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PREY SWITCHING AND VARIABLE FORAGING STRATEGIES OF BLACK-LEGGED KITTIWAKES AND THE EFFECT ON REPRODUCTIVE SUCCESS[1]

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Abstract. We studied the diets, foraging strategies, and reproduction of Black-legged Kittiwakes (*Rissa tridactyla*) during five years at two colonies within Prince William Sound, Alaska. Years with reduced occurrence of 1-year-old Pacific herring (*Clupea pallasi*) in kittiwake diets were associated with increased foraging trip duration, distance, and travel time at both colonies. Foraging range was consistently greater at the large, fjord colony with an annual mean trip duration of 4 hr and mean distance to the farthest feeding location of 40 km in years when 1-year-old herring dominated diets; these numbers increased to a maximum mean of 6 hr and 60 km during a year when kittiwakes consumed primarily young-of-year (YOY) herring and Pacific sand lance (*Ammodytes hexapterus*). Foraging trips of kittiwakes at the small, island colony averaged 2 hr and 5 km during years when 1-year-old herring dominated diets and increased when capelin (*Mallotus villosus*) and YOY herring and sand lance were consumed. Consequences of reduced herring availability were greatest at the large colony where alternative prey was limited, resulting in reduced reproductive success. In contrast, kittiwakes from the small colony were able to compensate for reduced herring availability by obtaining sand lance and capelin in relatively close proximity, and maintained above average reproductive success. Time spent traveling and trip distance increased with greater trip duration. However, search and prey capture times were only weakly related to trip duration and may reflect foraging strategies that vary with different species, age classes, or availability of prey consumed.

Key words: Black-legged Kittiwake, diet, foraging range, prey switching, radio tracking, Rissa tridactyla, *time budget.*

INTRODUCTION

Piscivorous seabirds are confronted with a variety of challenges in obtaining prey during the breeding season. Their primary prey are often distributed in patches that vary temporally and spatially within the marine environment (Schneider and Piatt 1986, Ostrand et al. 1998a). The spatial distribution of prey is further complicated by depth, creating a three dimensional realm in which prey can avoid predators. This third dimension is not available to surface feeding species such as Black-legged Kittiwakes (*Rissa tridactyla*) that are constrained to exploiting a two-dimensional environment. Therefore, kittiwakes can compensate for reduced availability of surface schooling prey only by intensifying search effort in a given area or increasing their foraging range to include potentially more productive areas. In either case, the primary goal is to obtain sufficient quantities of prey within a time frame that allows adequate provisioning of nestlings.

Although kittiwakes have the ability to capture many species of vertebrate and invertebrate prey that occur in surface waters (Furness and Monaghan 1987), relatively few forage species have been associated with kittiwake reproductive success. The most common of these species or groups are sand lance (*Ammodytes* spp.), capelin (*Mallotus villosus*), and cod (Gadidae; Springer et al. 1987, Hatch et al. 1993). In many instances, one prey species dominates seabird diets and declines in this prey item cause reduced reproductive performance. For example, Hamer et al. (1993) reported no change in the predominately sandeel (*Ammodytes marinus*) diet of kittiwakes during a year of low prey abundance that led to declines in reproductive success. Baird (1990) reported a decline in reproductive success in Black-legged Kittiwakes associated with a dietary change from capelin to sand lance, invertebrates, and other fishes. The fact that reproductive success declined even though kittiwakes were consuming sand lance, a potentially energy rich prey (Van Pelt et al. 1997, Anthony et al., in press), implies the effort involved in obtaining prey can be as important as the energetic value of the prey.

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Under some circumstances, variation in prey availability and associated changes in foraging effort for seabirds may not directly affect reproductive parameters such as clutch size, brood size, or nestling growth rates because adults are able to vary their foraging effort without affecting reproduction (Burger and Piatt 1990, Irons 1992). Therefore, the most immediate changes in forage fish distribution and abundance would presumably be detected in foraging effort of breeding adult seabirds (Cairns 1987). Although foraging effort of colonial seabirds is often implied by the length of time an adult is absent from the nest (Gabrielsen et al. 1987), foraging trip distance and time budgets are typically unknown or estimated based on infrequent observations of marked birds at sea (Anderson and Ricklefs 1987, Barrett 1996), flight speed and trip duration (Furness and Barrett 1985), or locations of feeding flocks (Springer et al. 1984, Gabrielsen and Mehlum 1989). Indirect estimates of foraging range, however, are prone to errors. If a bird does not fly directly to a feeding area, calculation of trip distance based on flight speed and time can be incorrect (Monaghan et al. 1994). Observations of unmarked birds at sea may underestimate foraging distances because detection probability decreases with increasing distance from the colony, and maximum distance that birds travel may exceed the survey area (Ostrand et al. 1998b). In addition, the unmarked birds may not represent activities of currently breeding adults, which may have very different foraging strategies than adults that are not provisioning young (Wilson et al. 1988). By following radio-tagged birds at sea we were not constrained by the above limitations and were able to record exact flight paths, foraging locations, and foraging behaviors of confirmed breeding adults.

Determining foraging strategies of seabirds confronted with varying environmental constraints is an essential link in solving ecological relationships between prey availability and reproductive success. Here we contrast the diets and foraging strategies of Black-legged Kittiwakes in Prince William Sound (PWS) during five years (1989, 1990, and 1995–1997) in which diets, foraging strategies, and reproductive success varied greatly. We also contrast how kittiwakes from two colonies within PWS respond to differences in the availability of several forage fish species.

METHODS

STUDY SITES

Prince William Sound is an inland marine and estuarine waterway located along the north coast of the Gulf of Alaska (Fig. 1). The abundant fjords, bays, and islands in PWS provide more than 4,000 km of shoreline habitat. This area also is characterized by heterogeneous bathymetry and large tidal fluctuation (5.5 m between high and low tide), although the water column is typically stratified throughout the summer (Ostrand et al. 1998a). Two kittiwake colonies were selected for study. The Shoup Bay colony is the largest (ca. 5,500 breeding pairs) in PWS and is located in a fjord in the northeastern region (Fig. 1). The Eleanor Island colony (ca. 220 breeding pairs) is located among the islands of central PWS. Studies were conducted during all five years at Shoup Bay and four of five years at Eleanor Island (excluding 1990). These colonies provide an interesting comparison of seabird foraging ecology because they are dramatically different in size and one colony is located far inside PWS (Shoup Bay), whereas the other (Eleanor Island) is closer to Hinchinbrook Entrance and the influence of Gulf of Alaska waters.

DIETS

We sampled kittiwake diets by collecting 1,051 regurgitations from nestlings and storing them in isopropyl alcohol or a freezer. Regurgitations were collected weekly throughout the colony for the duration of the chick-rearing period (ca. 1 July to 15 August). In most cases, only one sample was collected per nest ($n = 977$); two or more samples were taken from a single nest in 74 cases. Repeat samples from a nest were separated in time ($\geq$ 1 week) and were therefore considered independent. Because the nest was our sampling unit, samples from alpha and beta chicks were combined. Prey were identified using otoliths, morphological characteristics, scales, and bones. To relate foraging trip duration and distance to the spatial distribution of prey, we were interested in the number of species obtained per foraging trip, with each species weighted equally. Therefore, we present the diet data as the annual percent occurrence of prey types from regurgitations. Otoliths were measured to the nearest 0.01 mm using an ocular micrometer. Age classes of herring were inferred

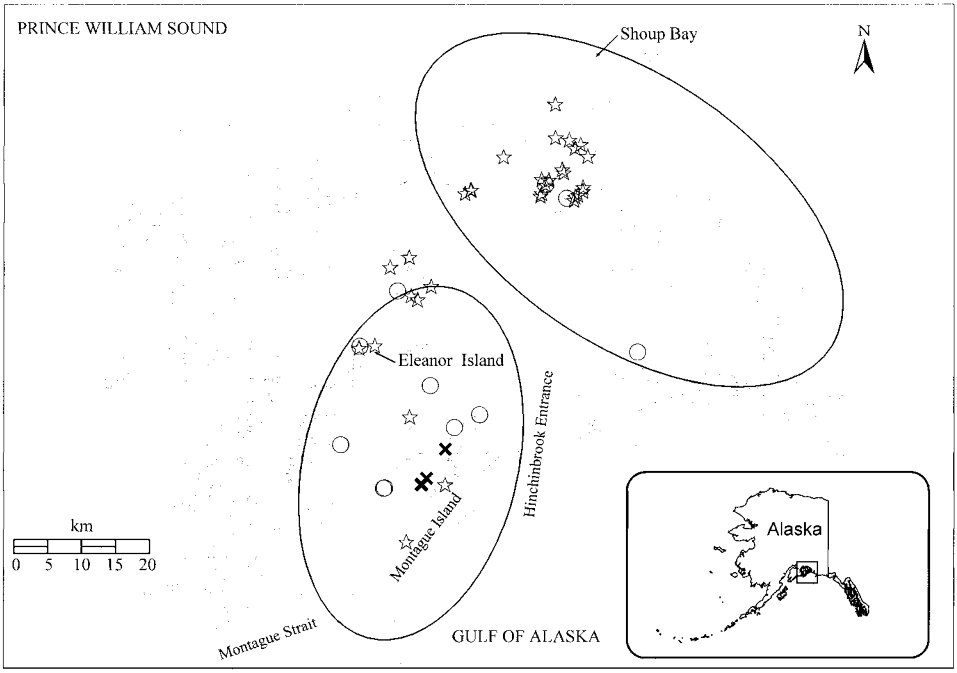

FIGURE 1. Location of the two study colonies, Shoup Bay and Eleanor Island, in Prince William Sound, Alaska. Oval boundaries encompassing colonies depict maximum foraging range of adult Black-legged Kittiwakes from respective colonies. Also shown is the species composition of forage fish schools sampled in 1997. Forage fish species included Pacific herring (☆), Pacific sand lance (○), and capelin (×).

from otolith length and the modes of length frequency distributions (1–2 mm for young-of-year [YOY], 2–3 mm for 1-year-old, and 3+ mm for age 1+ or 2-year old), which were confirmed by personnel from the University of Alaska Fairbanks and the Alaska Department of Fish and Game (Stokesbury et al. 1999, Kevin D. E. Stokesbury, pers. comm.).

FORAGING ACTIVITIES

We captured adult Black-legged Kittiwakes at their nests using a noose-pole (Hogan 1985) or leg-noose (Benson and Suryan 1999). We attached radio transmitters (164–167 MHZ, 9–11 g Advanced Telemetry Systems, Inc., Isanti, Minnesota) to 15–40 birds annually at each colony. Transmitters were secured ventrally to the base of the tail feathers (Anderson and Ricklefs 1987, Irons 1998) with two nylon cable ties and Loctite 494 instant adhesive (Loctite Corporation, Rocky Hill, Connecticut). In addition, we dyed (Nyanzol D and Rhodamine B-base) the head, breast, tail, and underwings of radio-tagged kittiwakes one of three color combinations. The dye permitted identification of kittiwakes during at-sea tracking.

We determined foraging trip duration, distance, location, and behavior by tracking radio-tagged kittiwakes with a receiver and a 4-element Yagi antenna from a 7.3 m Boston Whaler capable of traveling 65 km hr^{-1}. Radio-tracking was conducted throughout the chick-rearing period (nestling ages ranged from 1 to 30 days). Only kittiwakes provisioning nestlings were selected for tracking, and we attempted to obtain at least one track of each individual. In total, we attempted 160 tracks of 119 different kittiwakes during the five years of our study. Data from multiple tracks of a single bird were averaged for final analyses, therefore reported sample sizes represent individual kittiwakes. Observers waited nearby until a radio-tagged bird left the colony, then attempted to keep the kittiwake in view until it returned to the colony, constituting a complete track. Herein, we use only complete tracks in the analyses. The distance between the boat and radio-tagged kittiwake varied between ca. 700 m and less than 100 m depending on circumstances. In all cases, we remained at a maximum distance to prevent noticeable alterations of the kittiwake's activities while maintaining visual contact to record behaviors. Behaviors recorded included traveling (straight flight), searching for prey (back and forth flight), foraging (surface plunge or surface seize; Ashmole 1971), resting, and lost (bird out of view). Because duration of pursuit and handling of prey for kittiwakes is negligible compared to search time (Irons 1992), we combined feeding with searching in final analyses of time budget data. We determined locations of feeding kittiwakes and mapped flight paths of radio-tagged kittiwakes using a Lowrance LMS-350A global positioning system receiver (Lowrance Electronics Inc., Tulsa, Oklahoma). We used Atlas GIS software (ESRI Inc., Redlands, California) to plot the flight paths of kittiwakes and measure maximum foraging distance from the colony. Foraging trip distance is reported as the shortest distance between the colony and farthest feeding location without intersecting land.

REPRODUCTIVE SUCCESS

We estimated reproductive success (fledglings nest^{-1}) from an annual census of each colony (Irons 1996). Censuses were a single count of the number of nests at each colony in June or early July to determine the total number of breeding pairs. Nests were defined as any site containing new nesting material with or without an attending adult. We later counted the number of nestlings once in early to mid-August, immediately prior to fledging. Observers used binoculars (7× to 10×) and conducted counts of nests and chicks from a boat (7.6 m). The same methods for determining reproductive success were used in all years of the study (Irons 1996) and were conducted by the same two observers. We report reproductive success as deviations from the 14-year average (1984–1997) for each colony, thereby standardizing for differences in reproductive success that may inherently occur between large and small colonies.

SPATIAL DISTRIBUTION OF FORAGE FISH SPECIES

Throughout the 1997 breeding season, we identified the species composition of forage fish schools encountered within the approximate foraging range of kittiwakes from Shoup Bay and Eleanor Island colonies. Fish schools ($n = 47$ schools) were located by the presence of feeding birds and sampled opportunistically while radio-tracking or transiting the study area. Species identification was determined by collecting at least one fish per school (median = ca. 20 fish) using either a dip net or cast net. Mixed species schools were rare, less than 7% of the schools encountered.

STATISTICAL ANALYSES

We compared the percent occurrence of prey species in nestling diets among years and between colonies using contingency tables with chi-square analyses. For example, to compare the percent occurrence of herring in kittiwake diets at Shoup Bay, we used the number of diet samples with herring versus the number without herring among five years (Zar 1984). Tukey-type multiple comparison tests for proportions were used when significant differences were detected in chi-square analyses. In general, data of foraging activities did not exhibit normal distributions and, therefore, annual means were compared using nonparametric statistics. Mann-Whitney *U*-tests and Kruskal-Wallis *H*-tests were performed using SYSTAT software (SYSTAT 1997). We used a chi-square approximation of the Kruskal-Wallis *H*-test which is preferable for samples sizes of five or larger (Zar 1984, Sokal and Rohlf 1995). Relationships between independent and dependent variables were tested with linear regression. Results were considered significant at $\alpha = 0.05$.

RESULTS

DIETS AND FORAGING STRATEGIES

Kittiwake diets and foraging activities separated into two general categories, years when 1-year-old herring dominated diets and years when sand lance or YOY herring were more frequently consumed. During 1989, 1995, and 1996, diets at Shoup Bay were dominated by Pacific herring ($\chi^2_4 = 31.6$, $P < 0.001$; Fig. 2a) that were 1-year-old ($\chi^2_4 = 105.1$, $P < 0.001$; Fig. 2b). In other years (1990 and 1997), sand lance ($\chi^2_4 = 21.7$, $P < 0.001$) and/or YOY herring ($\chi^2_4 = 105.1$, $P < 0.001$) dominated the diets. Nearly all sand lance fed to nestlings were YOY (< 100 mm fork length, $n = 266$ of 294 otoliths). Other prey items were consumed (including; capelin, cod, fish offal, and salmon eggs [*Oncorhynchus* spp.]), but their occurrence was infrequent (<

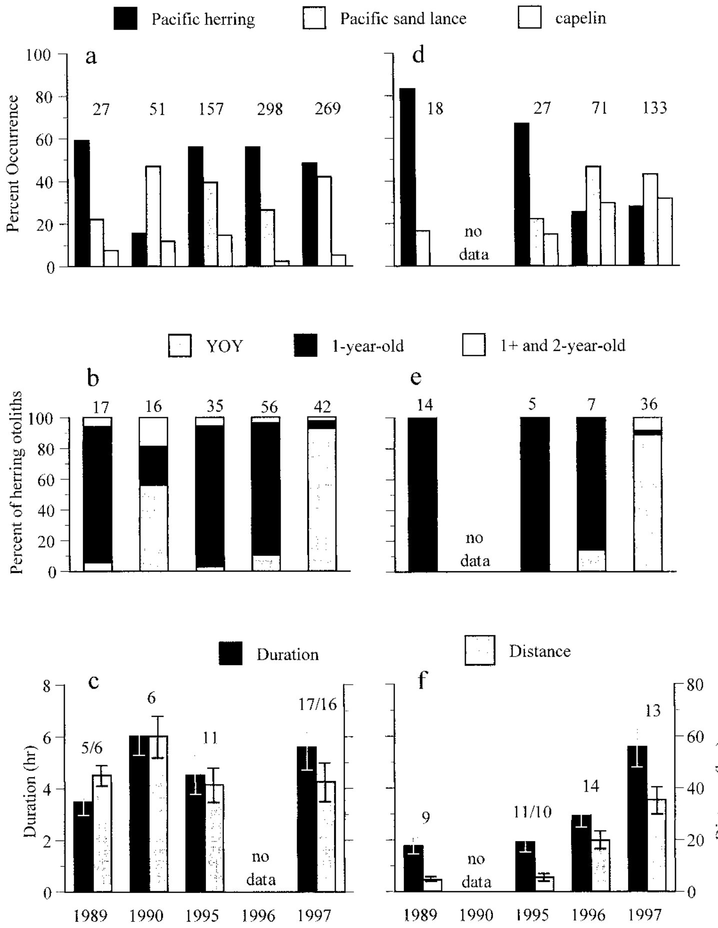

FIGURE 2. Annual percent occurrence of primary prey in nestling diets, age class of herring consumed (percent of otoliths recovered), and mean (± SE) foraging trip duration in hr and distance in km for adult Black-legged Kittiwakes nesting at Shoup Bay (a, b, and c, respectively) and Eleanor Island (d, e, and f, respectively) in Prince William Sound, Alaska. Numbers above bars are sample sizes.

20%) and never in sufficient quantity to compensate for lack of herring or sand lance.

In all years, foraging ranges were relatively large for kittiwakes at Shoup Bay with average trip durations from 3.5 to 6.0 hr and average distances from 45 to 60 km. Foraging trip duration and distance tended to increase during years with reduced occurrence of 1-year-old herring in diets (Fig. 2c); however, because of within-year variation in the data, these increases were not statistically significant at Shoup Bay ($\chi^2_3 < 4.1$, $P > 0.25$). Foraging range was greatest in 1990 with birds traveling 60 km from Shoup Bay on average and trip durations averaging 6 hr (Fig. 2c). The maximum distance traveled to the farthest foraging location was 120 km.

For kittiwakes at Eleanor Island, dietary changes resulted in considerable variation in foraging effort among years. During 1996 and 1997 there was a significant reduction in the occurrence of herring ($\chi^2_3 = 38.3$, $P < 0.001$) in diets and an increase in sand lance ($\chi^2_3 = 7.8$, $P = 0.05$) and capelin ($\chi^2_3 = 10.3$, $P < 0.03$; Fig. 2d). Eulachon (*Thaleichthys pacificus)* and cod also were consumed, but their annual occurrence was less than 12%. As at Shoup Bay, nearly all sand lance fed to nestlings were YOY ($n = 121$ of 129 otoliths). In 1997, nearly all herring consumed were YOY compared to previous years

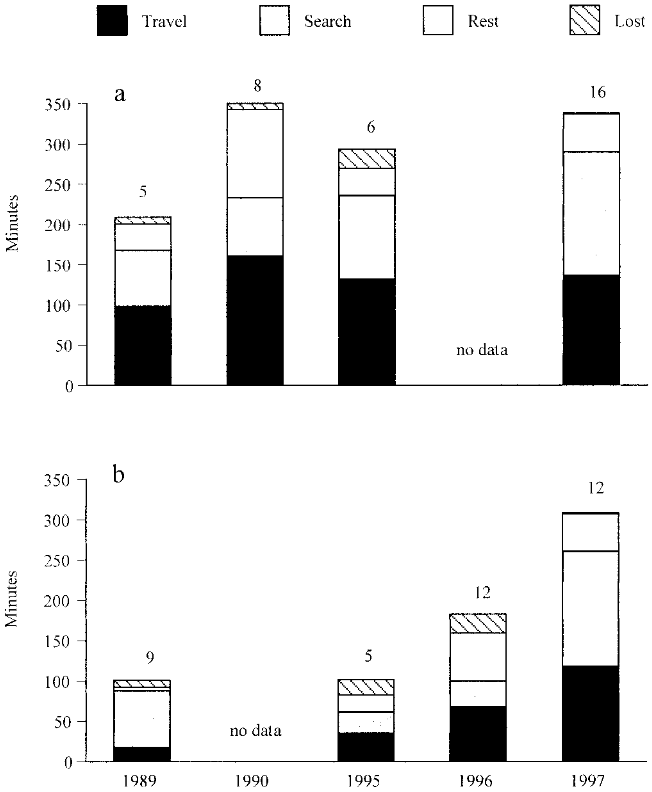

FIGURE 3. At-sea time budgets of foraging Black-legged Kittiwakes from (a) Shoup Bay and (b) Eleanor Island, Prince William Sound, Alaska. Numbers above bars are sample sizes and represent the number of individual kittiwakes.

(χ^2_3 = 51.6, $P < 0.001$; Fig. 2e), as also observed at Shoup Bay. These dietary changes in 1996 and 1997 corresponded with significantly increased foraging trip duration (χ^2_3 = 15.4, P = 0.002) and distance (χ^2_3 = 18.1, $P < 0.001$; Fig. 2f). Maximum distance to the farthest foraging location was 67 km. In all years except 1997, foraging trip duration ($U > 39.0$, $P \leq 0.05$) and distance ($U > 54.0$, $P \leq 0.001$) were significantly less for kittiwakes at Eleanor Island than at Shoup Bay.

Although Shoup Bay and Eleanor Island are in relatively close proximity (85 km straight-line distance), their respective food supplies were to some extent independent. Compared to Shoup Bay, the occurrence of herring in diets at Eleanor Island was significantly less (χ^2_1 = 21.6 and 18.2, $P < 0.001$) during two (1996 and 1997) of four years, respectively (Figs. 2a and 2d). During these two years, capelin was an important prey item at Eleanor Island but had minimal significance at Shoup Bay, occurring significantly more frequently at Eleanor Island than Shoup Bay ($\chi^2_1 > 56.8$, $P < 0.001$).

The species composition of forage fish schools sampled throughout our study areas in 1997 corresponded with the diet and foraging data obtained from kittiwakes. Net samples indicated schools of herring were more common in northeastern PWS (closer to Shoup Bay), whereas schools of sand lance and capelin were more frequent in central and southern waters (within the foraging range of kittiwakes from Eleanor Island; Fig. 1).

TIME BUDGETS

The amount of time spent traveling, searching, and resting during foraging trips varied markedly among years (Fig. 3); differences within colonies were significant at Eleanor Island (χ^2_3 > 14.0, $P < 0.005$) but not Shoup Bay (χ^2_3 > 7.38, $P > 0.05$). Overall, a strong, positive re-

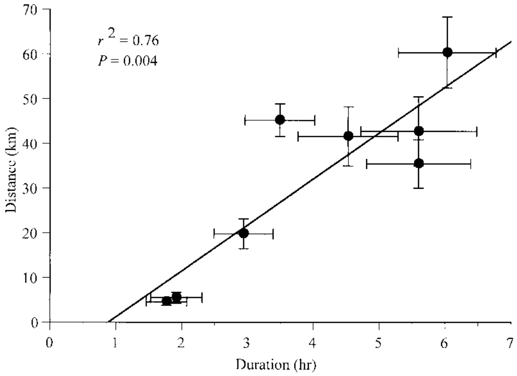

FIGURE 4. Relationship (linear regression) between mean (± SE) annual foraging trip duration in hr and distance in km for Black-legged Kittiwakes at Shoup Bay and Eleanor Island, Prince William Sound, Alaska.

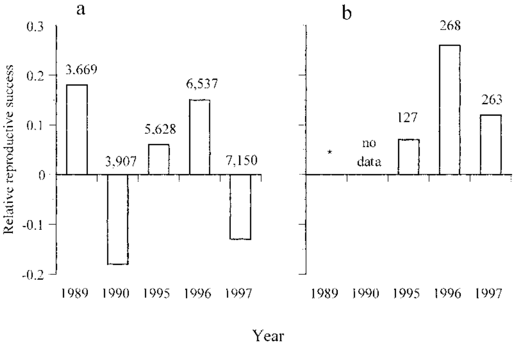

FIGURE 5. Reproductive success (fledglings nest^{-1}) relative to a 14-year average for Black-legged Kittiwakes nesting at Shoup Bay (14-year $\bar{x} = 0.47$) and Eleanor Island (14-year $\bar{x} = 0.21$), Prince William Sound, Alaska. Number of nests is reported above bars. Reproductive success at Eleanor Island in 1989 (*) was not reported because of disruption by the *T/V Exxon Valdez* oil spill (the path of the discharged oil included the Eleanor Island study area, but not the Shoup Bay study area; Irons 1996).

lationship existed between trip duration and travel time (linear regression, $r^2 = 0.91$, $P < 0.001$, $n = 8$). In addition, greater foraging trip durations were associated with birds traveling farther from the colony (Fig. 4). The amount of time spent searching for and obtaining prey was also positively related to trip duration ($r^2 = 0.54$, $P = 0.04$, $n = 8$), however, search time explained considerably less variation in trip duration than did travel time.

REPRODUCTIVE EFFECTS

Years of reduced consumption of herring and increased foraging effort for kittiwakes at Shoup Bay were coincident with reduced reproductive success (Fig. 5a). This relationship did not occur at the Eleanor Island colony, however, where kittiwakes maintained above average reproductive success in all years of the study (Fig. 5b).

DISCUSSION

Diets and foraging effort of kittiwakes were linked to a few key prey species: herring, sand lance, and capelin. In particular, reduced occurrence of 1-year-old herring in diets was associated with increased foraging trip duration and distance. Foraging range and trip duration were much greater for kittiwakes at Shoup Bay, because birds from Eleanor Island were able to obtain prey closer to the colony.

These two colonies provide several insights into seabird and forage fish relationships. First, they show dramatic regional differences in foraging range and diet while being located only 85 km apart. Second, individuals exhibited a wide range of foraging effort coinciding with changes in prey selection. Third, the frequent occurrence of herring in the diet is in contrast to most other colonies in the Gulf of Alaska (Baird 1990, Hatch et al. 1993), Bering Sea (Springer et al. 1987), and Chukchi Sea (Springer et al. 1984). Fourth, reproductive success in northern PWS (a region including the Shoup Bay colony) has been consistently higher since at least 1984 than most other colonies in the Gulf of Alaska, probably due to the availability of herring (Suryan and Irons 1998).

DIETS

The ability of an animal to switch from its primary prey to an alternative food source was termed prey switching by Murdoch (1969). Prey switching may be directly related to the abundance of potential prey items (Bergerud 1983) or be influenced by prey preference (Murdoch 1969), resulting in a sigmoidal response curve of predator abundance to prey abundance (Joern 1988). The ability of kittiwakes to switch prey during chick rearing can be restricted at some colonies because alternative prey are unavailable. Because kittiwakes are limited to both surface-schooling prey and the need to obtain energy-rich food for proper nestling development (Romano et al. 1998), they have a fairly specialized summer diet (Hatch 1987). In the North

Atlantic Ocean, Hamer et al. (1993) documented that kittiwakes did not change their diet when their principle prey, sandeels (*Ammodytes marinus*), declined; instead, kittiwakes increased their foraging effort to obtain sandeels. In PWS, several species of schooling fishes were available to kittiwakes, indicating the potential for prey switching. Prey switching, however, did incur a cost. This was particularly evident at Shoup Bay where kittiwakes increased their foraging ranges to an extreme to obtain sand lance in compensation for lack of 1-year-old herring, resulting in reduced reproductive success.

In contrast, prey switching was a viable alternative for kittiwakes at Eleanor Island where prey was located closer to the colony. As herring declined in their diets, these birds obtained sand lance locally or moderately increased their foraging range to acquire capelin. Capelin, in particular, are more associated with Gulf of Alaska waters, which have a greater influence on the central and southwestern waters of PWS than on its northern regions (Niebauer et al. 1994). The closer proximity of sand lance and capelin schools (along with other species potentially associated with the Gulf of Alaska, such as eulachon) allowed kittiwakes from Eleanor Island to compensate for lack of herring without increasing foraging ranges to such an extreme as that seen at Shoup Bay.

FORAGING TRIP DURATION AND DISTANCE

In years of high prey abundance in Atlantic and Barents Sea colonies, foraging trips of kittiwakes were reported to be 2 to 3 hr duration (Hamer et al. 1993), and distances (also reported as linear distance over water to the farthest feeding location) were less than 10 km (Gabrielsen and Mehlum 1989, Hamer et al. 1993). This is similar to what we observed at Eleanor Island. However, these numbers are markedly less than at Shoup Bay where foraging trip distances averaged 40 km in years of apparently high prey abundance. In a year of low prey abundance, Hamer et al. (1993) reported that average foraging trip distances of kittiwakes in Shetland were greater than 40 km (the maximum signal reception range from shore-based telemetry stations). Measured foraging distances of kittiwakes at Shoup Bay in years of apparently low prey abundance also were greater than 40 km on average, reaching a maximum average of 60 km. At Eleanor Island, foraging trip duration and distance increased as prey availability was apparently reduced, yet the adults never exceeded a 40 km average. It seems that an average foraging range for breeding kittiwakes in PWS of ca. 45 km and an average duration of ca. 5.5 hr may be the limits beyond which increased effort negatively affects reproductive performance.

PREY ABUNDANCE

Reduced occurrence of 1-year-old herring in diets and associated increases in foraging range of kittiwakes at Shoup Bay and Eleanor Island indicated reduced availability and/or abundance of 1-year-old herring during three years of our study (1990, 1996 at Eleanor Island only, and 1997). Independent fisheries data provide evidence to support this interpretation. Back-calculations from a known age structure of the adult herring population indicated that the abundance of 1-year-old herring was greatly reduced in 1990 in regions overlapping our study areas (Alaska Department of Fish and Game, unpubl. data). Additionally, Brown et al. (1996) and Norcross and Fransen (1996) identified low YOY herring survival in 1989, which probably contributed to reduced 1-year-old herring abundance in 1990. During the latter years of our study (1996 and 1997), Haldorson et al. (1999) conducted hydroacoustic forage fish surveys within the foraging ranges of kittiwakes from Shoup Bay and Eleanor Island. These surveys indicated very low biomass density of 1-year-old herring near Eleanor Island in 1996 and in both areas in 1997 (Haldorson et al. 1999). Fisheries data and hydroacoustic surveys provided additional evidence that the abundance of 1-year-old herring was at or above average in years when 1-year-old herring dominated kittiwake diets (1989 and 1995 in both study areas and 1996 near Shoup Bay). It appears that variation in the consumption of 1-year-old herring by kittiwakes in our study did correspond with fluctuations in the abundance of this prey item.

TIME BUDGETS

As food supply near a colony declines, seabirds may respond in two different ways: (1) extend their foraging range by increasing travel time away from the colony, or (2) spend more time searching for prey within a restricted foraging range. Individuals may invoke either of these strategies depending on current conditions and knowledge of available prey from the recent past

(Anderson and Ricklefs 1987, Irons 1998). Kittiwakes in our study typically increased travel duration and distance from the colony in years of apparently low prey abundance, but the amount of time spent obtaining prey did not consistently increase. This implied that kittiwakes primarily used the first strategy mentioned above. By increasing their foraging range, some birds were able to locate prey that was more abundant or otherwise easier to obtain (spending similar amounts of time obtaining food as in years of high prey abundance). In other instances, however, although birds increased their foraging range, they were unable to locate prey that was easy to obtain and the amount of search time greatly increased along with travel time.

In addition to the abundance of prey, the schooling characteristics of different prey species or age classes may have affected kittiwake search time. Capelin often occurred in large schools covering several square kilometers in locations near Montague Island that were persistent for weeks during mid July to mid August (Fig. 1). Kittiwakes from Eleanor Island were often observed extending their foraging range to these areas, and easily taking the post-spawning, male capelin that lethargically swam near the surface. In contrast, YOY herring and YOY sand lance were often observed in relatively small ($<$ ca. 100 m^2), ephemeral schools. When kittiwakes at Eleanor Island switched from consuming 1-year-old herring to smaller, YOY herring in 1997, their search time increased significantly compared to other years. This same pattern occurred at the Shoup Bay colony in 1997 (Figs. 2b and 3a).

CONCLUSIONS

We demonstrated that kittiwakes in PWS exhibited prey switching and a considerable increase in foraging range in response to an apparent reduction of a primary prey item, 1-year-old herring. Time spent searching and capturing prey also increased during years of low herring abundance, but this trend was not as strong as with increased travel time and distance during years of low herring abundance. Search and capture time was likely confounded by prey switching and the different foraging strategies required to obtain particular prey species and age classes. As the occurrence of herring in diets declined at Shoup Bay, kittiwakes appeared to have little alternative prey close to the colony. In contrast, kittiwakes at Eleanor Island were able to locate capelin and sand lance in relatively close proximity when herring was not available. Results of this study support the premise that seabird diets and foraging effort (distance, duration, and time budgets) are sensitive indicators of changes in prey availability (Cairns 1987, Montevecchi 1993) and that kittiwakes are able to dramatically vary their foraging effort in response to regional changes in prey availability.

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