

## ADULT PREY CHOICE AFFECTS CHICK GROWTH AND REPRODUCTIVE SUCCESS IN PIGEON GUILLEMOTS

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**ABSTRACT.**—Pigeon Guillemots (*Cephus columba*) are diving seabirds that forage near shore and feed their chicks demersal and schooling fishes. During nine years between 1979 and 1997, we studied chick diet, chick growth rate, and reproductive success of Pigeon Guillemots at Prince William Sound, Alaska, to determine factors limiting breeding populations. We found evidence for prey specialization among breeding pairs and detected differences in reproductive success between specialists and generalists. Pairs that specialized on particular prey types when foraging for their chicks fledged more chicks than those that generalized, apparently because they delivered larger individual prey items. Reproductive performance also varied among guillemot pairs as a function of the proportion of high-lipid schooling fishes fed to the chicks. Pairs that delivered primarily high-lipid fishes (Pacific sand lance [*Ammodytes hexapterus*] and Pacific herring [*Clupea pallasii*]) had higher overall reproductive success than pairs that delivered primarily low-lipid demersal fishes (e.g. sculpins, blennies, stichaeids, and pholidids) and gadids. The proportion of high-lipid fishes in the diet was positively related to chick growth, suggesting that piscivorous seabird chicks benefit from eating species with high-energy densities during development. The diet of Pigeon Guillemot chicks showed high annual variation from 1979 to 1997, presumably because of fluctuations in abundance of Pacific sand lance, a high-lipid schooling fish. Regression analyses suggest that the percent occurrence of high-lipid fishes in the diet affected chick growth rate at the population level. We conclude that Pigeon Guillemots benefit by specializing when selecting prey for their chicks, and that high-lipid schooling fishes enhance chick growth and reproductive success. Received 30 September 1998, accepted 5 May 1999.

WITHIN POPULATIONS of generalist predators, some individuals demonstrate high degrees of prey specialization (Werner and Sherry 1987, West 1988, Wendeln et al. 1994). Differences in patterns of prey choice among individuals within populations are of interest from an ecological standpoint because they represent alternate strategies to the general life-history challenge of maximizing lifetime reproductive success. Yet, relatively few studies have compared the reproductive performance of a population in which the adults specialize on different prey types (but see Trillmich 1978, Trivelpiece et al. 1980, Pierotti and Annett 1991, Spear 1993). Much more common are studies that relate intercolony differences in diet to reproductive performance (e.g. Harris and Hislop 1978, Monaghan et al. 1989, Hamer et al. 1991).

Guillemots (*Cephus*) are semicolonial seabirds that eat a wide range of prey types (Brad-

street and Brown 1985, Ewins 1993). Some individuals are highly specialized, however, and prey selection may differ markedly among birds within the same breeding colony (Drent 1965, Slater and Slater 1972, Cairns 1981, Kuletz 1983, Emms and Verbeek 1991). Thus, guillemot colonies present valuable opportunities for studies of foraging ecology in relation to chick growth and reproductive success.

Guillemots often forage solitarily, or in small groups, and they primarily select nearshore demersal fishes (sculpins, blennies, stichaeids, and pholidids) for their chicks (Drent 1965, Cairns 1987a, Ewins 1993). These prey tend to be dispersed but may be predictable in time and space (Rosenthal 1979, Cairns 1987a). In contrast, most other piscivorous alcids (e.g. murrens [*Uria*] and puffins [*Fratercula*]) feed in foraging flocks on dense aggregations of pelagic schooling fishes (e.g. Pacific sand lance [*Ammodytes hexapterus*], capelin [*Mallotus villosus*], Pacific herring [*Clupea pallasii*], and gadids; Piatt 1990, Hatch and Sanger 1992). Given that

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many pelagic schooling fishes have higher lipid content (gadids are an exception), and consequently higher energy density than demersal fishes (Montevecchi et al. 1984, Hislop et al. 1991, Anthony and Roby 1997, Van Pelt et al. 1997), it is perhaps surprising that guillemots do not prey on schooling fishes more extensively. High-lipid schooling fishes sometimes are available to guillemots, as instances of individual birds specializing on them demonstrate (Slater and Slater 1972, Cairns 1981, Kuletz 1983). Only rarely, however, have guillemots been reported to exploit schooling fishes to a large degree (Kuletz 1983).

To better understand the foraging ecology of guillemots, we studied chick diet, chick growth, and reproductive success of Pigeon Guillemots (*Cepphus columba*). We tested two main hypotheses, the first being that adults that are highly specialized when selecting prey items for their chicks have higher reproductive success than adults that are less specialized. This might be expected if specialization increases foraging efficiency by reducing prey handling time or enabling adults to select larger or more nutrient-rich prey (Futuyma and Moreno 1988). The second hypothesis is that reproductive success varies as a function of the percent of high-lipid prey items in the chick diet. Adults that select high-lipid prey for their chicks may be expected to have higher reproductive success than those that select low-lipid prey for a number of reasons. Field and laboratory studies of seabird nestling growth suggest that chicks fed high-lipid prey grow faster than chicks fed low-lipid prey because lipids are energy-rich (Harris and Hislop 1978, Massias and Becker 1990, Roby 1991). Because lipids tend to replace water and not protein, high-lipid prey fishes typically are not lacking in other nutrients (Harris and Hislop 1978). A further benefit of high-lipid prey is that they generally yield higher assimilation efficiencies by seabirds than do low-lipid prey (Massias and Becker 1990, Brekke and Gabrielsen 1994).

#### STUDY AREA AND METHODS

*Study site.*—We studied Pigeon Guillemots during nine years (1979 to 1981, 1989 to 1990, and 1994 to 1997) at Naked Island, Alaska (Fig. 1). Naked Island (ca. 3,862 ha) is located in central Prince William Sound (PWS) and is part of a complex of three islands. The nearshore habitat of this region is char-

acterized by numerous bays and passages with shallow shelf habitat (<30 m) radiating about 1 km from shore. Naked Island is forested to its 371 m summit, mostly with sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*). Pigeon Guillemots nest semicolonially along the island's rocky shorelines. They nest in cavities beneath tree roots that hang above crumbling cliffs, in rock crevices, or among boulders on talus slopes. From 1979 to 1997, guillemot numbers at the Naked Island complex declined from 1,871 to 670 birds (Oakley and Kuletz 1996, G. Golet unpubl. data). Other alcids that breed on these islands include Marbled Murrelets (*Brachyramphus marmoratus*), Parakeet Auklets (*Aethia psittacula*), Tufted Puffins (*Fratercula cirrhata*), and Horned Puffins (*F. corniculata*). Populations of these species have also declined appreciably in PWS since the 1970s (Agler et al. 1999).

*Chick diet and prey specialization.*—We determined chick diets and food delivery rates by observing prey items held crosswise in the bills of adults as they provisioned their chicks. Feeding observations were made with binoculars and spotting scopes from land-based blinds at five colonies. We watched from each blind for an average of four full days, alternating our observations among colonies to ensure that the diets of chicks aged 8 to 30 days were well documented. Because adults often paused on the water or on rocks in front of their nests before delivering food to their chicks, we were usually able to identify the prey items carried in their bills. Prey items were identified to the lowest possible taxon that we could distinguish and then grouped into the six categories listed in Table 1. Lengths of prey items were estimated visually as multiples of guillemot bill lengths. Because chick diets were determined solely by observations, adult behavior and chick growth were not influenced by this method of data collection.

Guillemot pairs were classified as generalists or one of five types of specialists. We classified pairs rather than individuals because we usually could not distinguish among mates. This classification was appropriate because the reproductive parameters we studied depended upon the prey deliveries of both adults. We included pairs in our analyses only if at least 10 deliveries were observed in which prey items were identified (see Pierotti and Annett 1991); on average, 29.3 (maximum = 148) deliveries were identified per pair. Pairs were classified as specialists when particular prey items or classes of prey items (as defined in Table 1) comprised >50% of their deliveries, and as generalists when they did not meet this criterion. Based on these classifications, we examined the distribution of specialist types among colonies and years.

To examine the effects of the proportion of high-lipid fishes in the diet on chick growth and reproductive success, we pooled specialist types according to the energy density of their prey. Sand lance

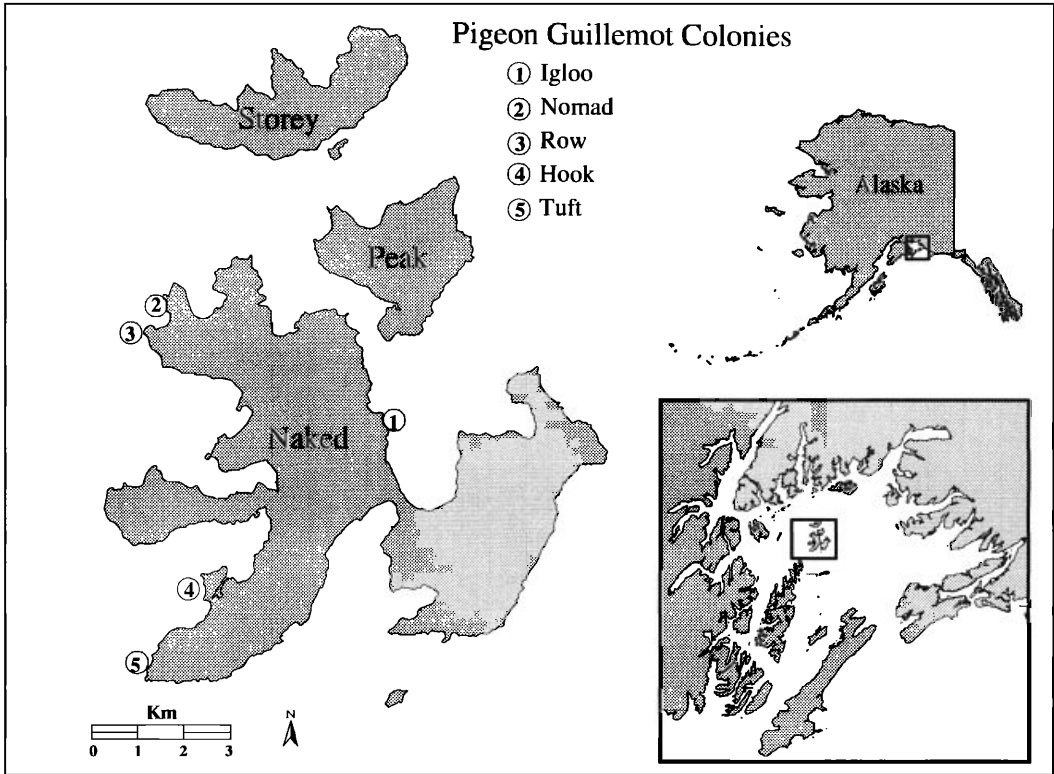


FIG. 1. The Naked Island group with the locations of the five Pigeon Guillemot study colonies indicated by numbered circles. Inset maps show the location of the Naked Island group within Prince William Sound (PWS), and the location of PWS within Alaska.

TABLE 1. Diet of Pigeon Guillemot chicks at Naked Island, Alaska, 1979 to 1997. Values are percent of deliveries in which prey was identified ( $\bar{x} = 81.5 \pm 3.5\%$  of total deliveries).

Year	<i>n</i>	Blennies <sup>a</sup>	Gadids <sup>b</sup>	Herring / smelt <sup>c</sup>	Sand lance <sup>d</sup>	Sculpins <sup>e</sup>	Other <sup>f</sup>
1979	525	20.6	1.5	0.0	60.4	15.4	2.1
1980	622	33.8	7.9	0.0	40.4	10.3	7.7
1981	431	22.3	1.4	17.6	25.8	12.3	20.7
1989	508	21.1	27.8	25.0	15.0	10.0	1.2
1990	646	38.7	19.7	2.2	11.5	13.0	15.4
1994	927	37.3	36.7	1.6	10.1	11.2	3.0
1995	689	49.3	8.7	11.8	10.2	13.9	6.1
1996	645	39.8	11.8	3.9	17.4	22.6	4.5
1997	541	35.9	7.6	7.0	22.9	19.0	7.6
All	5,534	33.2	13.7	7.7	23.7	14.2	7.5

<sup>a</sup> Crescent gunnel (*Pholis laeta*), slender eelblenny (*Lumpenus fabricii*), snake prickleback (*L. sagitta*), daubed shanny (*L. maculatus*), black prickleback (*Xiphister atropurpureus*), y-prickleback (*Allolumpenus hypochromus*), high cockscomb (*Anoplarchus purpureus*), penpoint gunnel (*Apodichthys flavoides*), northern ronquill (*Ronquillia jordani*), searcher (*Bathymaster signatus*), arctic shanny (*Stichaeus punctatus*), and snailfish (*Liparis* spp.).

<sup>b</sup> Pacific cod (*Gadus macrocephalus*), Pacific tomcod (*Microgadus proximus*), and walleye pollock (*Theragra chalcogramma*).

<sup>c</sup> Pacific herring (*Clupea pallasii*), and smelt (including capelin [*Mallotus villosus*]).

<sup>d</sup> Pacific sand lance (*Ammodytes hexapterus*).

<sup>e</sup> Ribbed sculpin (*Triglops pingelii*), slim sculpin (*Radulinus asperillus*), tidepool sculpin (*Oligocottus maculosus*), plain sculpin (*Myoxocephalus jaok*), roughspine sculpin (*Triglops macellus*), armorhead sculpin (*Gymnocanthus galeatus*), grunt sculpin (*Rhamphocottus richardsonii*), and red irish lord (*Hemilepidotus hemilepidotus*).

<sup>f</sup> Flatfish, including rex sole (*Glyptocephalus zachirus*), slender sole (*Lyopsetta exilis*), dover sole (*Microstomus pacificus*), rockfish (*Sebastes* spp.), Pacific sandfish (*Trichodon trichodon*), greenling (*Hexagrammos* spp.), lingcod (*Ophiodon elongatus*), salmon, and invertebrates (including shrimp [*Pandalus* spp.], squid [*Rossia pacifica*], and crabs).

specialists were grouped with herring/smelt specialists because these prey typically are energy-rich (energy densities range from 6 to 8 kJ/g fresh mass; Anthony and Roby 1997). The non-schooling fishes and gadids (which school but have low lipid content in the size classes that guillemots eat) were combined to form the low-lipid category (energy densities typically <5 kJ/g fresh mass; Anthony and Roby 1997). Generalists were also included in this category because on average they delivered only 25.3% high-lipid fishes.

Data from 1979 to 1981 were excluded from these analyses because of the small number of nests in which chick diet, nestling growth, and productivity were studied simultaneously. We report diet data from these early years (see Table 1), however, because they relate to the population-level effects that we describe between diet and growth rate (see Discussion).

*Chick growth and reproductive success.*—We determined chick growth and reproductive success to examine the effects of prey choice on reproductive performance. At hatching we recorded brood size and hatching order and marked the web of the foot of chicks with a permanent pen to distinguish them from one another until they were old enough to band. Chicks were weighed and measured at least once every five days from hatching until fledging (i.e. leaving the nest). Growth rate was calculated as the slope of the regression of mass on age for chicks between 8 and 18 days, the linear phase of the growth cycle (Emms and Verbeek 1991, Ewins 1993). Because this growth measure is not influenced by the particular asymptote that individual chicks attain (Gaston 1985), it has the advantage of being independent of peak and fledging mass, which we also report. We defined peak mass as the highest mass measured and fledging mass as the last mass measured prior to fledging. Peak and fledging mass have been shown to affect fledging success and subsequent survival, and they may represent the condition of nestlings at their time of highest energetic demand (Perrins et al. 1973). Based on observations made during nest visits, we determined hatching success (eggs hatched per egg laid), nestling survival (chicks fledged per egg hatched), and productivity (chicks fledged per egg laid).

*Statistics.*—We used general linear models (GLM) to test for the effects of prey specialization and the proportion of high-lipid prey in the diet on reproductive performance. We determined the degree of specialization of guillemot pairs with the modified Hill's ratio,  $F_{2,1}$  (Alatalo 1981):

$$F_{2,1} = \frac{\frac{1}{\sum_{i=1}^n p_i^2} - 1}{\exp\left(-\sum_{i=1}^n p_i \ln p_i\right) - 1}. \quad (1)$$

In this equation,  $p_i$  is defined as the number of prey type  $i$  delivered by the pair in a season divided by the total number of all prey types delivered by that pair in that season, and  $n = 6$ , the total number of prey types (Table 1). This diversity index has the advantage of not requiring an independent assessment of species richness, which is often a function of sample size (Alatalo 1981). We used  $F_{2,1}$  as an independent variable in our GLMs to test for effects of specialization on reproductive performance.

To examine the effects of the proportion of high-lipid prey in the diet on reproductive performance, we calculated a high-lipid prey index, which we also included in our GLMs. This was defined as the proportion of prey items delivered to each nest that was sand lance or herring/smelt. We also included "year" as a categorical random factor in all GLMs. For binomially distributed data, we compared multiple logistic regression models and tested for significance by assessing the deviance (expressed as a likelihood-ratio statistic) of saturated models and models lacking particular effects (Agresti 1996). We used the Lilliefors test to assess normality with variables having continuous frequency distributions, and compared variables identified as nonparametric with Kruskal Wallis tests or Mann Whitney  $U$ -tests. The remainder were contrasted with ANOVAs or  $t$ -tests assuming equal or unequal variance as appropriate. For contingency analyses, we used log-linear models (SYSTAT 1996),  $G$ -tests (Fienberg 1970), and Fisher's exact test. For  $G$ -tests involving only two classes, we applied Williams' correction to reduce the likelihood of Type I errors (Sokal and Rohlf 1995). Means are presented  $\pm 1$  SE, and all tests are two-tailed.

## RESULTS

*Effects of specialization and high-lipid diet on reproductive performance.*—Dietary diversity (degree of specialization) and the proportion of high-lipid prey in the diet affected reproductive performance of adult guillemots (Table 2). Dietary diversity was negatively related to overall productivity, suggesting that adults that specialize when selecting prey items for their chicks raise more young than those that generalize. The difference in reproductive output between specialists and generalists resulted largely from differences in nestling survival, suggesting that the benefits of specializing came during the later part of the nestling stage. Dietary diversity was not found to affect hatching success, chick growth rate, peak mass, or fledging mass. Differences in nestling survival apparently resulted from differences in the size

TABLE 2. Results of general linear model testing for effects of dietary diversity and % high-lipid fishes in the diet of Pigeon Guillemot chicks on reproductive parameters at Naked Island, Alaska, 1989 to 1990 and 1994 to 1997. Multiple logistic regression models<sup>a</sup> of the following type were constructed: parameter = diversity index (Hill's ratio  $F_{2,1}$ ) + % high-lipid fish in the diet + year. The  $G$ -statistic is a measure of deviance between the fully saturated model and the model lacking a particular effect. Improved reproductive performance was associated with reduced dietary diversity (increased specialization) and increased selection of high-lipid prey.

Effect <sup>b</sup>	Test statistic	<i>n</i>	<i>P</i>
<b>Chick growth (g/day)</b>			
Diet diversity	$F = 0.0$	41	0.99
% High-lipid prey	$F = 5.7$	41	0.023
<b>Peak mass (g)<sup>c</sup></b>			
Diet diversity	$F = 1.1$	62	0.31
% High-lipid prey	$F = 1.1$	62	0.24
<b>Fledging mass (g)<sup>c</sup></b>			
Diet diversity	$F = 2.6$	63	0.12
% High-lipid prey	$F = 1.6$	63	0.21
<b>Hatching success (eggs hatched/egg laid)</b>			
Diet diversity	$G = 0.8$	65	0.68
% High-lipid prey	$G = 3.7$	65	0.16
<b>Nestling survival (chicks fledged/egg hatched)</b>			
Diet diversity	$G = 4.5$	58	0.034
% High-lipid prey	$G = 4.2$	58	0.041
<b>Productivity (chicks fledged/egg laid)</b>			
Diet diversity	$G = 6.7$	58	0.01
% High-lipid prey	$G = 8.8$	58	0.003

<sup>a</sup> Diversity and proportion high-lipid prey were not autocorrelated (Pearson correlation coefficient = 0.096, Bonferroni probability = 0.32).

<sup>b</sup> Interaction term (diet diversity × % high-lipid prey) was nonsignificant in all cases.

<sup>c</sup> Year effect was also significant.

of prey items delivered to chicks, because dietary diversity was negatively related to prey size ( $F = 4.57$ ,  $df = 1$  and  $79$ ,  $P = 0.036$ ), but not to prey delivery rate ( $F = 0.09$ ,  $df = 1$  and  $70$ ,  $P = 0.77$ ).

The percent of high-lipid prey items in the diet was positively related to nestling survival and overall productivity (Fig. 2). Benefits of feeding chicks high-lipid prey fishes appeared early in the chick-rearing period, when a significant effect was detected on chick growth rate. The difference in growth rate appeared pronounced only among two-chick nests (Fig. 3). In nests with single chicks, growth did not differ according to diet. In two-chick nests, the difference was most apparent among beta (i.e.

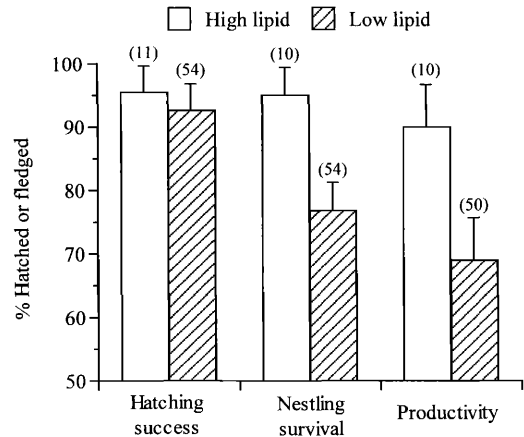


FIG. 2. Hatching success (eggs hatched per egg laid), nestling survival (chicks fledged per egg hatched), and productivity (chicks fledged per egg laid) at Pigeon Guillemot nests with adults that specialized in either high-lipid or low-lipid fishes at Naked Island, Alaska, 1989 to 1990 and 1994 to 1997. Sample sizes are in parentheses.

second-hatched) chicks, although alpha chicks also had lower mean growth rates when fed mostly low-lipid fishes. Chicks fed more high-lipid fishes did not, however, attain higher peak or fledging masses than chicks fed low-lipid fishes. The higher reproductive performance among adults that delivered more high-lipid prey apparently resulted from differences

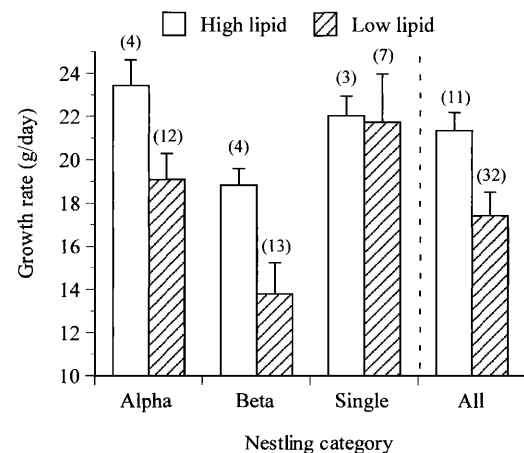


FIG. 3. Growth rates of Pigeon Guillemot chicks 8 to 18 days posthatching fed by adults that specialized in either high-lipid or low-lipid fishes at Naked Island, Alaska, 1989 to 1990 and 1994 to 1997. Sample sizes are in parentheses.

TABLE 3. Specialization of Pigeon Guillemot pairs on particular prey types at Naked Island, Alaska, 1989 to 1990 and 1994 to 1997. Values are percent of total pairs classified in that year.

Year	<i>n</i>	Sand lance	Herring/smelt	Blennies	Gadids	Sculpins	Total specialists	Generalists
1989	28	5.9	23.5	17.7	11.8	0.0	58.9	41.1
1990	25	5.6	0.0	22.2	5.6	5.6	39.0	61.0
1994	55	9.4	0.0	34.4	25.0	3.1	71.9	28.1
1995	29	11.8	11.8	41.2	0.0	5.9	76.5 <sup>a</sup>	23.5
1996	18	0.0	0.0	38.5	0.0	7.7	46.2	53.8
1997	29	11.1	0.0	38.9	0.0	11.1	61.1	38.9
All	184	8.8	5.8	32.2	7.1	5.6	58.9	41.1

<sup>a</sup> Includes one flatfish specialist.

in the nutritional value of the prey, as neither prey size ( $F = 1.42$ ,  $df = 1$  and  $79$ ,  $P = 0.24$ ) nor prey delivery rate ( $F = 1.60$ ,  $df = 1$  and  $70$ ,  $P = 0.22$ ) varied according to the percent of high-lipid prey delivered by adults.

*Prey specialization.*—Adult guillemots demonstrated preferences when selecting prey items for their chicks. Overall, from 1989 to 1990 and 1994 to 1997, 59% of nests had a particular prey type that comprised >50% of the observed deliveries (Table 3). The actual proportion of individuals that specialized was likely higher than this, however, because mates within a given nest sometimes differed in their habits of prey selection. Guillemots clearly differed in the diversity of prey items that they delivered to their chicks. A "flatfish specialist" (62% of 34 identified deliveries) occurred in 1995, although this prey item made up less than 5% of the diet in the guillemot population that year. The proportion of pairs that delivered primarily high-lipid fishes did not differ significantly among the three main colony areas between 1989 and 1997 ( $G = 2.00$ ,  $n = 95$  pairs,  $P = 0.59$ ). Thus, the availability of high-lipid fishes did not appear to vary among the guillemot colonies on Naked Island. However, the relative abundances of particular specialist types varied significantly from year to year ( $G = 37.9$ ,  $n = 114$  identified specialists,  $P = 0.009$ ; Table 3). This variability appeared to be influenced by the overall abundance of particular prey items in the diet (cf. Tables 1 and 3). Because guillemots have strong nest-site fidelity (Drent 1965), consistency in prey specialization may be examined by comparing prey selection at individual nests over multiple years. Among nests classified as a particular specialist type in one year, 50% were classified as the same specialist type in the subsequent year. This level of

consistency is substantially greater than would be expected by chance (20%). Interannual consistency appeared strongest among blenny specialists (73%) and generalists (55%).

*Differences among years.*—On average, we identified  $82 \pm 4\%$  of the prey items that we observed delivered to the chicks each year. Significant variability was found among years in the types of prey items delivered ( $G = 1,908$ ,  $n = 5,534$ ,  $P < 0.001$ ; Table 1), with schooling fishes fluctuating the most in percent occurrence. Pacific sand lance declined steadily from a high of 60% of the prey deliveries in 1979 to a low of 10% in 1994 and 1995. Variability was also high in the herring/smelt category (0 to 25%), and among gadids (1 to 37%). In contrast, the occurrence of demersal fishes such as blennies and sculpins remained relatively constant in the chick diets among years.

## DISCUSSION

*Benefits of prey specialization.*—Pigeon Guillemots that specialized when selecting prey items for their chicks had higher reproductive success than those that generalized, apparently due to differences in foraging efficiency. This finding is important, because empirical support for a tradeoff between foraging efficiency and dietary diversity is rare (Leigh 1990, Cockburn 1991). To forage efficiently, organisms must develop and maintain an accurate assessment of prey distribution and abundance (Dall and Cuthill 1997). Such assessments are always incomplete, however, because individuals are limited in terms of the time, energy, and cognitive resources that they can allocate to prey sampling (Real 1992). Moreover, representations of particular prey are expected to be less accurate for generalists than for specialists be-

cause of differences in the frequency of prey sampling (Dall and Cuthill 1997). Apparently, this was the case for guillemots in our study, although the particular mechanism whereby specialization led to increased foraging efficiency deserves further explanation.

Specialists did better than generalists not because they selected more energy-rich prey (this effect was factored out in the GLM), nor because they delivered prey more frequently, but rather because they selected larger prey for their chicks. In guillemots (which deliver prey items one at a time), it may be more advantageous to modify the size of the prey items delivered than the rate of delivery. Although both modifications may increase the rate at which energy is provisioned to nestlings, delivering larger prey likely entails smaller increases in energy expenditure than delivering prey more frequently, because it does not require additional trips to and from the foraging grounds. An additional benefit of increasing the size of prey delivered is that it does not necessarily increase the exposure of the nestlings to predators, as might more frequent nest visits. The main benefit of specializing appeared to be increased nestling survival. Specialization did not affect chick growth rates, suggesting that during the early stages of nestling development, prey quantity is less important than prey quality (see below).

*Patterns of prey choice in generalist predators.*—Benefits of a high-lipid diet were evident early in the nestling period. Growth rates were positively related to the percent of high-lipid prey in the diet, and this effect was especially pronounced among beta chicks. This finding supports the prediction of Kuletz (1983), who suggested that adults that deliver mostly low-lipid fishes are less likely to fledge a second chick. High-lipid fishes may be a better food source because they are more energy-rich, yield higher assimilation efficiencies (Massias and Becker 1990, Brekke and Gabrielsen 1994), and have less cartilaginous and bony parts than their low-lipid counterparts.

In other studies that demonstrated effects of diet choice on reproductive performance, the advantages of foraging on particular prey types varied. Delivery rates appeared important in several studies that attributed high reproductive success of particular groups of birds to close proximity of reliable prey. For ex-

ample, South Polar (*Catharacta maccormicki*) and Brown (*C. lonnbergi*) skuas that specialized on nearby penguin eggs and chicks were more successful raising chicks than those that fed mainly at sea on fish (Trillmich 1978, Trivelpiece et al. 1980). Similarly, Western Gulls (*Larus occidentalis*) that exploited nearby Common Murres (*Uria aalge*) and Brandt's Cormorants (*Phalacrocorax penicillatus*) had higher breeding success than gulls from the same colony that foraged elsewhere (Spear 1993). Among Herring Gulls (*Larus argentatus*), however, adults specializing on mussels had higher reproductive success than those specializing on petrels or human refuse, not because of differences in energy densities or delivery rates of prey, but because mussels contained a more complete complement of the nutrients required for laying viable eggs (Pierotti and Annett 1991). Thus, the mechanisms by which particular prey items benefit individuals appear to vary, supporting the view of Futuyma and Moreno (1988) that many sources of natural selection may favor one foraging strategy or another.

*Population-level effects.*—At the population level, the percent of high-lipid fishes in the diet also appears to have affected chick growth rates at Naked Island (Fig. 4). Chicks grew faster from 1979 to 1981, when high-lipid fishes comprised 40 to 60% of their diet, than in 1990 and 1994, when high-lipid fishes comprised only about 10% of their diet. Other studies of Pigeon Guillemots also have suggested that chicks grow slowly when they are fed few high-lipid fishes (Fig. 4). At Mandarte Island, chick growth was 15.6 g/day (calculated from Drent 1965) when *Ammodytes* (a high-lipid schooling fish) made up 4.7% of the diet. At Mitlenatch Island, Emms and Verbeek (1991) measured a growth rate of 14.5 g/day when chicks received 4.6% *Ammodytes* and 1% *Clupea*; and at Skidegate Inlet, Vermeer et al. (1993) measured a growth rate of 15.5 g/day when *Ammodytes* comprised 10% of the chick diet. These growth rates are comparable to the values we recorded at Naked Island when the percent of high-lipid fishes in the chick diet was the lowest in nine years of study.

Studies of Black Guillemots (*Cephus grylle*) in the North Atlantic further suggest that the proportion of high-lipid fishes in the diet affects chick growth. In Shetland, Black Guillemot growth rates were among the highest re-

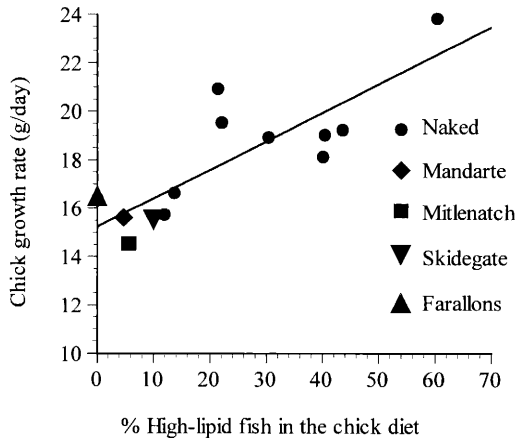


FIG. 4. Growth rate of Pigeon Guillemot chicks based on average percent high-lipid fishes in the diet ( $y = 1.17x + 15.1$ ,  $n = 13$  colony years,  $r^2 = 0.70$ ,  $P < 0.001$ ). The significant regression indicates that a high proportion of high-lipid fishes in the diet has a beneficial effect on chick growth. In all studies, the primary high-lipid fish was Pacific sand lance. Data are from Naked Island (this study); Mandarte Island, British Columbia (Drent 1965); Mitlenatch Island, British Columbia (Emms and Verbeek 1991); Skidegate Inlet, Queen Charlotte Islands, British Columbia, (Vermeer et al. 1993); and Farallon Islands, California (Ainley et al. 1990). The regression is also significant for Naked Island alone ( $n = 9$  years,  $r^2 = 0.53$ ,  $P = 0.026$ ). Growth rates were calculated with the linear slope method (Emms and Verbeek 1991, Ewins 1993) by the original authors, except for Mandarte Island, where values were derived from our analysis of Drent's (1965) measurements of chick mass.

recorded for the species (16.9 g/day) when *Ammodytes* made up 52% of the chick diets (Ewins 1990, 1992). This contrasts with the relatively low growth rate (14.2 g/day) measured for Black Guillemots in Hudson Bay when *Ammodytes* made up less than 1% of the chick diets (Cairns 1987a).

An effect of diet on reproductive performance was also found in guillemots at the Farallon Islands (Ainley et al. 1990). In years of cold water, when rockfish (*Sebastes* spp.) comprised a large portion of the chick diet, fledging masses and reproductive success were higher than in years of warm water when rockfish were fed to chicks less often. Although growth rates of chicks were not affected by the percent rockfish in the diet, chicks grew slowly in all years (16.5 g/day,  $n = 6$  years) relative to what

we observed at Naked Island (19.1 g/day,  $n = 9$  years). Perhaps chicks grew more slowly at the Farallon Islands because high-lipid fishes were lacking in their diets. Rockfish tend to have lower lipid content, and hence lower energy density, than *Ammodytes*, *Clupea*, and *Mallotus* (Van Pelt et al. 1997). Rockfish also may be digested and assimilated less easily than high-lipid fishes because they contain numerous spines and thick scales (Eschmeyer and Herald 1983).

Cairns (1987b) hypothesized that among polyphagous seabirds, the availability of a principal prey item may vary considerably before changes occur in parameters such as chick growth rate. Our findings suggest otherwise. In years when the proportion of high-lipid fishes was low in chick diets, growth rates also were low (Fig. 4). Hamer et al. 1991 obtained similar results in a 15-year study of Great Skuas (*Catharacta skua*). Sandeels (*Ammodytes marinus*), a high-lipid fish, varied from 5 to 95% of the skua chick diet, and their use was positively correlated with chick growth rate. Apparently, for some generalist foragers no suitable replacements exist for high-lipid fishes in years when they are absent from the chick diet. These results suggest that chick growth is sensitive to the percent occurrence of a principal prey item in the diet, particularly when pervasive differences occur in prey quality.

*Foraging strategies of guillemots.*—Comparisons among years and studies suggest that chick growth and productivity of guillemots are maximized when high-lipid fishes comprise a major portion of the prey fed to chicks. Nonetheless, low-lipid fishes (e.g. blennies and sculpins) form the staple of the chick diet in most guillemot populations. Given the apparent selective advantage of foraging on high-lipid schooling fishes, why haven't guillemots evolved (as have other piscivorous alcid) to become more highly specialized in feeding on these prey? The explanation may lie in the relative predictability of prey types. In Prince William Sound, high-lipid fishes such as *Ammodytes* have a distribution that is temporally and spatially variable (Blackburn 1979). Low-lipid fishes, by contrast, are predictable because they do not show marked movements during the breeding season (Rosenthal 1979). As a result, it is probably easier for guillemots to specialize on low-lipid fishes than on high-lipid fishes.



Because specialization per se can confer benefits (e.g. increased prey size), foraging on predictable low-lipid fishes may present a viable alternative to the more common alcid strategy of foraging on ephemeral high-lipid schooling prey.

#### ACKNOWLEDGMENTS

We thank Mary Cody, Brian Duggan, Conor Geisler, D. Lindsey Hayes, Kirk Lenington, Melissa Luanglue, John Maniscalco, Mark Russell, Scott Shaffer, Bev Short, Ted Spencer, Dave Tessler, and Ed Vorisek for valuable field assistance. The manuscript was improved thanks to insightful discussions with D. Lindsey Hayes, Michael Litzow, A. David McGuire, Karen Oakley, and Pamela Seiser. We are grateful to an anonymous reviewer, Carlos Bosque, George Divoky, Julian Fischer, Denis Lepage, and John Piatt for critically reviewing earlier drafts of the manuscript. Deborah Golet helped with analyses, and Steven Kendall produced the study site figure. This study was supported by the U.S. Fish and Wildlife Service, the *Exxon Valdez* Oil Spill (EVOS) Trustees Council, and grant no. BAA-52ABNF400104 from NOAA to D. D. Roby. This study was a component of, but does not necessarily reflect the views of, the EVOS Trustee Council-funded Alaska Predator Ecosystem Experiment (APEX) during 1994 to 1997. Permission to work on Naked Island was granted by the United States Forest Service.

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Associate Editor: C. Bosque