2	0	1	0		0	16	2	N CABIN BAY	4
08/16/95	2			50	0	0	0	200	0	252	1	E BOB DAY BAY	5
08/16/95	0	0		4	0	1	1	0	0	6	2	W BOB DAY BAY	6
08/16/95	1	2		14	0	4	0	0	0	21	2	MACPHER.	7
08/20/95	0	0	1	150	1	2	0	500	0	654	2	FUEL-CABIN BAY	8

Table 3

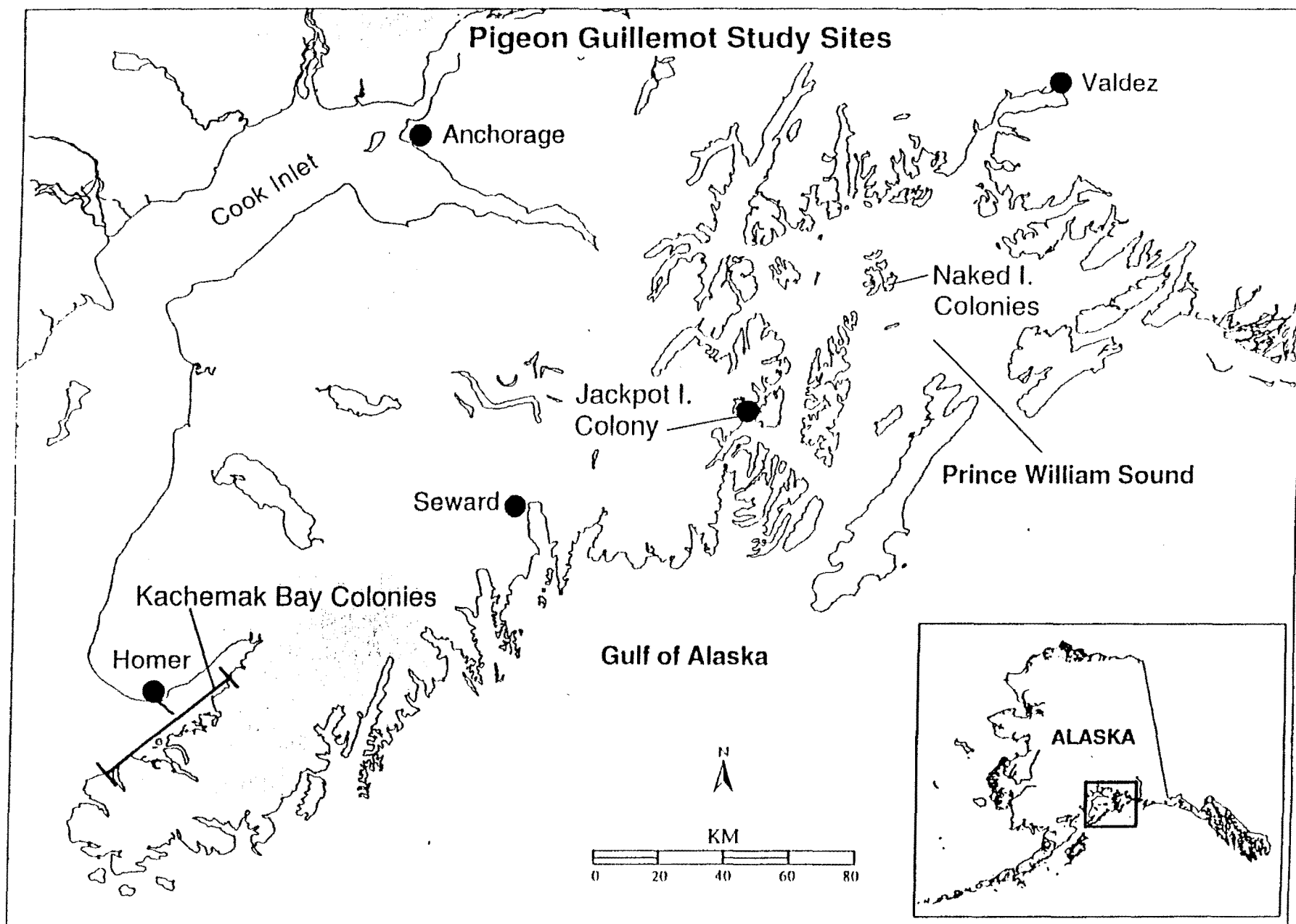


Figure 1

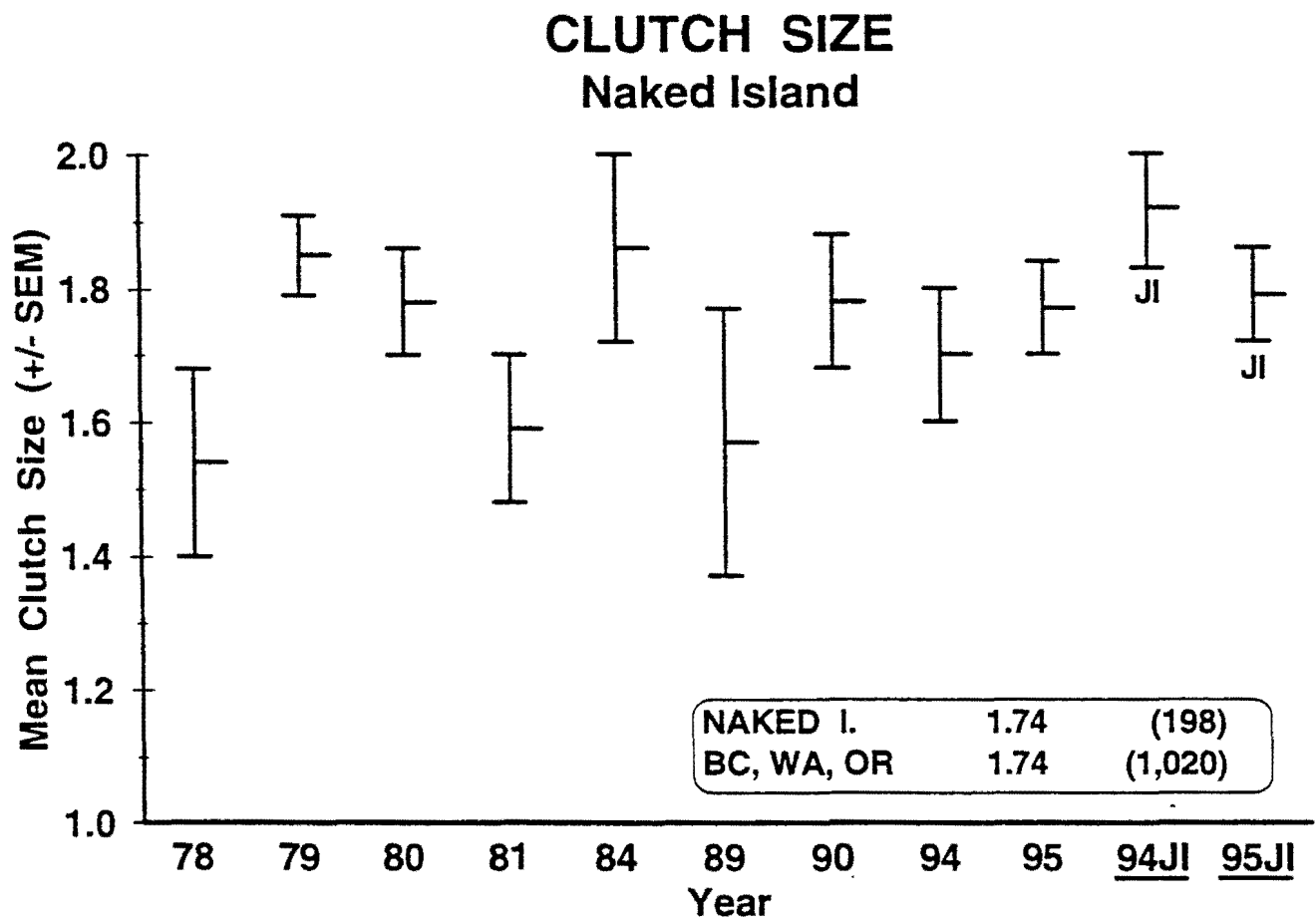


Figure 2

HATCHING SUCCESS Naked Island

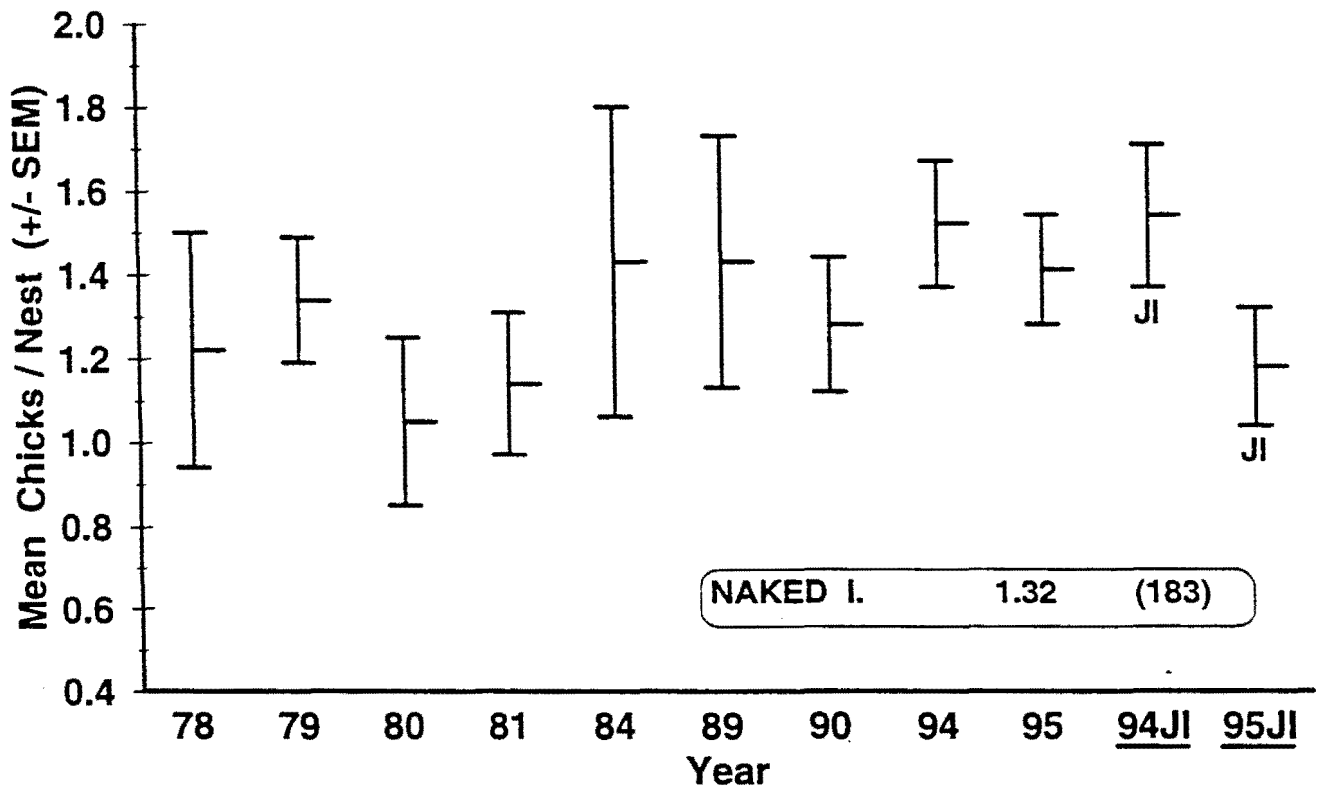


Figure 3

FLEDGING SUCCESS Naked Island

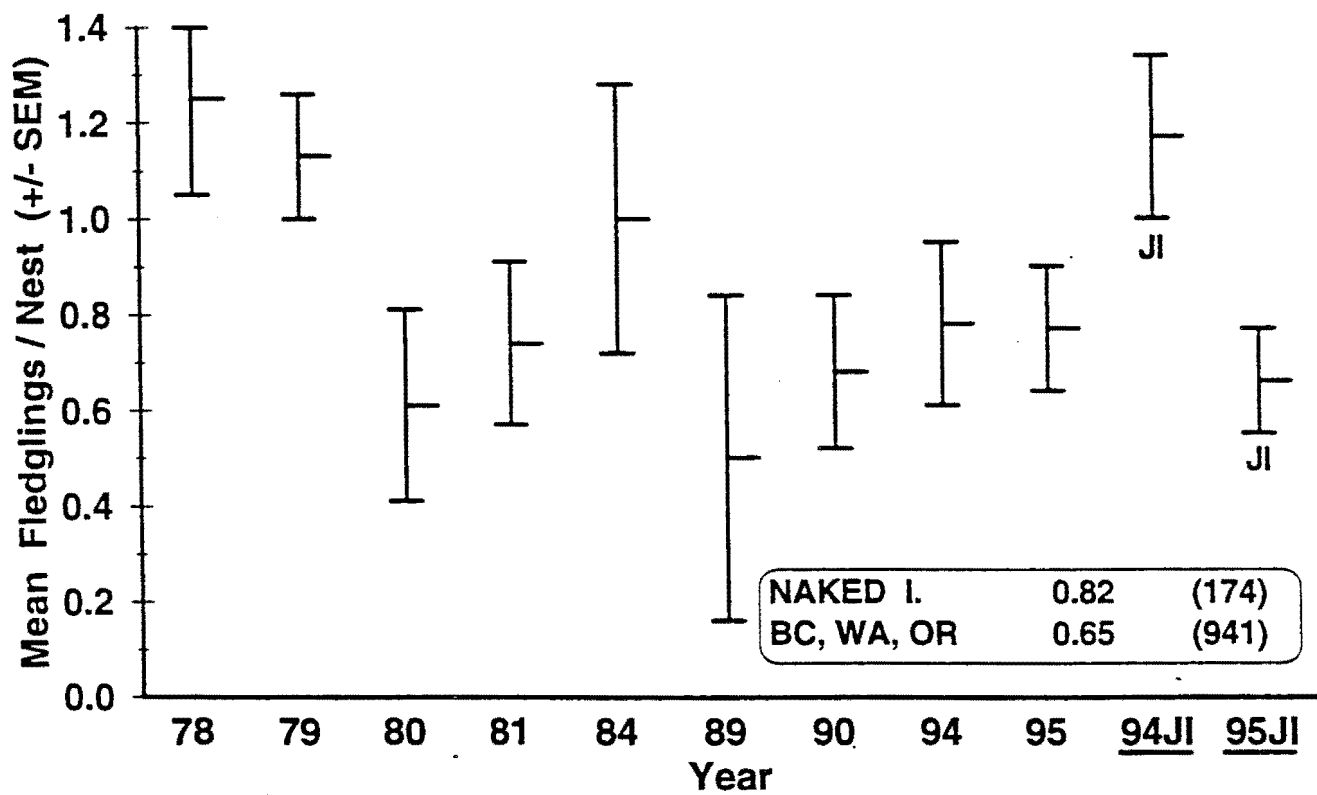


Figure 4

TEMPORAL DISTRIBUTION OF DELIVERIES

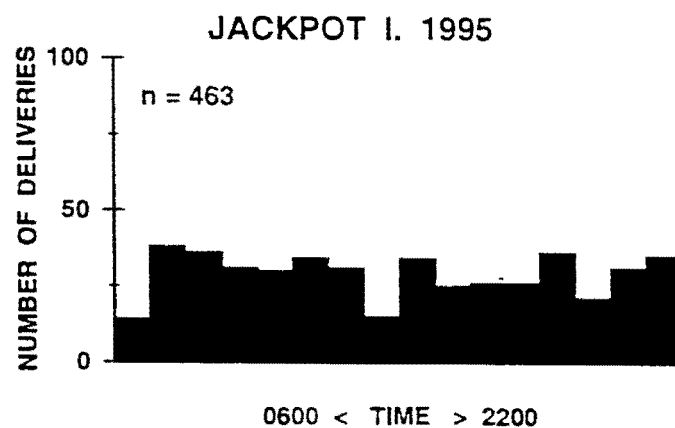
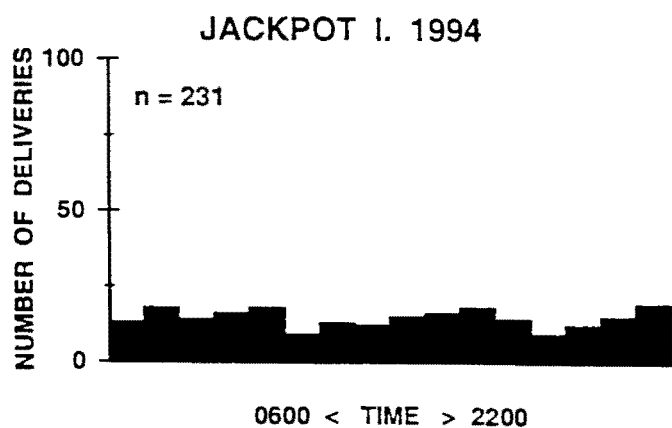
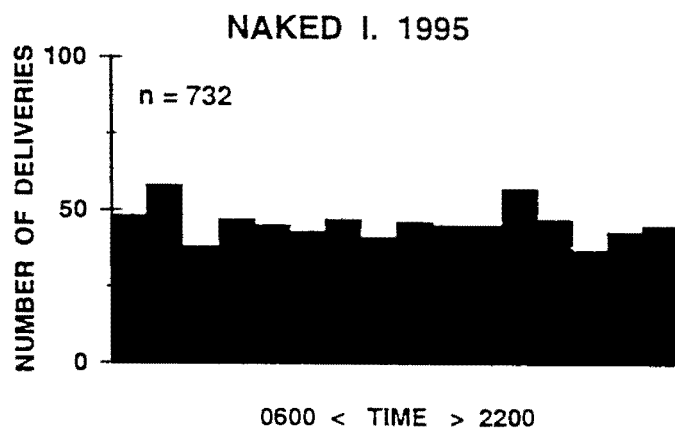
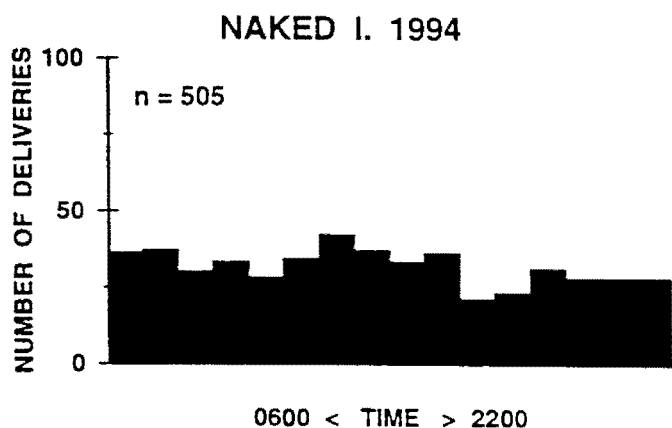
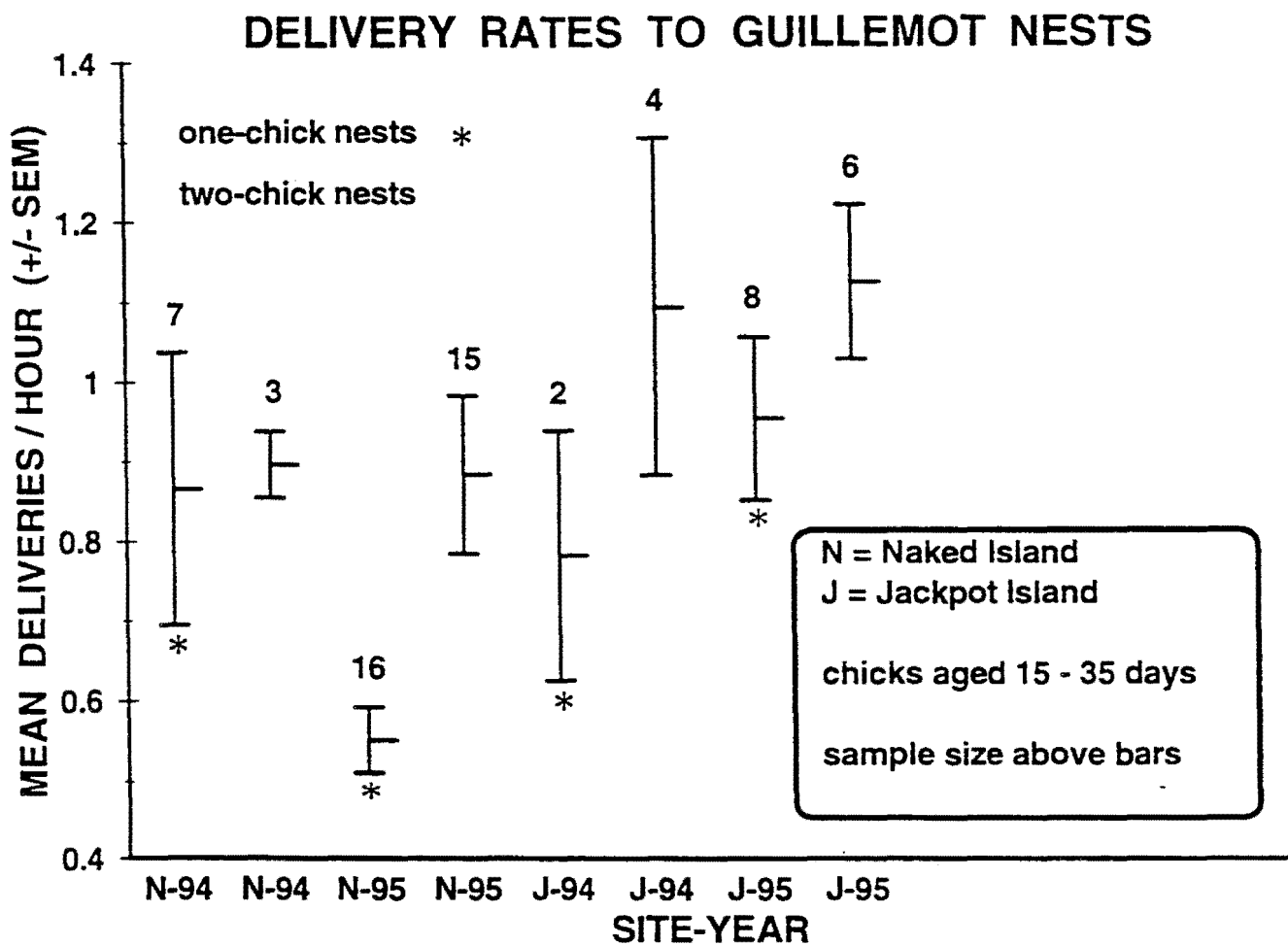


Figure 5

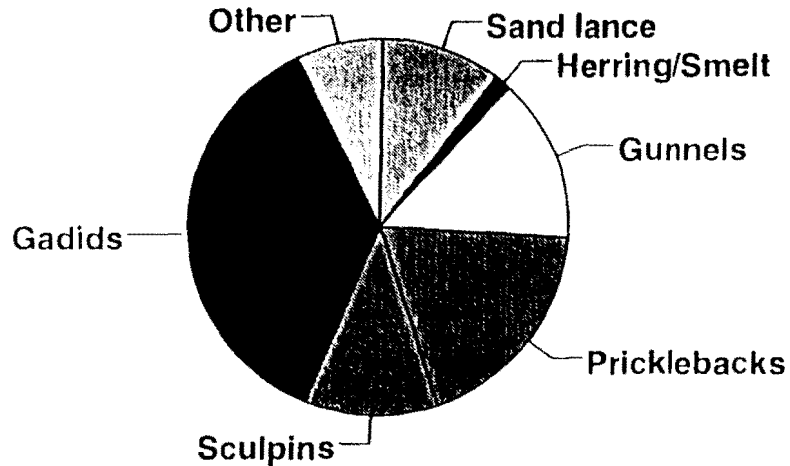


670 kJ/nest-day NI
1230 kJ/nest-day JJ

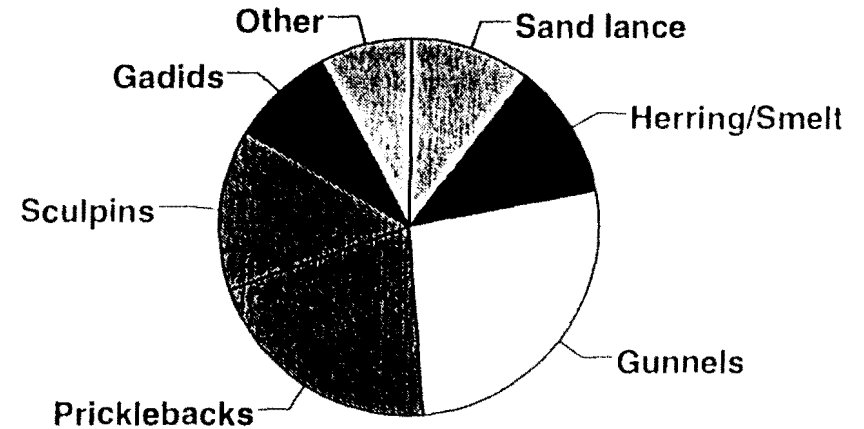
Figure 6

PIGEON GUILLEMOT CHICK DIET

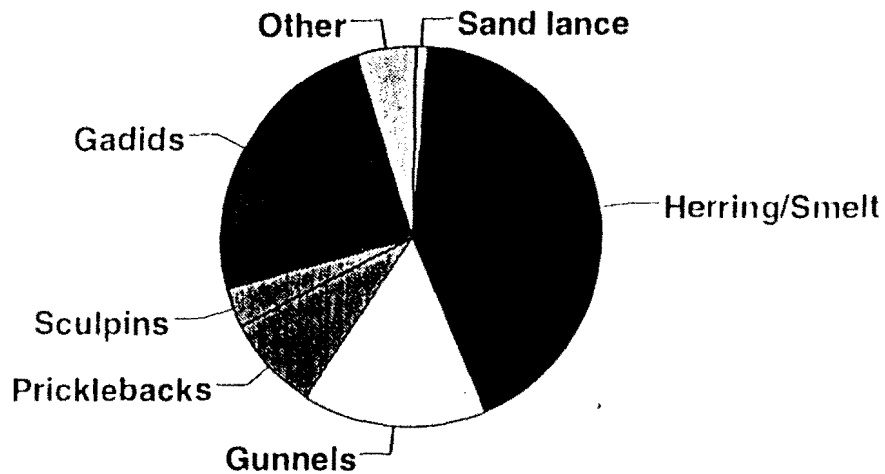
NAKED I. 94 (n = 927)



NAKED I. 95 (n = 689)



JACKPOT I. 94 (n = 291)



JACKPOT I. 95 (n = 629)

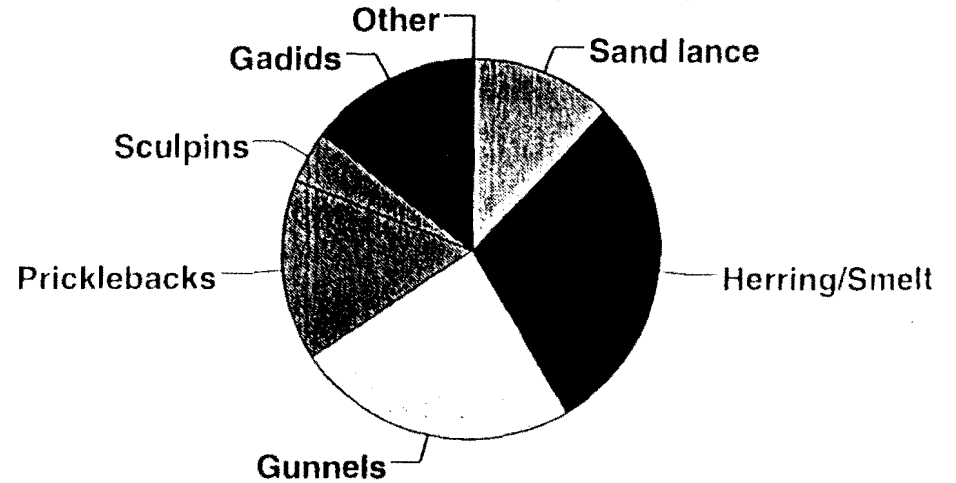


Figure 7

PIGEON GUILLEMOT CHICK DIET Naked Island

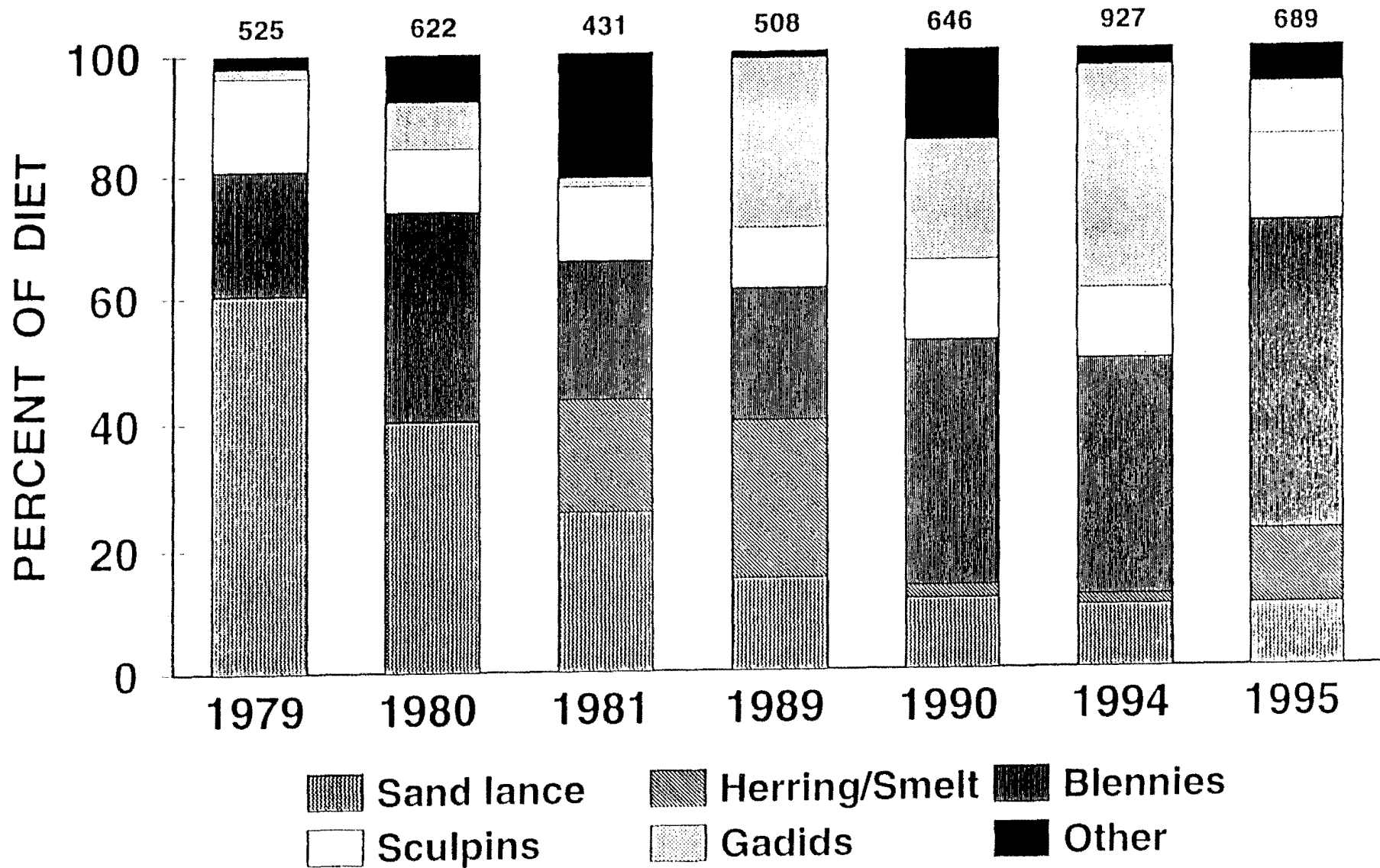


Figure 8

APPENDIX

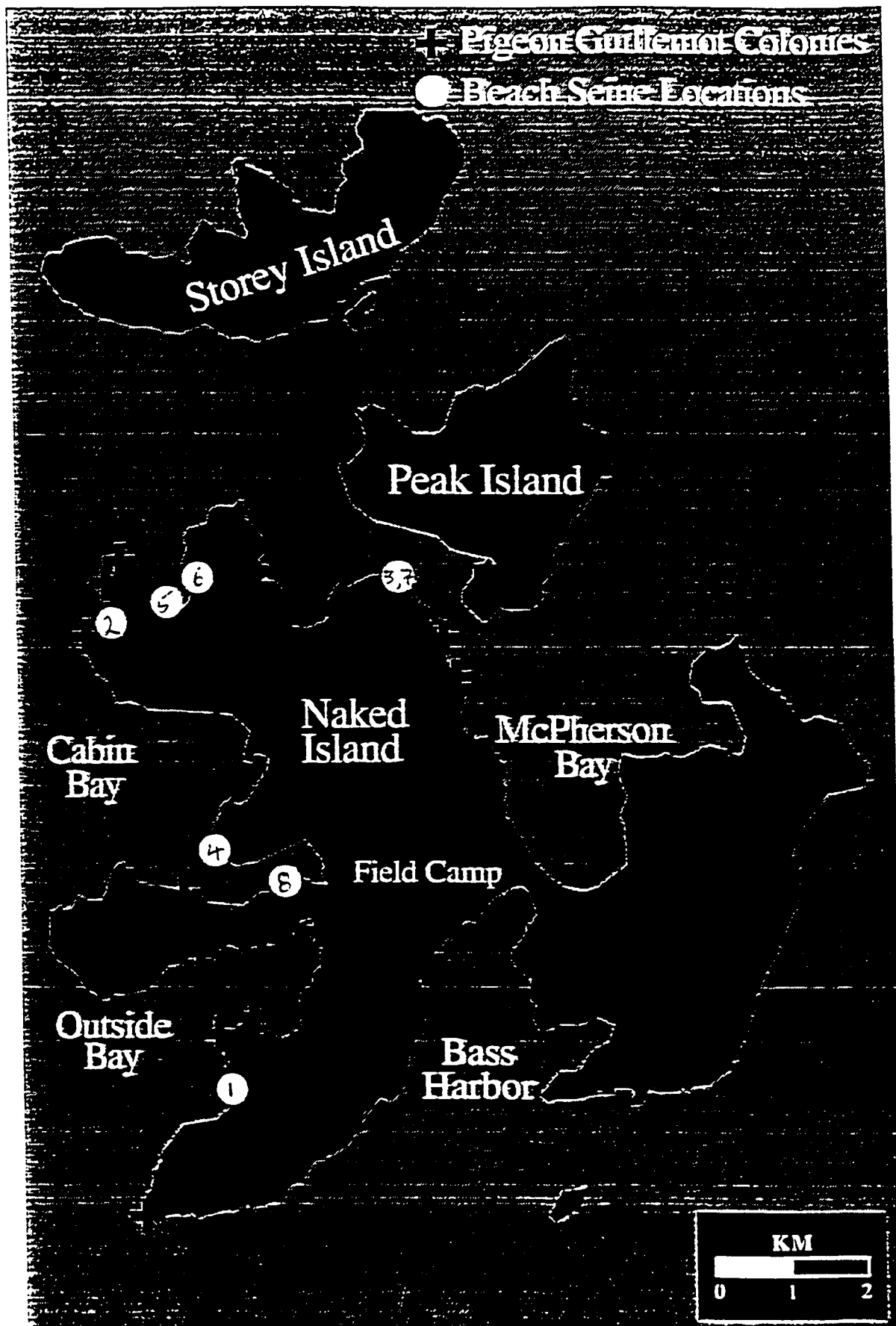


Figure A1

Table A1. Growth rates of pigeon guillemot chicks raised at Naked Island and Jackpot Island, Prince William Sound, Alaska, before (< 1989) and after the T/V Exxon Valdez oil spill.

Year	Number of Chicks	Mean Growth Rate (g/d) ^a	Standard Error	Minimum Growth Rate (g/d)	Maximum Growth Rate (g/d)
Naked I					
1978	15	19.6	1.4	7.4	31.7
1979	16	23.8	1.2	17.1	32.0
1980	^b 1	19.0	--	--	--
1981	11	19.2	1.8	11.4	34.3
1989	5	18.1	2.5	11.5	23.4
1990	12	16.6	1.2	10.1	23.6
1994	10	15.7	2.1	5.0	29.0
1995	13	19.5	1.2	11.8	26.7
Jackpot I					
1994	6	20.3	1.4	15.0	23.5
1995	16	17.4	.7	12.4	22.6

^aMean number of grams gained per day during the linear growth phase, which is the period between 8 and 18 days after hatching (Koelink 1972).

^bFew chicks were measured in 1980 because of loss of nests from netting and tagging of adults for foraging studies (Kuletz 1983).

Note: Data from before 1994 from Table 14 (Oakley and Kuletz 1994).

Table A2. Fledging weights^a of pigeon guillemot chicks raised at Naked Island and Jackpot Island, Prince William Sound, Alaska, before (< 1989) and after the T/V Exxon Valdez oil spill.

Year	Number of Chicks	Mean Fledging Weight (g)	Standard Error	Minimum Weight (g)	Maximum Weight (g)
Naked I					
1978	29	467	9	291	542
1979	17	506	12	427	590
1980	^b 2	517	52	466	569
1981	13	428	29	202	546
1989	10	507	16	420	570
1990	13	438	16	310	510
1994	17	453	13	357	525
1995 ^c	22	455	16	311	561
Jackpot I					
1994	17	508	9	440	585
1995 ^d	10	468	14	392	521

^aThe last weight obtained from a chick that was measured within one week of fledging.

^bFew chicks were measured in 1980 because of loss of nests from netting and tagging of adults for foraging studies (Kuletz 1983).

^cThe last weight obtained from a chick that was measured within 24 hours of fledging.

^dThe last weight from a chick that was measured within 72 hours of fledging.

Note: Data from before 1994 from Table 13 (Oakley and Kuletz 1994).