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EVALUATION OF RADIO-TRACKING AND STRIP TRANSECT METHODS FOR DETERMINING FORAGING RANGES OF BLACK-LEGGED KITTIWAKES[1]

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Abstract. We compared strip transect and radio-tracking methods of determining foraging range of Black-legged Kittiwakes (*Rissa tridactyla*). The mean distance birds were observed from their colony determined by radio-tracking was significantly greater than the mean value calculated from strip transects. We determined that this difference was due to two sources of bias: (1) as distance from the colony increased, the area of available habitat also increased resulting in decreasing bird densities (bird spreading). Consequently, the probability of detecting birds during transect surveys also would decrease as distance from the colony increased, and (2) the maximum distance birds were observed from the colony during radio-tracking exceeded the extent of the strip transect survey. We compared the observed number of birds seen on the strip transect survey to the predictions of a model of the decreasing probability of detection due to bird spreading. Strip transect data were significantly different from modeled data; however, the field data were consistently equal to or below the model predictions, indicating a general conformity to the concept of declining detection at increasing distance. We conclude that radio-tracking data gave a more representative indication of foraging distances than did strip transect sampling. Previous studies of seabirds that have used strip transect sampling without accounting for bird spreading or the effects of study-area limitations probably underestimated foraging range.

Key words: Black-legged Kittiwakes, habitat use, Prince William Sound, radio-tracking, Rissa tridactyla, *seabirds.*

INTRODUCTION

Radio-tracking and strip transects have been commonly used to evaluate resource selection by animals (Litvaitis et al. 1994). However, few habitat selection studies of seabirds used radio-tracking (Harrison 1981, Trivelpiece et al. 1986, Anderson and Ricklefs 1987); strip transects is the more common method (Heinemann et al. 1989, Piatt et al. 1989, Erikstad et al. 1990). Consequently, comparison between techniques have not been made with colonial seabirds. A subjective comparison of the relative bias and precision of each method should benefit field biologists considering these techniques. Furthermore, we anticipate that our comparisons will be useful in the interpretation of earlier studies of seabirds that used either method.

Comparison of these techniques using traditional statistical approaches is problematic due to differences in the nature of the data sets. Radio-tracking data consist of the locations of individual birds from a known colony, whereas strip transects generate a set of chance encounters. We used randomization tests to compare radio-tracking and strip transect data collected on Black-legged Kittiwakes (*Rissa tridactyla*) in Prince William Sound, Alaska (PWS) to determine the relative benefits of each method. We also used bootstrapping methods to simulate the effect of reducing sampling effort on both techniques.

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METHODS

BACKGROUND/MODEL RATIONALE

We assumed that there would not be significant differences in measures of habitat use determined by either radio-tracking or strip transect sampling methods if data were collected on the same population during the same time period. If differences were observed, we assumed they resulted from bias associated with the sampling methods. We also examined how data variability changed with decreasing sampling effort to determine the effect of changing sample sizes, and compared the precision of both methods.

We observed that as birds flew farther from the colony, the area of available habitat increased. Hence, if the number of birds at any distance from the colony remained constant, bird density would decrease as distance increases (this concept is hereafter referred to as bird spreading). Consequently, the probability of detecting birds also would decrease as distance from the colony increased. We suggest that detection probability is a function of the area of the marine habitat available to birds for foraging. Island colonies, because they are surrounded by water and thus have the greatest available foraging area, should have the greatest bias associated with strip transect sampling. To describe this bias, we adapted a model from Kinder et al. (1983) and Decker (1995). We considered the available foraging habitat of an island colony as a series of concentric rings. The number of birds expected to be observed (n_i) in any ring (i) is inversely related to the area of a ring and can be calculated by:

$$n_i = N_i a_i / \pi(ro_i^2 - ri_i^2) \qquad (1)$$

where N_i is the total number of birds within ring i, ri_i is the inner radius and ro_i is the outer radius of ring i, and a_i is the area surveyed within ring i. If foraging patches are equal in quality, then birds should select patches near the colony (Stephen and Krebs 1986); thus as distance from the colony increases N_i should decrease. The attenuation of bird numbers as distance from the colony increases could be modeled by adding additional terms to the right side of equation 1. We suggest that attenuation should have affected both strip transect and radio-tracking data sets similarly. Therefore, to present the simplest possible models and to focus this exercise on bird spreading, we have assumed: (1) no attenuation, (2) the probability of detecting birds within rings remains constant, and (3) birds are randomly distributed within rings. For fjords, bays, or areas in which all marine habitat was not suitable, the above formula can be modified by introducing a variable (j_i), the proportion of the area in ring i that was available marine habitat:

$$n_i = N_i a_i / j_i \pi(ro_i^2 - ri_i^2) \qquad (2)$$

This equation may be solved to approximate the total number of birds within a ring when the number of birds observed is known:

$$N_i = n_i j_i \pi(ro_i^2 - ri_i^2)/a_i \qquad (3)$$

We approximated equation 2, using an assumed N_i, and compared the predicted n_i values to those obtained from strip transect sampling to test our predictions based upon bird spreading.

We anticipated four additional sources of bias that could influence the comparison of data collection methods: (1) the potential maximum distance from the colony obtained from radio-tracking was unlimited, whereas the farthest point observed during the strip transect data was constrained by the survey design. If the survey did not cover the full extent of the foraging range of the radio-tracked kittiwakes, then a smaller mean distance would be obtained from the strip transect data; (2) transmitters were only attached to birds with chicks. Birds without chicks, free of provisioning and nest attendance requirements, may be more likely to range farther during foraging flights (Wilson et al. 1988). Observations of non-nesting kittiwakes would tend to increase the mean distance from the colony for the strip transect data set; (3) Gessamen and Nagy (1988) and Gessamen et al. (1991) have demonstrated that the attachment of radio transmitters can increase the energy demands of flight in domestic pigeons (*Columba livia*). Acorn Woodpeckers (*Melanerpes formicivorus*) have been shown to have shorter flight distances when carrying radio transmitters (Hooge 1991). If the kittiwakes in this study were affected similarly, then this bias would have reduced the mean distance from the colony for the radio-tracking data set; (4) kittiwakes from neighboring colonies may have occurred within the strip transect study area. Influence of this source of bias would depend upon where the area of overlap between colonies occurred. If the overlap was distant from the study colony, then the sighting of birds from neighboring colonies

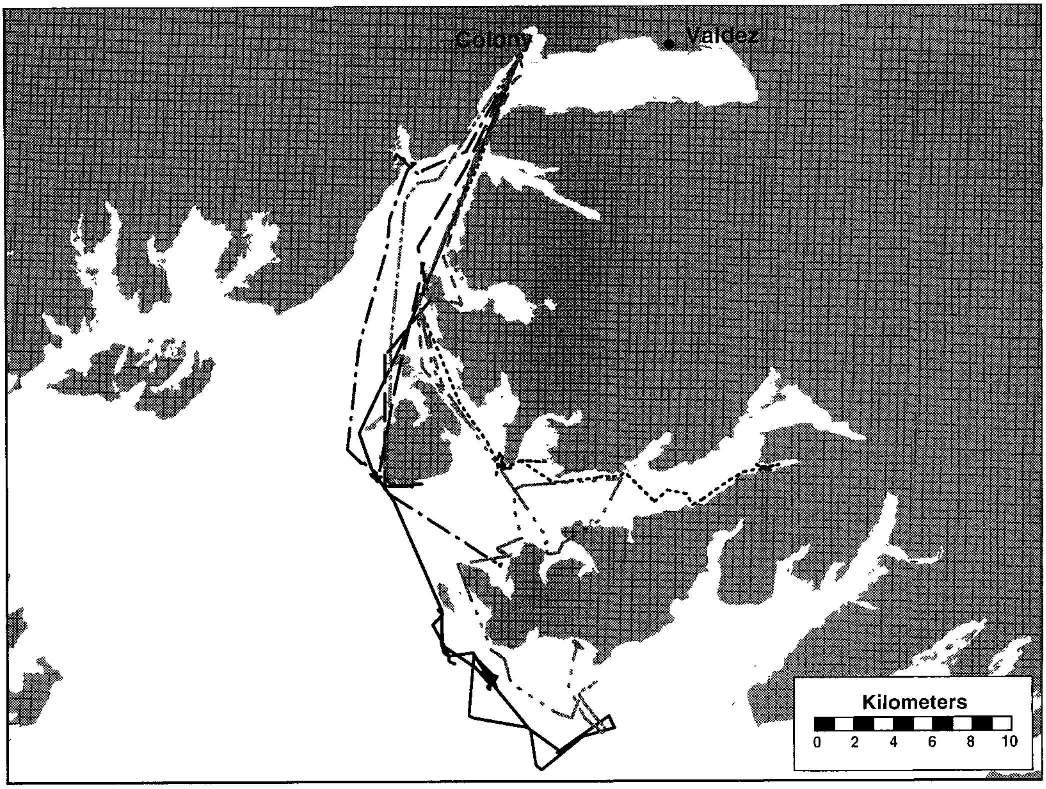

FIGURE 1. The flight tracts of seven Black-legged Kittiwakes followed by boat during radio-tracking studies conducted in Valdez Arm, Prince William Sound, Alaska.

would inflate the sample mean distance birds were observed from the study colony during strip transect surveys. Conversely, if overlap occurred near the study colony, the bias would have decreased the sample mean distance from the colony.

DATA COLLECTION

We conducted this study in PWS, an embayment of 8,800 km^2, located on the southern central coast of Alaska. The climate is maritime with a mean annual precipitation of 1.6 m and moderate temperatures for the subarctic. The coastline of PWS is rugged, with mountains up to 4-km in elevation and numerous fjords and tidewater glaciers.

We selected the Black-legged Kittiwake colony located at Shoup Bay (61°09′N, 146°35′W), the largest in PWS with 5,628 breeding pairs in 1995 (Irons 1996), for the focus of this study. Shoup Bay adjoins Port Valdez and Valdez Arm in northern PWS (Fig. 1).

For the radio-tracking study, birds on nests located throughout the colony and containing eggs or chicks were captured with a noose-pole. Advanced Telemetry Systems, Inc. (Isanti, Minnesota) radio transmitters were attached to 24 adult birds. The radio packages weighed approximately 9 g, $< 2.5\%$ of an adult kittiwake's average body weight, and were attached to the ventral surface of the base of the tail feathers (see Anderson and Ricklefs 1987, Irons 1992, for description of attachment method). Flight tracks were determined by following radio tagged birds in an 8-m boat, capable of speeds up to 65 km hr^{-1}, during 14 July–5 August 1995. Birds were tracked both visually and with radio-tracking equipment. A following distance of 50–100 m was maintained and appeared to have minimal effect on kittiwake behavior (Irons 1992).

Locations of radio tracked birds were determined using a commercial global positioning system instrument (GPS). GPS data have an accuracy of about ± 100 m (Leick 1992). Only tracking efforts that were successful in determining the farthest point from the colony during a foraging trip were used (n = 7). Five birds were tracked once and one bird was tracked twice, on different days. Return flight locations were incomplete and not included in the analysis (Fig. 1).

We chose the boundaries for the strip transect study area based upon the expected foraging range of Black-legged Kittiwakes from the Shoup Bay colony, determined from previous radio-tracking studies at this colony (Irons 1992). The latitude of the initial east-west transect was randomly located within the first 2′ latitude of the southern study area boundary. We added east-west transects at 2′ latitude intervals north of the initial transect and zigzag transects to increase data collection of nearshore habitats. Zigzags were inserted where the running distance between east-west transects was located near land (Fig. 2). There were 23 transect segments, 15 east-west ($\bar{x}$ ± SD length = 6.6 ± 4.9 km) and 8 zigzag ($\bar{x}$ ± SD length = 1.5 ± 0.7 km), for a total length = 111.4 km. Typical of other strip transect surveys (Erikstad et al. 1990, Decker 1995, Leopold et al. 1995), our survey design resulted in a greater proportion of habitat surveyed within concentric rings near the colony than those at greater distance (Fig. 2).

We replicated the strip transect survey twice, on 26–28 July and 5–7 August 1995. Observations were made from the second deck, 8 m above the water, on a 24-m vessel, operated at approximately 11 km hr^{-1}. One person made observations using 8×42 binoculars, while a second person recorded data. Each observer had more than one field season experience recording seabird data in PWS. Continuous counts were made of all kittiwakes observed within 100 m of the starboard side of the vessel. Observers calibrated their ability to estimate the transect

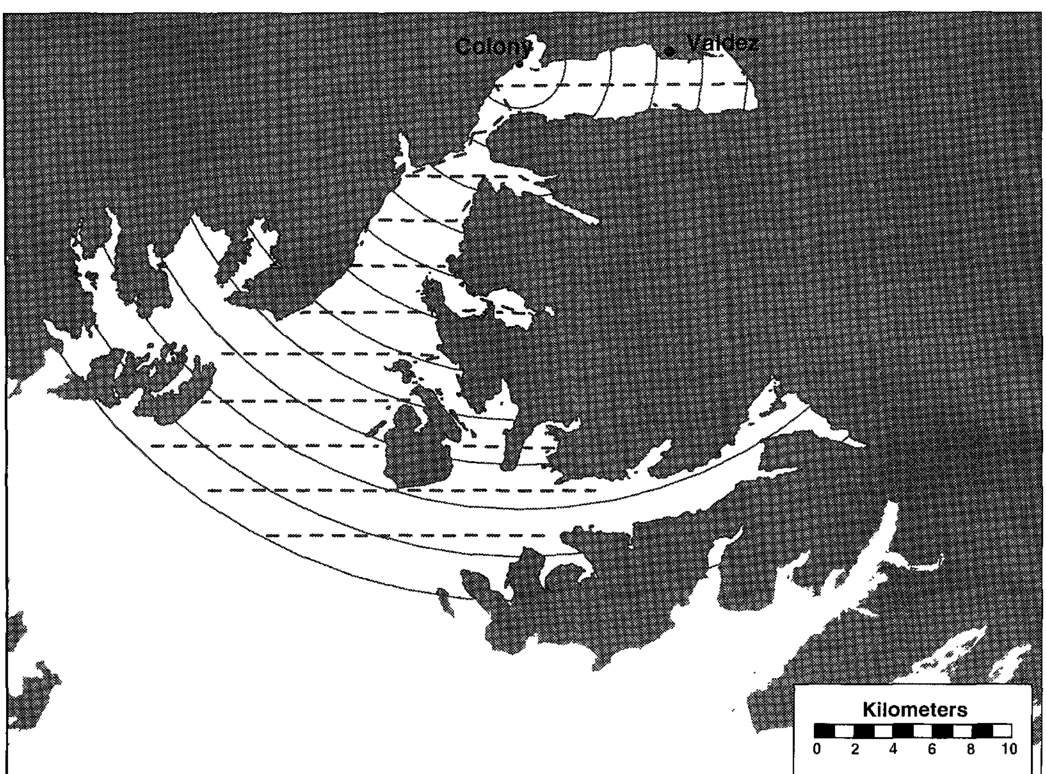

FIGURE 2. Transects (dashed lines) conducted to obtain location data on Black-legged Kittiwakes are overlaid on concentric rings (solid lines) extending out at 2 nautical mile intervals from the Shoup Bay kittiwake colony located in Valdez Arm, Prince William Sound, Alaska.

width during each survey by viewing a seabird replica, on the water, at a measured 100 m. To be consistent with radio-tracking data on bird flights, we used only locations of flying birds on strip transects ($n = 255$). Observations were made prior to a detectable influence of the ship's presence on behavior. Bird locations were recorded when the ship was closest to the point at which the birds were first observed. We recorded data directly into a computer file using custom software that recorded the number of birds observed and accessed a GPS to record the ship's position and time for each entry.

STATISTICAL ANALYSIS

To compare data collection methods we developed a set of random locations from the radio-tracking data to mimic the chance sightings of the strip transect data. To do this we assumed that the birds flew in a straight line between the GPS locations that had been recorded during flight following. A geographic information system (GIS) was then used to convert the GPS locations into contiguous tracts. To reduce tracts to a data set of manageable size, we next converted these routes to a series of points spaced 100 m apart ($n = 1,504$). For each point, we calculated the distance to the study colony. This set of points then was used as the pool of potential kittiwake locations from the radio-tracking method. We also used the GIS to calculate the distance to the Shoup Bay colony for each bird location recorded along transects.

To compare radio-tracking and strip transect data, we modified a randomization program (Noreen 1989). A data subset, equal in size to the number of bird locations from transects ($n = 255$), was randomly selected from the radio-tracking point set. Mean distances from the study colony were calculated for each data set and their difference became our test statistic. We then conducted a randomization test, by randomly selecting 255 points from the radio-tracking set, with replacement. These new radio-tracking points were then combined with the strip transect observation locations to form a pooled data set. Next, two dummy sets ($n = 255$) were randomly selected from the pooled data. We calculated the mean distances from the colony for each dummy set and compared them. We repeated this procedure for 1,000 trials, each with a new selection of 255 points from the radio-tracking set. The number of times the absolute value of the difference of means of the dummy sets exceeded the test statistic divided by 1,000 was the P value of the test statistic (Noreen 1989).

We determined the maximum distance from the study colony on the strip transect survey and the greatest distance that radio tagged birds were observed from the colony. To reduce the effect of unequal maximum distances from the colony between data sets and isolate the effect of bird spreading, all values greater than the smaller maximum value were deleted. We compared the reduced data set to the original set using the randomization test, described above, to determine if the deletions resulted in a significant change in the data set; n = the size of the reduced data set. We then reran the comparison of the strip transect and radio-tracking data using the reduced data set.

To test the model of decreasing bird detection due to bird spreading, we calculated expected values of n_i using equation 2 and a conservatively chosen N_i, then compared them to the mean n_i values observed during the two replicates of the strip transect survey. To accomplish this, we used GIS to measure the area of available foraging habitat within 12 concentric rings around the colony, each with widths of 2 nautical miles (Fig. 2). The outermost ring contained the farthest distance from the study colony surveyed by the strip transects. We determined the mean number of kittiwakes observed in each ring during the two strip-transect surveys. We multiplied the total transect length within each ring by the transect width, 100 m, to determine the area surveyed within each ring. For the innermost ring we used values for area available, area surveyed, and number of birds observed, in equation 3 to determine a value for N_1. Following the conservative assumption that each ring contained the same number of birds, we used the calculated value of N_1 for all N_i and the respective values for area surveyed and available area in equation 2 to determine values for n_i for all rings. We compared the expected n_i values thus calculated with the mean observed values graphically (Fig. 3) and with a chi-square test.

To evaluate the effect of reducing sampling effort, we wrote a bootstrapping program that simulated decreased sampling. We randomly selected 46 transects, with replacement, from the strip transect data set and used the kittiwake locations from those transects to create a simulated survey. Mean distance from the Shoup Bay colony was then calculated for the bird locations in the simulated survey. We repeated this process for 1,000 trials and calculated the mean and standard error of mean distances. We repeated the randomization with successively fewer transects (n = 46, 45, . . . , 1). We applied the same bootstrapping program to the radio-tracking data set, simulating the effect of reducing the number of kittiwake flights (n = 7, 6, . . . , 1).

All of the statistical analyses were intended for the comparison of sample data and to examine bias associated with those data. Statistical inferences from these procedures are limited to the two sets of sample data (255 points from the strip transect observations and 1,504 points from the radio-tracking observations). The number of unique birds involved in the 255 sightings from shipboard transect lines is not known and thus limits the use of more common statistical methods. Conclusions relative to the applicability of these results to the Shoup Bay colony are presented in the Discussion. Our statistical methods should not be applied to studies in which the objectives are to make inferences about the behavior of birds at a colony. In all comparisons we assumed $P \leq 0.05$ to be significant.

RESULTS

The mean distance from the Shoup Bay kittiwake colony in the radio-tracking data was significantly greater than in the strip transect data, 35.5 km and 22.2 km, respectively ($P = 0.001$). The maximum distance to the colony for the radio-tracking data set was 62.3 km compared to 47.3 km for the strip transect survey; therefore, we deleted 314 locations from the radio-tracking data set with values greater than 47.3 km. Consequently, the mean distance to colony for the radio-tracking data was reduced significantly to 29.4 km ($P = 0.001$). After deletions, the radio-tracking mean distance to colony remained significantly greater than the strip transect value ($P = 0.001$).

Our expected numbers of kittiwakes obtained using equation 2 was different from the numbers observed in rings ($\chi^2_{11} = 37.9$, $P = 0.001$). The observed values were consistently equal to or below the expected values (Fig. 3).

Simulating a reduced sampling effort for both strip transect and radio-tracking studies resulted in exponentially increasing variability (Fig. 4). The standard error for the radio-tracking data set (2,976) was greater than that obtained by the strip transect method (2,628). A standard error value (2,891) most similar to that obtained by the radio-tracking method was achieved by reducing the sampling effort to 34 transects out of 46.

DISCUSSION

Our comparison of radio-tracking and strip transect data isolated two sources of bias. Differences in the mean distances from the colony obtained by the two sampling methods were significantly different; these differences were the result of underestimating the foraging range of kittiwakes when designing the strip transect survey. However, this source of bias does not account for all error. By eliminating distances from the radio-tracking data set that were larger than those that could be obtained from strip transects, we removed the influence of unequal maximum distance to examine the effects of bird spreading separately. The deletions resulted in a significant reduction in mean distance from the colony of the radio-tracking set that we attributed to bias associated with unequal maximum distances. Following deletions, the mean distance from the colony of the radio-tracking data set remained significantly larger than the mean obtained from strip transects, indicating residual bias. We suggest that the source of this remaining bias is the result of reduced detectability of birds at increasing distance due to bird spreading.

We do not know to what extent the energy costs of carrying radio transmitters and using only birds with chicks affected our results. However, as previously indicated, we anticipated that the most probable influence of these factors, if any, was that the mean trip distances of our radio-tracked birds would be less than the mean of the rest of the population in the colony. These sources of bias did not reduce the mean flight distance of the radio-tracking data set to less than the strip transect mean and they do not account for a greater mean obtained from radio-tracking.

We did not quantify the extent to which observations of birds from other colonies may have affected our results. However, the nearest colony, i.e., > 50 pairs, was located at Eaglek Island (296 breeding pairs; U.S. Fish and Wildlife Service, unpubl. data, Anchorage Alaska), 75 km, over water, from the Shoup Bay colony. The

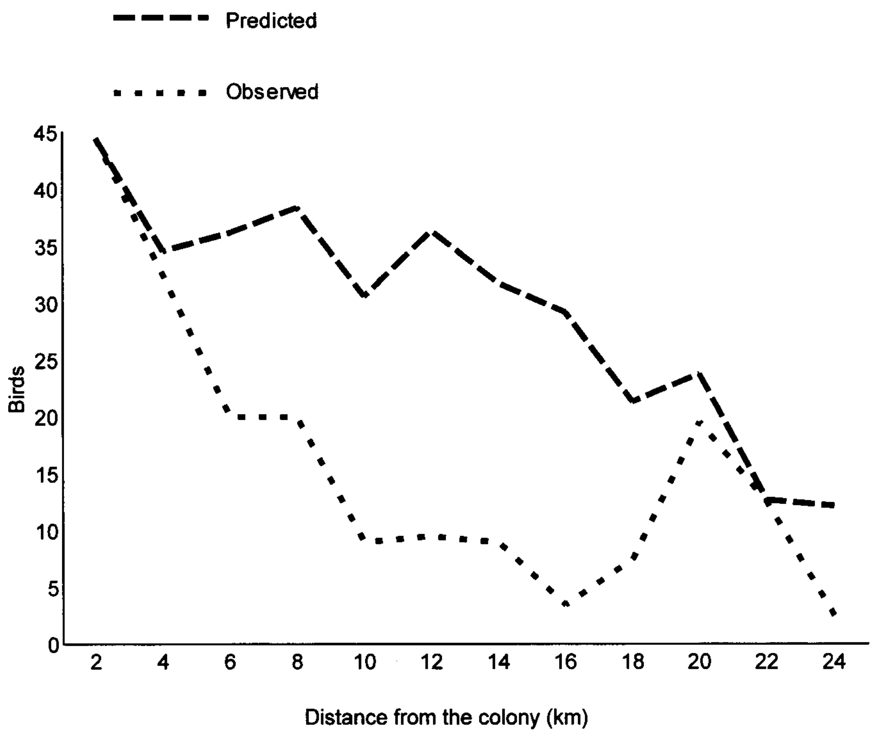

FIGURE 3. Comparison of the number of Black-legged Kittiwakes observed within concentric rings (Fig. 2), extending from the Shoup Bay Colony, Prince William Sound, Alaska, to numbers predicted by a model of the decreasing probability of detection due to bird spreading. Field data were obtained on two surveys of systematically arranged transects (Fig. 2).

closest point of the strip transect study area to the Eaglek Island colony, 33 km, was located on the southwest edge, 47 km from the Shoup Bay colony. These distances were within the foraging range of kittiwakes that we observed, and it is possible that birds from the Eaglek colony occurred within our study area. The area of potential overlap of colony foraging ranges would have originated at the portion of the study area that was most distant from the study colony. Hence this source of bias would tend to inflate the distance at which birds were observed on the strip transect survey. Due to the smaller size of the Eaglek Island colony, 5.3% as large as the Shoup Bay colony, we assumed that this bias was small, and we observed that its influence was not enough to increase the strip transect mean distance to a value greater than that of radio-tracking.

Consistent with Decker's (1995) application, strip transect observations were significantly different than the predictions of the model of the decreasing probability of detection due to bird spreading. Differences may have resulted from assuming no attenuation of bird numbers as distance from the colony increases. The initial greater rate of decline in the number of birds observed compared to predicted numbers may indicate that attenuation was having an effect on the number of birds observed (Fig. 3). However, an equal number of birds predicted and observed at 22 km suggests that at this distance the bird numbers had not attenuated to a level detectable by our sampling. These findings indicate a general conformity to the prediction of decreased detection due to bird spreading and possibly attenuation. The results of both our randomization comparison and modeling efforts suggest that our strip transect data were biased due to spreading. We conclude that radio-tracking data gave a more representative indication of foraging distances than did data from strip transect sampling. Studies that have used strip transect data to describe the distribution of birds relative to colony location, and have not accounted for bird spreading (Wilson et al. 1988, Leopold et al.

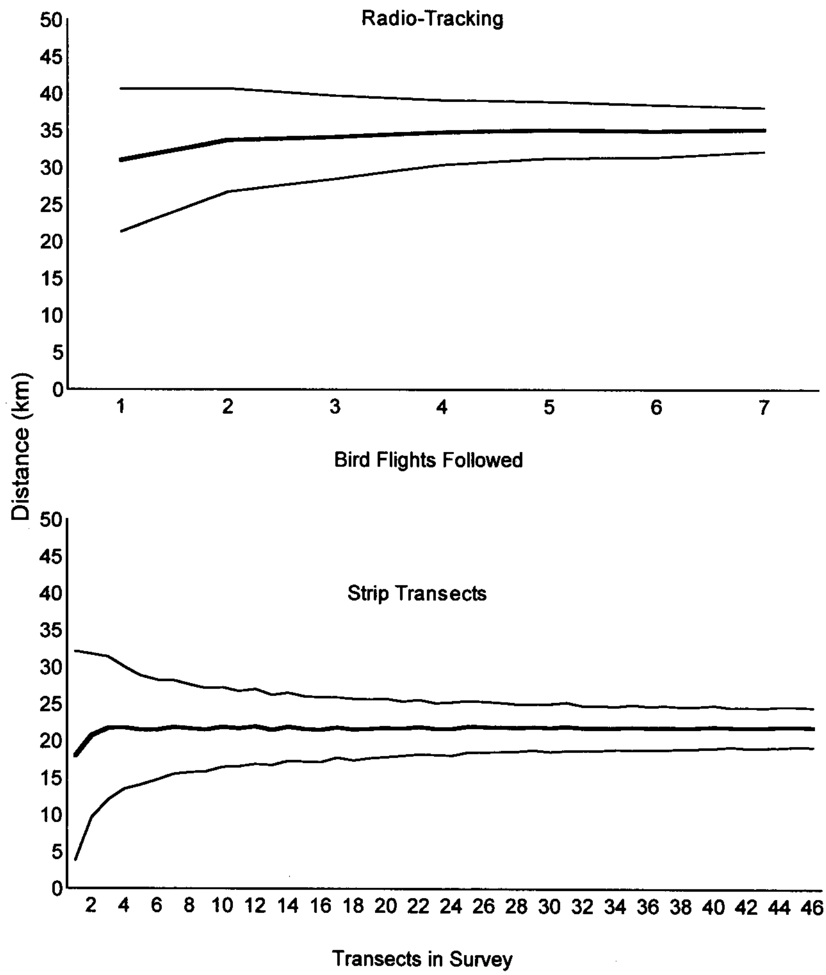

FIGURE 4. The results of a bootstrapped simulated reduction of the sampling efforts of radio-tracking and strip transect studies of Black-legged Kittiwake in Valdez Arm, Prince William Sound, Alaska. The simulation demonstrated how the mean (bold lines) and standard error (fine lines) values for the distance birds were observed from their colony changed as sampling effort was reduced.

1995), probably underestimated foraging ranges. This bias could be reduced by applying weighted averages, that account for the areas surveyed and available, at distance from the study colony, instead of our use of simple means. We have used mean distances from the colony to make comparisons between our data sets; however, these types of data are more frequently used to determine foraging ranges or foraging distance (Wilson et al. 1988, Leopold et al. 1995). Weighted means may not be applicable to these more common methods of analysis, yet spreading remains a source of bias. In these applications, bias can be reduced by sampling the same proportion of the total area within each ring.

Our simulation of reducing sampling effort resulted in exponential increases in variability as sample size was decreased for both methods; however, the rate of change in variability was greater for the radio-tracking data (Fig. 4). This comparison indicates that strip transect sampling yielded more precise data in a shorter time, but the trade off for low variability and less field time was a failure to detect the longer flight distances made by kittiwakes. We caution that this analysis is intended to detect biases between the two sampling methods. If parameters with measures of precision (e.g., confidence intervals on mean foraging distance) are to be estimated for the colony using radio-tracking or strip transect data, then other statistical procedures are required which identify a proper sampling unit in order to avoid pseudoreplication

In a review of empirical studies of animal dispersal, Koenig et al. (1996) identified study areas that are smaller in extent than maximum dispersal distance and a decreasing probability of detection as distance from the point of dispersal increases as major sources of bias associated with transect sampling methods. They compared results obtained from transect studies to both radio-tracking and genetic studies and determined that transect studies consistently underestimated dispersal distances. The topic of central place foraging by kittiwakes, discussed here, is similar to that of dispersal but differs in temporal scale. Foraging takes place daily, whereas dispersal from a central place may occur only once during the life of an organism. That both Koenig et al. (1996) and this study found the same sources of bias suggests that the limitations of transect sampling of animal movements may extend across taxa and temporal scales.

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