HOME RANGE SIZE AND HABITAT USE PATTERNS OF THE SANDERLING (<u>CALIDRIS</u> <u>ALBA</u>) ON THE OREGON COAST NONBREEDING RANGE, AND COMPARISON WITH HOME RANGE SIZES IN CALIFORNIA AND PERU

by

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A THESIS

Presented to the Department of Biology
and the Graduate School of the University of Oregon
in partial fulfillment of the requirements
for the degree of
Master of Science

June 1990

An Abstract of the Thesis of

Maureen L. de Zeeuw for the degree of Master of Science
in the Department of Biology to be taken June 1990

Title: HOME RANGE SIZE AND HABITAT USE PATTERNS OF
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Approved: ___________________________________
Dr. Peter W. Frank

During the nonbreeding season I observed the degree of site faithfulness of individual Sanderlings, Calidris alba, on the Pacific coast of southcentral Oregon, and the linear home range size was estimated. Home range size of Oregon birds and range sizes of individuals wintering in coastal areas of California and Peru were compared to determine if annual migration distance from the high arctic breeding ground is positively correlated with home range size. Oregon sanderlings on average remained within a minimum range of 17 km during the nonbreeding season from October through April, although spring data are sparse. The Oregon home range is significantly larger than that of birds in Bodega Bay, California, and similar to that of birds in Peru. Therefore home range size is not correlated with

distance from the breeding ground.

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Ornithological research grant, Frank M. Chapman Memorial Fund, American Museum of Natural History, 1990

AKNOWLEDGMENTS

I wish to thank my advisor, Professor Peter Frank, for his invaluable advice and assistance with the analyses and manuscript, and for the support and sense of humor that encouraged me. In addition, I wish to thank Dr. J.P. Myers for the impetus he gave in forming the hypothesis of this study and for the training in field techniques and procedures. Very special thanks are due to Suzanne Fellows for her assistance in the field, and particularly for the time, patience, and training in computer usage which she gave me. I am grateful for the help of Professor James Carlton, Dr. Jan Hodder, Doug Warrick and Chad Hewitt. Last but not least I wish to thank my family for their support and inspiration. The National Audubon Society provided the use of the three-wheeler. This investigation was supported in part by a grant from Sigma Xi, and by a grant from the Frank M. Chapman Fund, American Museum of History.

Dedicated to the memory of Brian B. Hoover

TABLE OF CONTENTS

APPENDIX

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

An individual's relation with its environment is reflected in its patterns of space use or level of organization in space and time. Myers (1984) defined four levels of spatial behavior seen in shorebirds: (1) individual (moment to moment spacing, as in adjustments in flock size or tightness, on a scale of centimeters to hundreds of meters) (see also Myers 1983), (2) local (movements of hundreds to thousands of meters within a day or the tidal cycle, and, spatially, within the home range), (3) regional (nomadism vs. faithfulness to a particular site during either its nonbreeding or breeding season, with movements on a scale of tens to hundreds of kilometers and space use patterns varying over a period of days to months), and (4) global (migratory patterns involving up to in excess of thousands of kilometers over a year or more).

Where a shorebird occurs, its space use or "spacing behavior", during its nonbreeding season can have profound influence on population structure, affecting how many and which conspecific individuals each may encounter during its lifetime. Cox (1985) concluded that population density, for example, of migrants is limited by conditions during the nonbreeding as well as breeding season. Nonbreeding range refers to where an individual or conspecific group occurs on the regional level of spatial organization during the nonbreeding season of the species. Individual birds of some species occur within their own home ranges within the nonbreeding range of the local population. These individual home ranges may be defined as those areas within which a bird is found a given high percentage of the time. Comparisons between characteristics (e.g. size) of different nonbreeding home ranges of members of the same species can provide valuable information about the bird's habitat requirements.

Sanderlings (Calidris alba) breed in the summer in the high arctic, and the nonbreeding ("winter") range of the species has an immense geographic scope. They begin to migrate southward from the breeding grounds as early as July, and from October to early May are abundant on sandy beaches world-wide (see Cramp and Simmons 1983, Myers 1987 for an extensive description of range), including the Pacific shores of North and South America from Washington to Chile. Because of their high numbers and ubiquity in a geographic zone which is essentially two-dimensional and has good visibility owing to sparse vegetation (the sandy shoreline), they are excellent birds for research on spatial behavior, and Myers (1988) mentions that they have become a "white rat" for shorebird research.

Myers, Schick, and Castro (1986) conducted studies on the space use patterns of Sanderlings on their nonbreeding ranges in coastal areas of Bodega Bay, California and Peru. They concluded that most sanderlings exhibit site faithfulness (occasionally described as "site tenacity", see Gauthreax 1982), confining most of their activity during the nonbreeding period to distinct home ranges along the length of the beach. Therefore, they stated, patterns of association among conspecifics at this regional level of spatial behavior are highly ordered, and an individual Sanderling will interact with a particular subset of all Sanderlings that occur along that coast. Additionally, it will interact with a somewhat restricted array of competitors and predators.

Specific home range sizes, expressed as length along the line of the beach, were determined in the course of the same study, and those in California and Peru were compared. Peruvian birds occurred in a broader area during the nonbreeding season than Californian birds. California Sanderlings have also been found to wander more broadly in August than in the late fall and winter months, and more so in the spring (defined as March and April) than in the autumn (September and October) or winter (Myers 1984, Myers et al. 1986). (Parallel studies have not been conducted in Peru).

One hypothesis for the observed difference between Californian and Peruvian home range size is that the annual migration distance from the breeding ground is positively correlated with home range size (Myers pers. comm.). Sanderlings numbering in the low thousands winter on beaches of the southcentral Oregon coast, a site approximately 650 km north of Bodega Bay, California but relatively close to it in distance relative to California and Peru from the arctic breeding range (approximately 4500 km and 11,000 km, respectively) (see Figure 1). If this hypothesis is correct, Sanderlings on these Oregon beaches should have range sizes similar to or narrower than those in Bodega Bay, and distinctly narrower ones than those in Peru.

In this study, I evaluated Sanderling spacing behavior for degree of site fidelity, and estimated individual home range size on the southcentral Oregon coast during the nonbreeding season. Site faithfulness and home range size were compared to those recorded for Californian and Peruvian beaches. This study also considered the effect of season (autumn, winter, and spring) on site faithfulness in Oregon, comparing it with a seasonal change in home range size in California. Distance between successive sightings of the same individual is used as a measure of site faithfulness. Unless a bird occupies a fixed home range, as time intervals between sightings of an individual increase, distance between these sightings are expected to increase. Therefore, to examine the effect of temporal contingency on site faithfulness, the effect of time in days elapsed was also evaluated.

Additionally, to tease apart possible separate classes of Sanderling spatial behavior on the Oregon coast, I compared birds that were sighted only once or twice overall with the time (date during the nonbreeding season) of their sightings. I also looked for differences in the number of sightings during the nonbreeding season of birds belonging to different age classes and sexes.

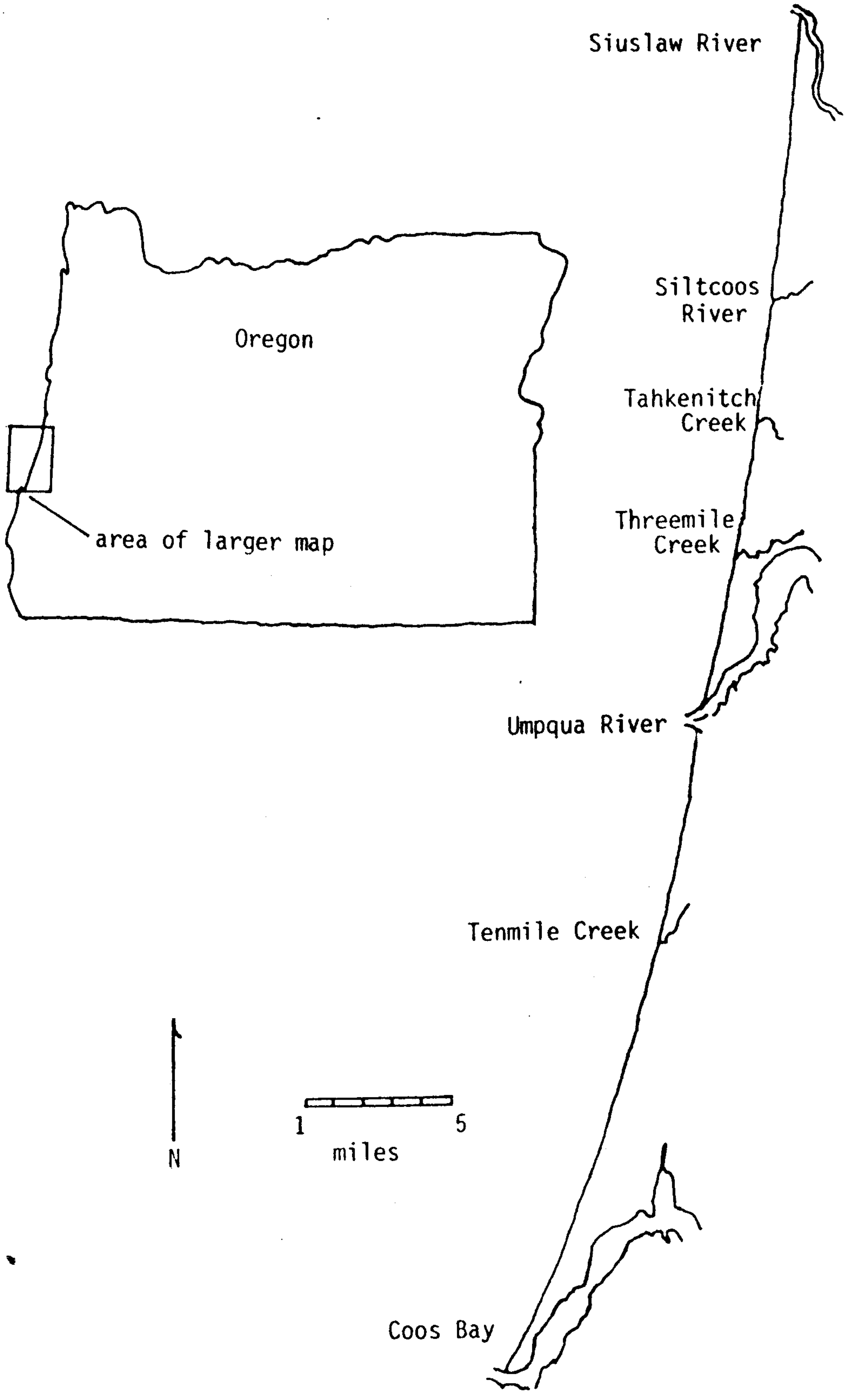
FIGURE 1: Relative distances of Sanderling nonbreeding populations from the arctic breeding range. (Actual migratory pathways not shown.)

METHODS

Study Site

Open sandy beaches of the Pacific Ocean on the southcentral coast of Oregon were surveyed for locations of individual Sanderlings. The study area extended from the north jetty of Coos Bay (43 21 N lat, 124 20 W long) northward to the south jetty of the Siuslaw River (44 01 N lat, 124 08 W long). This is a shoreline of approximately 75 km, and I searched the width of the beach (see Figure 2). Except for creek mouths and the Umpqua River mouth (approximately 0.5 km) and its artificial rock jetties (constructed perpendicular to the shore), this site is a continuous sandy beach. It is bounded to the south by Coos Bay which has a narrow (approximately 0.7 km) river-like opening between two rock jetties. Extending approximately 15 km south from Coos Bay are expanses of rocky headlands which are broken occasionally by small (1.0 km or less in length) sandy beaches. Steeply sloped narrow sand beaches continue for another approximately 7.5 km until widening again into open beach ("Bullards Beach"). To the north the study area is bounded by the Siuslaw River opening (approximately 0.5 km) between rock jetties. Wide

FIGURE 2. Study area on the Oregon coast of the Pacific Ocean.


Siuslaw River
Oregon
area of larger map
Siltcoos River
Tahkenitch Creek
Threemile Creek
Umpqua River
Tenmile Creek
N
1
5
miles
Coos Bay

sandy beaches continue northward for approximately 8 km, with intermittent rocky and vegetated headlands and sandy beaches for 60 km further. The beaches comprising the study area are wide and backed by low foredunes covered with European beach grass (Ammophila arenaria). The entire ocean boundary (approximately 61 km) of the Oregon Dunes National Recreation Area is included within the study area.

In the nonbreeding season Sanderlings forage on these beaches for invertebrates. Sanderlings may be found across the width of the open sandy beach, from the surf zone to the area between the upper rackline and the seaward side of the foredune but are normally found within 2 m of the tideline (pers. obs., Stinson 1979). Because of the relative narrowness of this beach area, the study site is essentially linear.

The study area, approximately 650 km north of Bodega Bay (38 20 N lat, 123 04 W long) and 8000 km north of Myers et al.'s (1986) Peruvian field site (12 15 S lat, 76 55 W long), was chosen because of the large number of banded Sanderlings found there each winter (see Procedures, below). The central portion (from the Umpqua River to Three Mile Creek) was the capture site for the birds that were banded. The boundaries of the study site were chosen because they are approximately half the length of the study site, to the north and south, from the central banding "node", and because of logistical problems in surveying beyond these points. The total length of the site is significantly greater than the recorded width of Sanderling home ranges in Bodega Bay (approximately 10 km) and in Peru (up to 25 km) (Myers et al. 1986).

Procedures

Sanderlings were caught and banded on the beach between the Umpqua River and Three Mile Creek in the autumns of 1986, 1987, and 1988 by a research group led by J.P. Myers. The birds were leg-banded with unique color combinations of plastic rings so that each individual was identifiable. In the wild, the rings or bands are easily distinguished on the birds with a spotting scope. The unobstructed sandy beach habitat in which the birds forage allows ready viewing of each bird present.

Both juveniles (birds hatched in the summer of the year they were banded) and adults were banded. The banded birds were released at various sites between a small beach near the jetty on the south shore of Coos Bay ("Coast Guard Beach") and Three Mile Creek (the capture site). Others were released on various California beaches as part of a separate, unpublished transplant study of J.P. Myers (see Myers et al. 1986). In 1988 only birds banded as adults were released in Oregon.

The study site is accessible to off-road vehicles from five points. The entire study site was essentially divided into five separate tracts because creeks and rivers between them are too deep to be passable. Vehicles are allowed on the beaches between October 1 and April 30, except for approximately 0.8 km in an area north of the Siltcoos River, and for 10.5 km south of the Umpqua River. Vehicles are also generally not allowed to cross the creek estuaries.

The study site was traversed using a "three-wheeler" type off-road vehicle, and every Sanderling not in flight was checked for bands by spotting scope. The three-wheeler was fitted with an odometer so that distance travelled from point to point could be recorded. The beach was surveyed by travelling in straight line fashion along the beach so that distance traversed could be used to determine location at any one point. The location, to the nearest kilometer, of each banded Sanderling along the line of the beach was thus recorded along with date and time of sighting. If the same bird was seen more than once in one day, only sightings that occurred within different kilometers were recorded. For the remaining discussion note that "sighting" is not equivalent to "bird" because there were cases of several sightings in a given day of one bird. The presence of the three-wheeler did not appear to frighten the Sanderlings or affect their movement.

My study was conducted during two consecutive nonbreeding seasons. I began surveying on 26 October 1988, and searches continued throughout the winter and until

5 May 1989. Data were also available for a small section of the study site for July through October 1988. During the second nonbreeding season, observations were confined to the fall, from 18 September until 9 November 1989.

Surveys were attempted daily throughout the two study periods, but were actually conducted between four and nineteen days per month. Weather, mechanical, and other conditions prevented a greater frequency of searches. It was not possible to cover the entire study area in one day. One or two of the five tracts of the study site, an average of 14.5 km, were searched in a day. I attempted to survey every section of the beach an equal number of times over the study period (see Analysis).

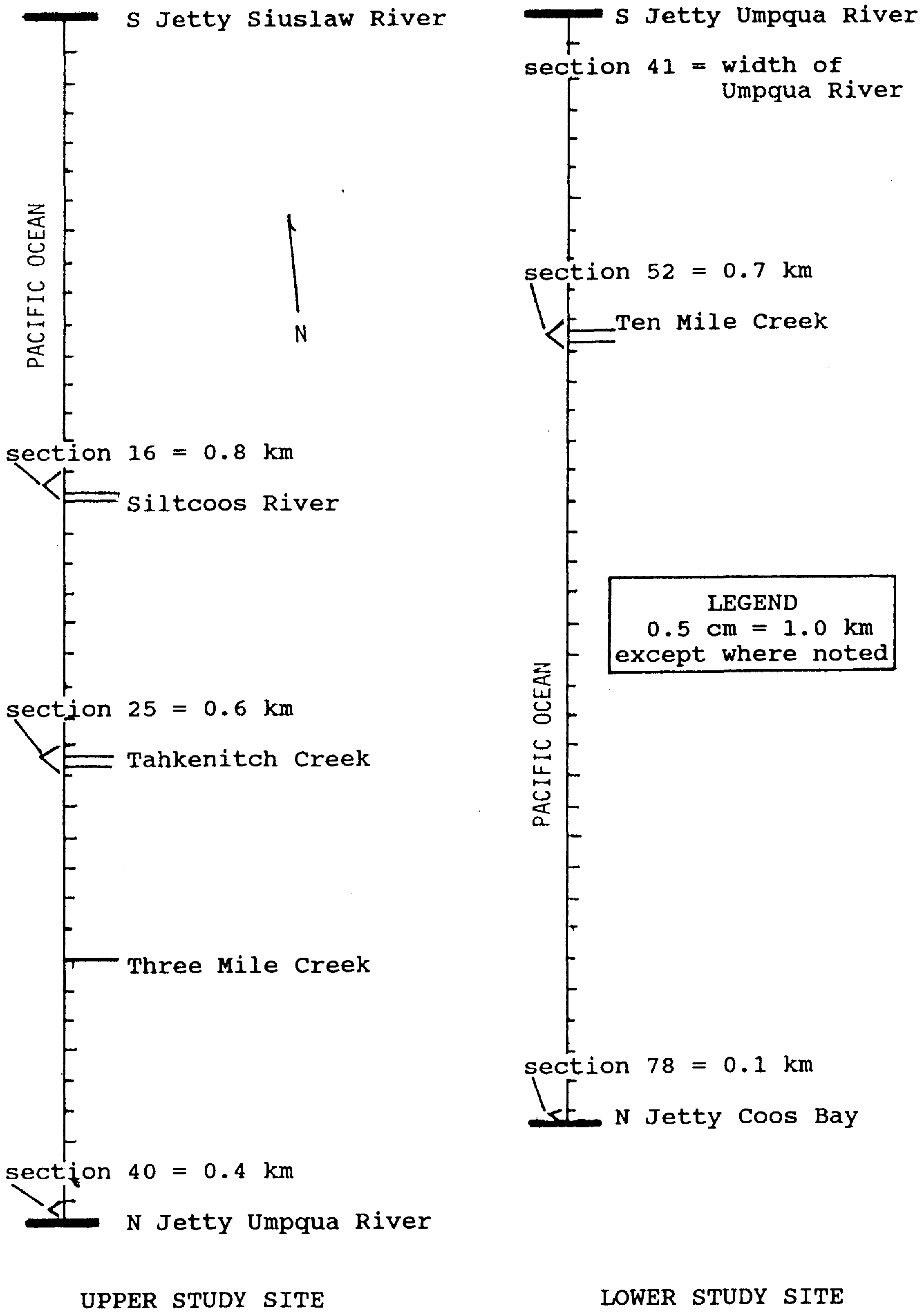
Observations were during daylight hours and when the tide was low enough to permit operation of the three-wheeler on the beaches, which were sometimes narrow and bounded by low storm-cut cliffs or wide, log-strewn wracks at the high tide line. Except for that consideration, surveys were conducted during all periods of the tidal cycle.

Analysis

For the analyses, the study area was divided into 78 one-kilometer sections. However, because the site was surveyed as five separate tracts and not travelled and measured continuously from one end to the other, exceptions resulted. None of the five tracts was an integer number of kilometers in length, and some creek widths were impossible to measure precisely. This resulted in six of the 78 sections (see Figure 3) being all somewhat less than 1 km long. Hereafter the 78 "sections" are taken to be synonymous with kilometers, and the departure from reality will be addressed in the Discussion.

Because all sections were not searched equally often, a data set composed only of sightings under conditions of equal search intensity had to be derived. In other words, all of the resighting points used in the analyses came from a set of an equal number of searches of all 78 sections of the beach (with an exception for section 41, the Umpqua River). In this way, sampling bias was removed. This set was determined by examining the data for all non-overlapping contiguous time periods within which all sections were searched at least once. Searches that occurred at other time periods were not included. Within each of these periods some sections had been searched more than once. For these, dates with the largest number of sightings of banded birds were selected. All other searches of those sections were not used. It should be noted that, for these purposes, the number of sightings were generally not determined for each of the 78 sections, but for a continuous line of sections searched on one day. For example, on one day within the time period sections 25 through 31 may have been searched with 12 sight records overall. On another day

FIGURE 3. Schematic view of study area: Oregon coast shoreline from Siuslaw River to Coos Bay. (Landmarks not drawn to scale).


S Jetty Siuslaw River
PACIFIC OCEAN
N
section 16 = 0.8 km
Siltcoos River
section 25 = 0.6 km
Tahkenitch Creek
Three Mile Creek
section 40 = 0.4 km
N Jetty Umpqua River
UPPER STUDY SITE
S Jetty Umpqua River
section 41 = width of Umpqua River
section 52 = 0.7 km
Ten Mile Creek
LEGEND
0.5 cm = 1.0 km
except where noted
PACIFIC OCEAN
section 78 = 0.1 km
N Jetty Coos Bay
LOWER STUDY SITE

within the same time period sections 25 through 31 may been searched with 8 sight records. The latter search would be the one deleted from the "equal probability set" because of the lower number of sightings overall. This method resulted in data with an equal number of searches of each of the five tracts, but a maximum number of observations. (See Table 1 for a list of the search dates and sections used.) Only sightings of birds which were seen at least twice were included in this set and contributed to the estimates of range. These data were the basis of the following analyses, unless use of the "total set" (all data) is noted.

Distance between successive sightings of an individual was used as a measure of site faithfulness. To determine if time between sightings during one nonbreeding period has an effect on site faithfulness, the distance, to the nearest kilometer, between each resighting of an individual bird was determined. The distances used were only from one sighting to the next, in chronological order, and not from the first to the third sighting, etc.. Distances between these successive sightings and the times in days between each successive sighting were calculated for all birds. The difference in distance was plotted against days elapsed. Additionally, a multiple regression analysis, as described below, was performed.

To evaluate whether or not there is a seasonal effect on resighting distance, kilometers between successive

TABLE 1. Dates and sections searched with equal intensity during two nonbreeding seasons

Date (mo.day.yr)	Days since July 7 1988	Sections searched	Date	Days since July 7 1988	Sections searched
I.11.15.88	131	1-40	VI.09.20.89	440	35-40
11.18.88	134	42-52	09.22.89	442	29-34
11.20.88	136	53-78	09.23.89	443	66-78
			09.24.89	444	53-65
II.01.28.89	205	1-15	09.25.89	445	42-52
01.29.89	206	52-78	09.26.89	446	17-25
02.12.89	220	27-40	09.28.89	448	31
02.13.89	221	25-26	09.29.89	449	26-28
		42-51	09.30.89	450	1-16
02.14.89	222	17-24			
			VII.10.14.89	464	32-33
III.02.15.89	223	25	10.17.89	467	17-31
		42-52	10.20.89	470	1-16
02.17.89	225	53-78			42-51
02.25.89	233	26-40	10.24.89	474	52-78
02.26.89	234	17-24	10.25.89	475	34-40
02.27.89	235	1-16			
			VIII.10.27.89	477	25-35
IV.04.11.89	278	42-78	10.28.89	478	1-16
04.12.89	279	17-40	10.29.89	479	17-24
04.14.89	281	1-16	10.30.89	480	42-52
			10.31.89	481	36-40
V.04.29.89	296	53-78	11.03.89	484	52-78
05.01.89	298	36-52			
05.04.89	301	17-35			
05.05.89	302	1-16			

resightings were compared with the absolute time in days elapsed since the beginning of the study. This date was July 7, when the first sightings were made of banded Sanderlings in the study area. In this way, the difference in kilometers between each sighting of a bird and the next sighting of the same bird was plotted against the date of the resighting, and results were given as both nonbreeding seasons combined.

A multiple linear regression analysis for effects of year (1988-1989 and autumn of 1989), as well as time (days elapsed between successive sightings within a single year) and season (days elapsed after July 7) on resighting distance was performed for the "equal probability" data set.

To estimate home range size, the distance between successive sightings of an individual bird was again used. If time between successive sightings is found to have no effect on distance between them, these particular pairs of sightings are a suitable sample of all pairs of sighting distances. The frequency distribution with which birds were seen at different distances was then obtained. This absolute number of times that a Sanderling may be found within a particular length of beach was plotted. From the absolute numbers, the percentage of successive resightings at any given distance apart was determined, as was the cumulative percentage or frequency for increasing distances. Results were expressed as cumulative percentage of time or probability that an individual appears within a given length of beach.

This result was compared with an estimate of home range size as implied by the standard deviation, since home range was taken to be unidimensional. If two sightings are assumed to be random locations within a fixed home range, the distance between them is estimated to be the square root of 2 times the standard deviation of the distribution. A home range size for a normally distributed array of sightings may then be calculated for a given confidence interval.

As an additional examination of home range size, individual home ranges of the birds that were seen most often during all searches were calculated. Because all sightings (the "total set") and not only the sightings of equal probability with respect to area searched were used, results were expressed not as proportion of appearances within a given range but simply as the area within which all sightings occurred.

To ascertain if low numbers of sightings of an individual indicated a particular pattern of space use by some Oregon coast Sanderlings, I compared number of individuals that were no more than two times with the date of sighting. The data for this analysis came from the total set of all survey dates, and were not confined to the equal probability set, because the concern here is not specifically where the bird is seen, but when it was ever seen anywhere on the Oregon Dunes beaches.

Finally I examined the data from the total set of searches for any differences between the sexes and three age classes in the number of times an individual was seen. The number of birds that were seen only once, twice, three times, etc. was calculated for females and compared with the same data for males. The numbers of birds of each age class seen only once, twice, etc. were similarly compared. The age classes are as follows: birds that were adults (at least one year old) when banded in the autumn of 1986 are known to be three or more years old in the autumn of 1988, when my surveys began. Birds that were juveniles (hatched in the summer) when banded in autumn of 1986 are known to be two years old in autumn of 1988. Birds that were juveniles when banded in autumn of 1987 are known to be one year old in the autumn of 1988. No birds banded as juveniles in the autumn of 1988 were released in Oregon and none appeared during my survey periods. Therefore the three age classes for which number of sightings was examined were birds three or more years old, two years old, and one year old in the autumn of 1988. Birds that were adults when banded in 1987 could be two or three or more years old, and birds banded as adults in 1988 could be one or two or three or more years old, and therefore these two categories of birds, which could overlap with the known age classes, were not used. Results for both the sexes and age classes were expressed simply as frequency of individuals of each class with a given number of sightings.

RESULTS

During both nonbreeding seasons, the maximum number of sightings of banded birds recorded on one search day was 42 (on October 30, 1988 on the tract from section 25 to section 41), with 0 sightings being the minimum. A total of 148 banded birds were seen, and 107 of these were seen at least twice. Twenty-eight birds were seen at least 10 times each, with one bird seen a maximum of 20 times, during the total period of both survey seasons.

Table 1 shows the dates and sections in which birds were searched for with equal intensity. Five continuous time periods of surveys of equal sampling intensity with respect to area searched were derived for the 1988-1989 nonbreeding season, and during the autumn of 1989, all sections were searched with equal intensity three times. (See Appendix A for list of all dates of observations). Sixty-seven birds were seen at least twice during these "equal probability" searches. The maximum number of sightings during these searches was 8 for any one bird. (See Appendix B for list of sightings of equal probability with respect to area searched).

When sightings of all birds seen only once during the "equal probability" searches were deleted, and the differences in time and distance between successive sightings were derived (thereby translating n sightings into n - 1 "differences"), the data were pared to 141 points (see Appendix C). These were the resighting differences in time and distance used for all analyses that required there be no sampling bias.

Effect of Time

Time in days elapsed between successive resightings of an individual is shown to have no effect on difference of distances between sightings when plotted (Figure 4). The multiple regression analysis (Table 2) does, however, show time almost to be significant, but the probability is

TABLE 2. The regression analysis for effects of year (1988-1989 = 1; autumn 1989 = 2), season (days after July 7), and time (days between successive sightings within a single year) on distance between successive sightings

Source of variation		DF	Sum of squares	Mean square	F	Prob.
model	b0= 0.9996	3	1362.442	454.147	5.01	0.0025
year	b1=-0.2012	1	0.188	0.188	0.00	0.96
season	b2= 0.0295	1	92.021	92.021	1.00	0.32
days	b3= 0.0578	1	295.715	295.715	3.22	0.075
Error		137	12,410.721	91.931		
Total		140	13,773.163			

$Y = b0+b1*x1+b2*x2+b3*x3$, where $x1$ = year, $x2$ = season, $x3$ = days elapsed between successive sightings.

Note: Data of equal probability with respect to dates and area searched was used.

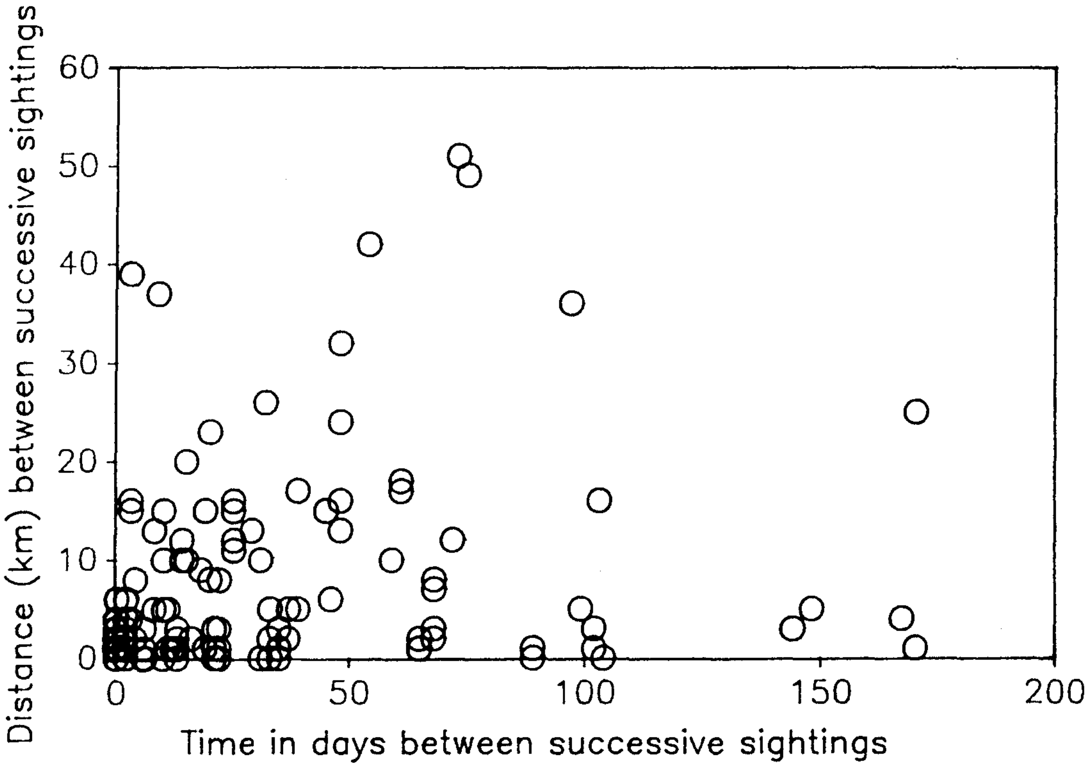


FIGURE 4. Effect of time on distance between successive sightings.

greater than 5% and there is no strong indication that any one of the variables considered has a strong effect (see below).

The lack of an effect of time between sightings on distance travelled during the nonbreeding season differs from the expectation that successive sightings (of an individual) which are close together in time will be a shorter distance apart than successive sightings that are comparatively farther apart in time. This result indicates that the scale (in kilometers) of a nonbreeding home range in Oregon presents no difficulties to Sanderlings, or at least that the birds are capable of moving over the distances involved here in short time periods. In fact, Myers (1984) observed that one Bodega Bay bird moved between two locations 20 km apart at least four times in 12 days.

Effect of Season

Season, in terms of the fall, winter, and spring periods of the nonbreeding period, is found to have no effect on difference of distances between successive sightings of an individual. This result is evident in the random scatter plot of Figure 5. The multiple regression analysis also shows that the season variable is not significant. This result contrasts with the conclusion of Myers et al. (1986) for Bodega Bay birds that Sanderlings range more broadly in the spring, spending 82%, rather than more than 95% as in the winter, of their time within a 10 kilometer home range.

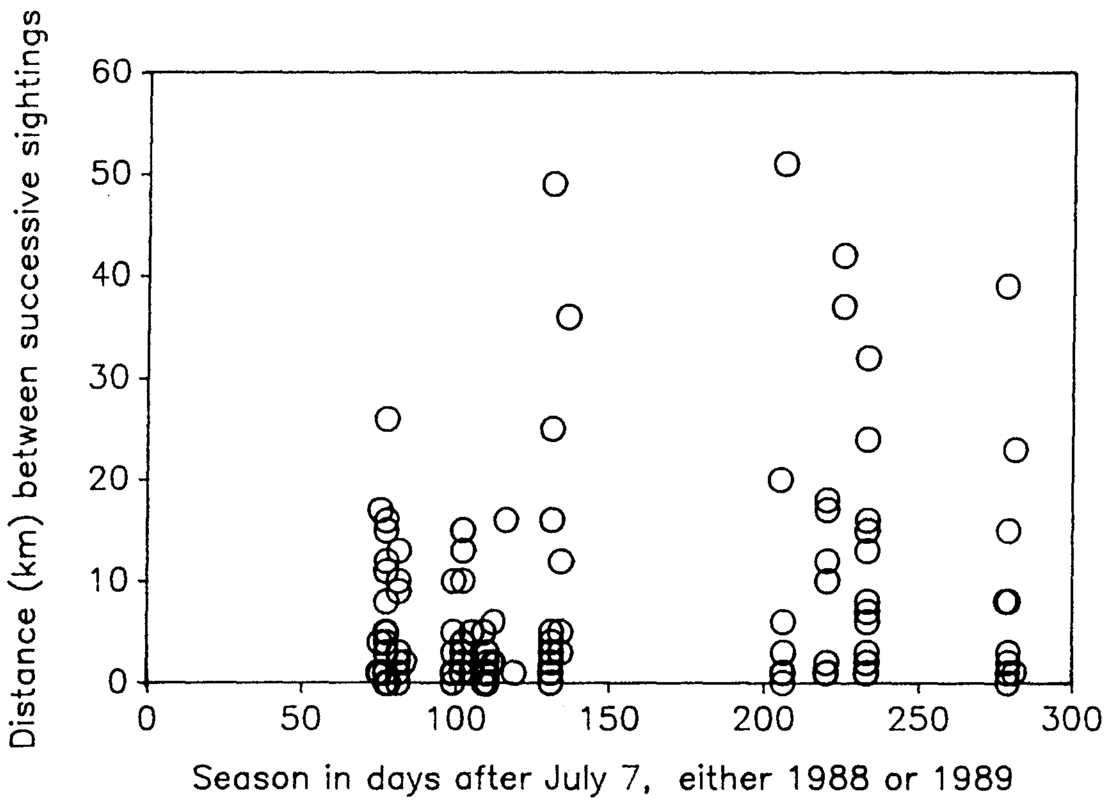


FIGURE 5. Effect of season on distance between successive sightings within one nonbreeding season.

Effect of Year

The multiple regression analysis also shows that the year of the nonbreeding season itself is not significant. In other words, the two survey periods (the nonbreeding season of 1988-1989 and the autumn of the nonbreeding season of 1989-1990) do not differ in distance between sightings of a bird.

Home Range Size

During the daylight hours of the nonbreeding season, 90% of a Sanderling's appearances occur within a 17 km length of beach (Figure 6). In other words, in Oregon an individual can be expected to exhibit site faithfulness and to be found within a home range of 17 km 90% of the time. Above 90% the curve begins to level out. If time between sightings had an effect on resighting distance, one could not have confidence in this calculation of range size, since distance between resightings would increase with time. However, time was shown to be unimportant.

The calculation of home range size from the standard deviation yielded an estimate of 19 km when the average distance between 141 successive sightings of single birds along the Oregon coast (6.86 km) was multiplied by 0.7071 to give a standard deviation of 4.85 km. A 95% confidence interval for the distance over which a bird occurs is, for a normal curve, 3.92 times the standard deviation, or 19. This is similar to the range size determined above.

The ranges of the 28 birds seen at least 10 times each during all searches averaged 28 km, with 3 birds seen at distances more than 40 km apart. Only 6 of the 28 were seen within ranges of less than 18 km (Table 3). The calculations for these particular estimates are not derived from an equal probability of searches with respect to area searched, but any error is at the maximum, not the minimum, boundary of range size. That is, with additional observations, an individual might have been found at some more distant location, and therefore within a larger home range. It could only be said to have a smaller home range than that shown by these "non-equal probability" sightings if, upon removing sampling bias, it were found regularly and often (say 90% of the time) within a shorter range, and the larger range calculated had been the result of one or 2 stray, rare forays to the extreme point.

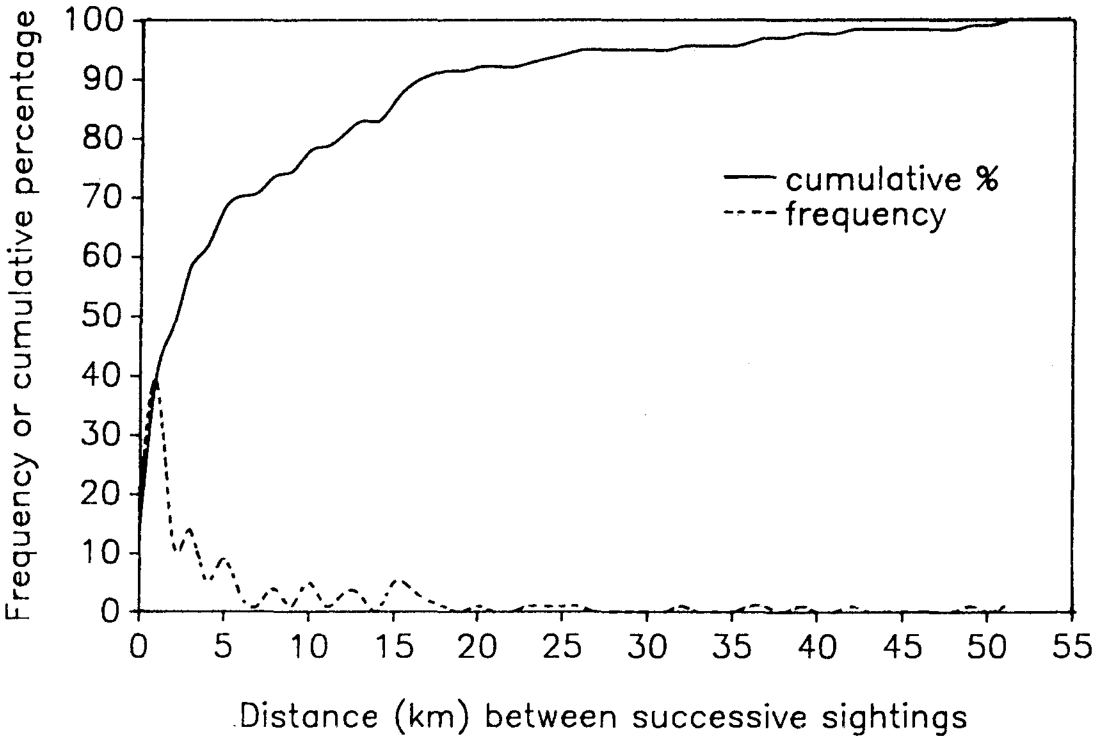


FIGURE 6. Frequency distribution of successive sightings as a function of distance between sightings.

TABLE 3. Home range sizes of banded Sanderlings seen ten or more times during two nonbreeding seasons

Bird	Home range size (area within which all sightings occurred)	Home range size not including March/April sightings
1	22.3 km	6.0km
2	3.0	3.0
3	40.0	18.1
4	32.3	8.0
5	22.2	4.0
6	16.5	16.5
7	16.5	16.5
8	27.3	6.0
9	31.3	5.0
10	41.0	9.1
11	40.0	15.5
12	36.0	21.6
13	24.3	5.0
14	63.6	62.6
15	32.3	29.3
16	31.0	8.0
17	38.6	38.6
18	30.3	12.5
19	29.3	12.5
20	26.3	26.3
21	30.3	5.0
22	25.3	9.5
23	45.6	18.5
24	28.3	4.0
25	23.3	10.5
26	12.5	12.5
27	7.0	4.0
28	10.7	6.3
Average	28.11	14.09

Note: "Total Data Set" (see text) was used.

Low Sighting Numbers

Most birds which were seen only one or two times during the course of the study appeared on the site only in the autumn or spring periods of the nonbreeding seasons (see

Figure 7). The vast majority (25) of birds seen only once in the first study year appeared before December, with 4 appearing in early December and only 2 sightings occurring during the remainder of the winter. In April and May, 6 single sightings were recorded. The second study period ended on November 9, and there had been 4 single sightings in the autumn by then. Fifteen birds were seen only twice each over the course of both study years, and all but one of these 30 sightings were recorded in the "pre-autumn" (July and August), autumn, and spring periods. Birds with low numbers of sightings show a clear pattern of appearing before the winter, with another low pulse in the spring.

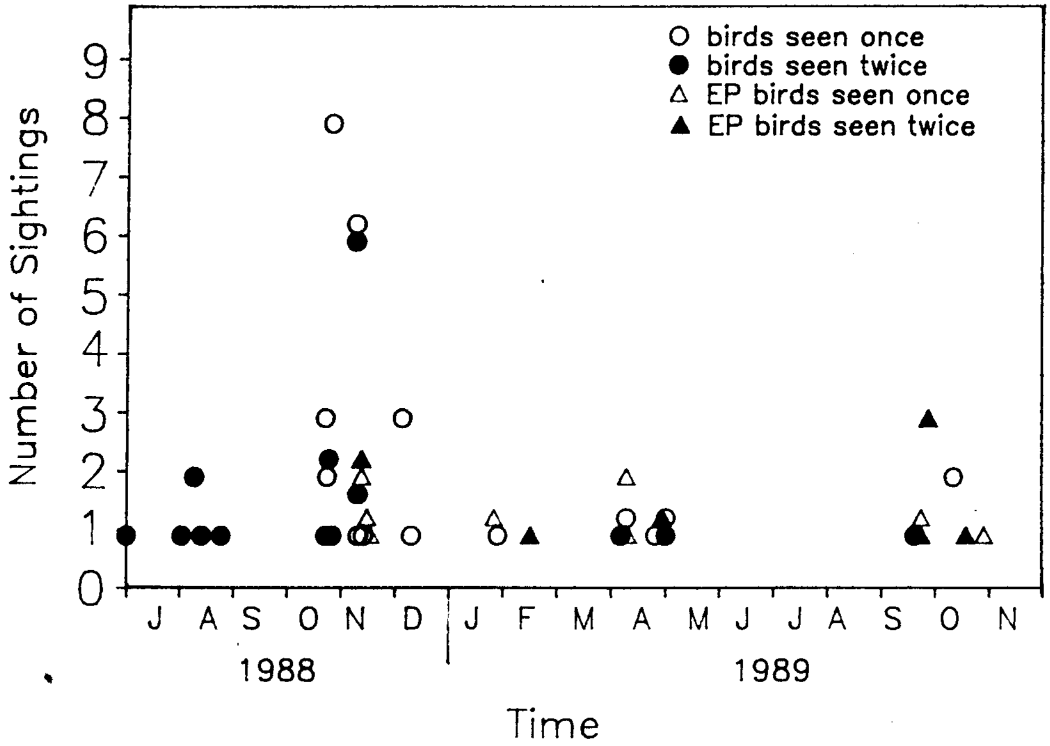


FIGURE 7. Dates of sightings of birds seen only once or twice. EP refers to "equal probability" dates explained in text.

Sexes and Age Classes

Female birds are found to have slightly, but not significantly, more sightings each than males (Figure 8). There is no apparent pattern in the number of sightings of different age classes of adult Sanderlings (Figure 9). These findings are consistent with Myers' (1981) conclusion that adult Sanderlings are not segregated by sex or age on the nonbreeding grounds.

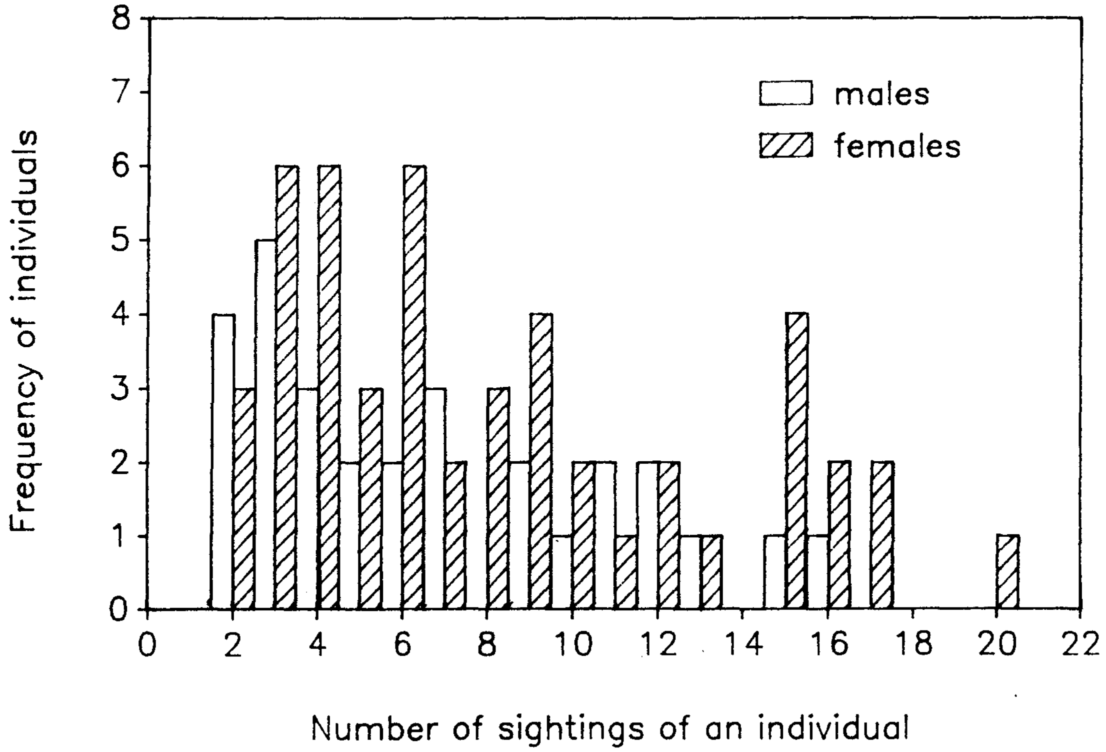


FIGURE 8. Comparison of sighting numbers of male and female Sanderlings (for all birds of known sex, during all searches).

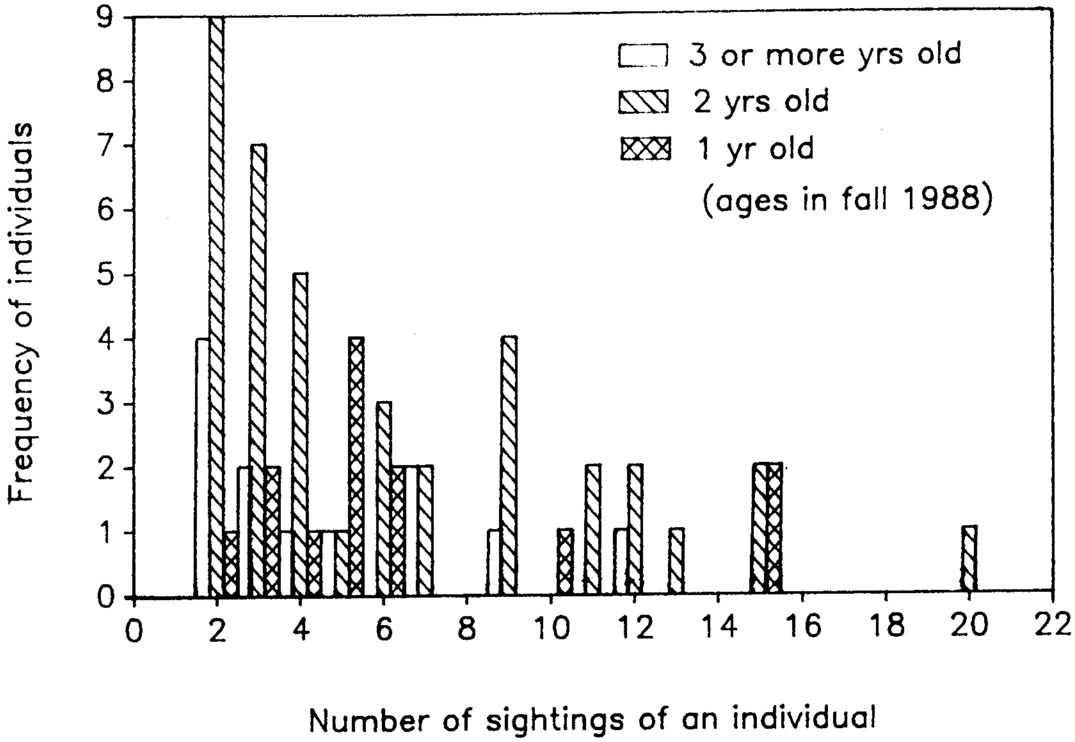


FIGURE 9. Comparison of sighting numbers of three age classes of adult Sanderlings (for all birds of known age, during all searches).

DISCUSSION

Home Range Size

Sanderlings do exhibit site faithfulness on the southcentral Oregon coast, although a bird with an Oregon home range may appear at some time during the nonbreeding season more than 60 km from the site of some other appearance (Table 3).

The Oregon home range size, a minimum of 17 km, is wider than that observed in Bodega Bay, California by Myers et al. (1986) where individuals were shown to remain within a 10 km home range more than 95% of the time. That investigation also found that birds which spend the nonbreeding season in Peru occur within a 5 km sector 60% of the time while 30% of their activity occurs within a secondary 5 km sector located up to 15 kilometers away.

The hypothesis that annual migration distance is positively correlated with nonbreeding home range size is rejected, because the home ranges in Oregon are distinctly longer than those recorded in California, and at least approach the length of those recorded in Peru. It seems more likely that some localized environmental factor or factors influence the home range size of Sanderlings during the nonbreeding season (see Concluding Discussion).

Effect of Season

My results also do not show Oregon home ranges narrowing in the early winter and then broadening again in the spring, as Myers and his co-workers have observed at Bodega Bay, California. However, I believe there is reason to believe that more intensive sampling in the spring might alter the results.

First, the data used for the calculations of seasonal effect included only 11 spring sightings made during the selected searches of equal probability with respect to area searched. No dates in March were included in the "equal probability" data, and in fact because of harsh weather conditions there were only four searches of any sections made during March, as well as two periods of more than a week when no searches occurred. However, on 31 March 1989 I returned to sections 1 through 16, the northernmost tract of the study site, for the first time in over 30 days, and made 28 sightings of 18 banded birds. During the searches in April, 45 sightings of 25 banded birds were made on the same tract. These observations are significant because only four sightings of banded birds had been made there during all previous searches of that beach since July 1988. One bird that was seen 15 times over both years and always within just a 3 km section disappeared from the study area in March, April, and May, though the tract on which it normally appeared was searched 10 times during those months. If all April and May sightings of the 28 birds seen at least 10 times are ignored, the average home range size of these individuals is reduced by half: from 28 kilometers to 14 kilometers (Table 3).

I also observed, though without compiling corroborating records, a change in occurrence of flocks in late March and April, with larger tight flocks (occasionally of 500 or more individuals) moving rapidly (by walking and flying) along the beaches at this time. Conversely, large stretches of beach where I was accustomed to seeing Sanderlings were frequently devoid of them in the spring. Consequently, I speculate that some variation in patterns of space use does occur on the Oregon coast in the spring. More intense sampling, perhaps over a longer study area, is needed to further investigate a seasonal effect.

Two possibilities at variance with the results of this study are that home ranges extend beyond the boundaries of this study site, and that a secondary "node of activity", as described by Myers et al. (1986) for Peruvian birds, may exist outside the study site in the spring. This latter hypothesis is supported by the large number of sightings of banded birds in late March and April at a site 20 to 40 km from where those birds were seen several times at other times during the nonbreeding season.

Low Sighting Numbers

The pattern of appearances of birds seen only once or twice can indicate several possibilities. One is that some Sanderlings appear on the Oregon Dunes study site only while passing through on their continued migration. Because of the pre-winter results, this seems particularly likely for birds which may be continuing southward on their autumn migration. They also may appear on the Oregon Dunes because they are sampling sites in the autumn before settling into or developing a home range and/or exhibiting migratory restlessness or staging in the spring. Myers (1984) found Sanderlings did wander broadly in the fall, reappearing in Bodega Bay in the winter. These findings are consistent with the hypothesis that birds appearing only in the fall settle in a home range somewhere outside the Oregon Dunes shoreline. The low number of sightings may indicate birds which have a very wide home range, extending beyond the Oregon Dunes, or no home range at all (nomadic behavior), or simply be the product of poor sampling. These latter explanations seem unlikely though, given the strong seasonal pattern indicated.

The distinct temporal pattern of sightings of birds with low numbers of sightings therefore apparently describes birds which do not have home ranges within the study site and are continuing to migrate southward in the autumn.

Similar spring sightings indicate, though not as strongly, birds migrating from farther south, or wandering widely at that time from ranges either farther to the north or south. However, it is possible that birds seen only once in the fall later died, though this possibility is not easily answerable. Alternatively it may be that this stop was not a regular stop on their annual migratory route. Evidence for a class of nonsitefaithful "nomads" on the Oregon coast would have included birds seen rarely with no effect of season, but this was not found.

Sexes and Age Classes

The lack of a significant difference in how often males vs. females and different age classes are sighted does not defy any expectations. It is assumed that all ages of adult Sanderlings have the same space use patterns, and comparisons with juveniles should be made. Further research on space-use differences between the sexes and age classes, requiring more data than those obtained in this study, could focus on comparing their home range sizes.

Assumptions

Several problems with this study need to be addressed, beginning with assumptions made. It was assumed that the banded birds are a representative random sample of all Sanderlings (which appear at some time during the nonbreeding season in Oregon). This may be true, considering that Myers (1983) concluded that Sanderlings of a local population within a nonbreeding range (e.g. Bodega Bay or the Oregon Dunes shoreline) move independently of one another, and thus groups caught and banded each year will be a random sample. However, resightings of individuals are used to determine site faithfulness, and those birds seen more than once are among the most site faithful of Sanderlings. That is, nothing can be determined about the ranges of birds that are only seen once, or, indeed, never seen again after they are banded. Furthermore, those philopatric birds seen in the study area during both nonbreeding seasons represent even less of a random sample of space use patterns, because they obviously belong to the most sitefaithful subset of individuals.

The assumption that the study site was large enough to encompass the home range size of local birds should also be examined. Where indeed were the birds when I did not see them? It is possible that they move to some bayshore sandflat, as they do regularly during the nonbreeding season in Bodega Bay (see Myers 1980, Connors et al. 1981), or other inland region. It appeared reasonable, given the ranges recorded in California and Peru, to confine the study site to a length of 75 km. There is no evidence that a significant number had home ranges that exceeded this length. Approximately every two months during the study banded birds were looked for on Bullards Beach, the 7 km long open sandy beach approximately 20 km south of Coos Bay, but no banded birds were ever seen there.

Procedural techniques may need to be re-examined and may have adversely affected the results. First, search intensity differed from day to day, depending on visibility, weather conditions, and other factors. An assumption implicit in this study is that if a bird was present or "there to be seen", it was observed. There is no way of assuring this. This variable is further confounded by the spatial behavior of the birds on the "local" level (as defined by Myers 1984, see Introduction) in the following way: when birds were in tight flocks the legs (banded or not) of many were not visible. There is no way to calculate what effect this had on the data, since records were not kept for flocking. Of course banded birds in flight were likewise not identified. Banded birds which were roosting on one leg or sitting down could not be identified. It is also possible to misidentify bands, and birds can lose bands (see Anderson et al. 1985). Since some birds are banded with 5 rings and others with 4, loss of a fifth ring can lead to misidentification (birds with 3 rings were occasionally seen but not recorded).

One further difficulty arising from the analytical procedures was the arbitrary setting at 1 km of several sighting sections whose actual length was from 0.1 to 0.8

km. This caused some home range estimates (those that included any of these sections) to be improperly lengthened. However, given the scale of the Oregon home ranges, this underestimate iss of little moment. A second problem arises here because those pairs immediately north and south of both Tahkenitch Creek and Ten Mile Creek, all shorter (probably even when taken as a pair plus the creek), than 1 km, were treated in the calculations as one number (kilometer). In fact, the sections were searched separately, as part of the tracts to the north or to the south of the creeks. Both creeks were impassable boundaries to observation, and if, say, the section immediately north of Tahkenitch Creek was searched in one day, a search of section 25 would be recorded when in fact the southern portion of section 25 had not been searched. So in the cases of sections 25 and 52, incomplete searches were recorded as whole searches. Because of missed sightings in some "kilometers", this problem may be of some importance, particularly if a creek were to be a significant boundary to a bird's range, and at all times it was more likely to be found on one side of the creek than the other. In that case the number of sightings of a bird in one of those sections would be halved. However, again this is a problem on a scale of only one kilometer, which is not significant in terms of the overall home range length estimated for the study site.

Calculations

Ford and Myers (1981) compared several methods of estimating home range size, including the minimum convex polygon method, a parametric probabilistic estimator used by Jennrich and Turner (1969), and a nonparametric probabilistic estimator of Ford and Krumme (1979). They determined that the latter estimator had the most advantages. My estimation of home range size differs significantly from the three methods described in that my study estimates a one-dimensional home range, while they were examining methods to determine polygonal range sizes. However, the Ford and Krumme procedure begins with the same variables that are used in my estimation and a comparison is interesting: their estimation is based on a frequency distribution of pairwise distances measured between all observation points, as mine is. They then use a computer algorithm to estimate the minimum area that will contain a given proportion of the "space use" of the individual. This estimator becomes more accurate with increasing sample size, but is found to be affected by time elapsed between observations ("temporal contingency"). For the calculation method used in this study more intensive sampling is not likely to be helpful in further resolving the boudaries of home range size, (in contrast with further resolution of seasonal variation in behavior). As sample size increases, the limits of the home range size, defined as the area within which a bird is likely to be seen a given proportion of the time, are not expected to change.

Comparison of Procedures

Comparisons between the results of my estimations of seasonal effects and home range size and those of Myers' studies are unlikely to be influenced by the differences in methods and calculations employed. To determine intrayear site faithfulness Myers et al. (1986) used a one-dimensional adaptation of the Ford and Krumme method for straight-line distance between pairs of observations of the same bird, calculated for all birds. Results were expressed as proportions of a bird's activity occurring within a given distance measured in opposite directions from the central banding site. I would hesitate to define presence as "activity" as he does. The Ford and Krumme adaptation for linear home ranges was not used in my calculations because of unspecified problems with it that have recently been discerned by J.P. Myers (pers. comm.).

Concluding Discussion

Given that the most site faithful Oregon birds may be found 90% of the time within a home range at least 17 km in length, and that migration distance from the breeding range has no effect, what can explain the differences between

Oregon, California, and Peruvian range sizes?

Numerous studies, particularly among small mammals, have been conducted relating home range size of a species or taxonomic group to body size or weight, and there is evidence that energetic requirements determine these home range sizes (see Greenwood and Swingland 1983 for review). Mace et al. (1983) listed three factors as important determinants of home range size: habitat productivity, the animal's energetic needs (determined mainly by body size), and an interaction between body size and habitat productivity. "Interactions" and the broad scope of "habitat productivity" indicate the probably complex nature of the forces influencing home range size.

Little work has been done on the causes of variations of individual nonbreeding home range sizes within a species. Such work, involving migratory species with large nonbreeding ranges, will be closely tied to the study of the influences affecting the evolution of habitat use behaviors, particularly nomadism vs. site fidelity (see Myers 1984 for discussion of the relationship of these behaviors to seasonal variation in individual home range size); territoriality, which not only may share influencing factors with home range size (see Myers et al. 1979, Myers et al. 1981, Mace et al. 1983), but can affect estimates of home range size (e.g. a bird may spend a greater proportion of its time at its territory boundaries); and migration (see

Gauthreaux 1982, Pienkowski and Evans 1984 for discussion of factors affecting nonbreeding "distribution" of migratory birds). Interestingly, studies that have been conducted thus far have generally been for nonmigratory species. Some examples follow: seasonal variation in home range size of the Florida Sandhill Crane (Grus canadensis pratensis) has been linked with water level fluctuations (Bennett, 1989). Gatti et al. (1989) found some evidence that the home range size of female Ring-necked Pheasants (Phasianus colchicus) is positively correlated with area of food patches. Range sizes for female Ring-necked Pheasants (Gatti et al. 1989), and territorial male Ruffed Grouse (Bonasa umbellus) (Thompson and Fritzell 1989) have been inversely correlated with survivorship. The definitions and calculations of home range size obviously vary widely among these studies.

To answer the question, "What can account for the observed differences in individual home range size among populations of nonbreeding Sanderlings?", further examination of space use patterns is needed, and local environmental parameters including prey availability (see Myers et al. 1979; Myers et al. 1985; Maron and Myers 1985) will have to be described and compared.

Foraging behavior should be examined for variations over the photoperiod and the tidal cycle (Burger 1984, Puttick 1984) in Oregon and compared with observed patterns of habitat use in California and Peru. For example, Chilean

Sanderlings roost according to the time of day, independent of the tidal cycle, while, interestingly, Bodega Bay birds have roosting cycles that are dependent on both photoperiod and tidal cycle. Overall, Chilean birds spend much less time feeding than do California birds (Myers et al. 1985). Roosting cycles in Oregon may have affected the results on home range size and seasonal effect of the present study, if, for example, a communal roost existed during the daylight search hours. Furthermore, habitat use patterns give some indication of resource variability.

Flocking behavior was likewise ignored in this study but may both have affected results and can be used as an indicator of local environmental conditions. Not only did flocking impede observation, but having a home range and flocking may be two types of spatial behavior which overlap and affect one another. For instance, Stinson (1980) showed for several species of shorebirds that the threat of predation influences flocking. It is possible that Sanderlings leave or extend their movements outward from their home range as part of a flock if a predator is present. However, a 17 km home range would presumably allow for much predator avoidance and flocks could well form within it with little effect on home range size.

Predator presence, as an environmental factor possibly influencing home range size, needs to be investigated further for all nonbreeding ranges. Page and Whitacre

(1975) show a significant predation risk by raptors at Point Reyes in central California, with 13% of the Sanderlings present being eaten in one winter. Myers (1984) observed that Sanderling home ranges of 1500 m increased to 3200 m during weeks when raptors were hunting in Bodega Bay. I very rarely (less than 5 times overall) noted hunting raptors at the Oregon study site, and the scales of range size vary drastically between his California observations and mine in Oregon, but data on predation risk (mortality) are still needed in Oregon and Peru. See Myers et al. (1985) for discussion of possible effects of predation on migration.

Further hypotheses for predicting differences in home range size among different wintering sites have to do with spatiotemporal variability in food resources. Prey reliability might have a significant influence on size, and if so then such contributing effects as weather may be important. In contrast to Peru, the central California site experiences frequent winter storms, but the Peruvian coast experiences the profound ecological effects of an El Nino current every six to seven years (see Myers et al. 1985). Comparisons with the variability of invertebrate prey items, and possible effects of weather on this variability, have not been made for Oregon, and data are sketchy for all sites.

Different levels of prey abundance may also help predict home range size. Myers et al. (1985) surmised from admittedly sparse data that food availability is higher in coastal Peru than in Bodega Bay, though potential competitors are more abundant. Crowe and Crowe (1985) and Myers and McCaffery (1985) demonstrate that inter- and intraspecific interference competition may exist among shorebirds on the nonbreeding range. See Cox (1985) and Fretwell (1980) for discussions of the influences of intraspecific competition and food availability on the evolution of migration. On Oregon beaches I observed very few (although significance of number is unknown) individuals of potentially competitive species, although the incidence of Western Sandpipers (Calidris mauri), Dunlin (Calidris albina), and other waders may have been higher in the autumn and spring periods of the nonbreeding season. I commonly noted solitary gulls (species undetermined) following a group of Sanderlings and harassing any that uncovered food items too large to swallow immediately. As Myers et al. (1985) stated (while investigating why some Sanderlings migrate to North American beaches and other continue to South America), "we lack baseline information on the availability of food and on the effect of bird density on foraging success".

One additional hypothesis to explain the observed differences in home range size of populations of Sanderlings is that size is in some way correlated with habitat availability. The area of open sandy beach available to Sanderlings is significantly less in the Bodega Bay area than at the Oregon and Peruvian study sites, and less in Peru than Oregon (see Myers et al. 1985 for description of Peruvian and Bodega Bay study sites and surrounding areas). The area of estuary or availability of bay tidal sandflat for each area should likewise be compared. There are no quantitative and very little qualitative data available for tidal sandflat use by Sanderlings at the Oregon Dunes, and any use of these areas, within or outside the southern and northern boundaries of the study site, could certainly affect the results of "length" of study site. Because range size in the present study was calculated as a linear distance along the shore, cyclic use of other areas would almost certainly affect results. For example, Oregon birds may have a cyclic (e.g. daily or tidal) pattern of use of exposed sandflat in the Umpqua River, Siuslaw River, or Coos Bay estuaries. Other than incidental sightings of flocks of Sanderlings in some of these areas, there is no evidence of a regular pattern of birds leaving the open coast, but such cycles have been documented elsewhere.

APPENDIX A

ALL DATES ("TOTAL SET") WHEN SEARCHES MADE DURING TWO NONBREEDING SEASONS

Date (mo.day.yr)	Sections searched	Date (mo.day.yr)	Sections searched
07.07.88	31	02.25.89	26-40
07.14.88	31	02.26.89	17-24
08.07.88	31	02.27.89	1-16
08.14.88	31	02.28.89	42-78
08.18.88	30,31	03.12.89	32-40
08.21.88	30,31	03.29.89	54-78
08.29.88	31	03.30.89	15-16,42-52
10.26.88	25-40	03.31.89	1-16
10.27.88	25-40	04.02.89	25-40
10.28.88	30-40	04.03.89	52-78
10.30.88	25-40	04.06.89	42-52
11.12.88	25-31	04.07.89	25-40
11.13.88	25-31	04.08.89	25-40
11.15.88	1-40	04.09.89	25-40
11.16.88	25-32	04.10.89	66-78
11.18.88	42-52	04.11.89	25-40,42-78
11.20.88	52-78	04.12.89	17-40
11.21.88	42-51	04.14.89	1-16
12.08.88	27-31	04.19.89	54-78
12.12.88	25-40	04.21.89	1-15
12.13.88	42-44,51	04.23.89	42-52
12.14.88	65,66	04.24.89	1-16
12.18.88	31-32	04.25.89	17-24
01.14.89	25-40,52-65	04.26.89	42-52
01.16.89	30-40	04.27.89	17-24
01.18.89	32-40	04.28.89	1-15
01.28.89	1-15	04.29.89	52-78
01.29.89	52-78	05.01.89	32-52,66-78
01.30.89	31-40	05.03.89	25-40
02.10.89	42-52	05.04.89	17-40
02.11.89	1-15	05.05.89	1-16
02.12.89	27-40		
02.13.89	25-52,54-78	09.18.89	36-40
02.14.89	17-24	09.20.89	35-40
02.15.89	1-15,25-52	09.22.89	29-34
02.17.89	25-40,53-78	09.23.89	66-78

Date (mo.day.yr)	Sections searched	Date (mo.day.yr)	Sections searched
09.24.89	52-65	10.20.89	1-16,42-52
09.25.89	42-52	10.24.89	52-78
09.26.89	17-25	10.25.89	34-40
09.28.89	31	10.27.89	25-35
09.29.89	17-31	10.28.89	1-16
09.30.89	1-16,52-78	10.29.89	17-24
10.06.89	73-78	10.30.89	42-52
10.07.89	66-72	10.31.89	32-40
10.10.89	34-40	11.03.89	52-78
10.13.89	54-65	11.08.89	25-32
10.14.89	29-34	11.09.89	42-52
10.17.89	17-31		

APPENDIX B

SIGHTINGS OF BIRDS SEEN AT LEAST TWICE DURING "EQUAL PROBABILITY" SEARCHES

Bird	Location	Days since July 7	Days between successive sightings*	Distance between successive sightings
1	30	131	NA	1
	29	77	4	8
	21	81	21	3
	18	102	NA	NA
2	31	131	0	2
	29	131	NA	4
	33	99	11	1
	34	110	2	1
	33	112	NA	NA
3	31	301	NA	1
	30	77	25	12
	18	102	0	3
	21	102	8	13
	34	110	NA	NA
4	32	220	0	1
	31	220	61	18
	13	281	NA	18
	31	83	16	2
	33	99	11	1
	34	110	2	1
	33	112	NA	NA
5	29	233	45	15
	44	278	20	8
	36	298	NA	5
	31	77	0	1
	30	77	NA	NA

Bird	Location	Days since July 7	Days between successive sightings*	Distance between successive sightings
6	34	220	13	2
	36	233	NA	2
	34	77	33	0
	34	110	2	0
	34	112	NA	NA
7	10	131	170	25
	35	301	NA	14
	21	81	33	2
	19	114	NA	NA
8	70	109	10	0
	70	119	NA	NA
9	32	131	167	4
	36	298	NA	NA
10	20	279	0	2
	18	279	19	15
	33	298	NA	2
	31	77	22	1
	32	99	13	0
	32	112	NA	NA
11	32	77	39	5
	37	116	NA	NA
12	38	75	2	4
	34	77	32	26
	60	109	NA	NA
13	31	233	NA	10
	21	102	NA	NA
14	34	77	25	16
	18	102	NA	NA
15	37	233	0	1
	38	233	48	32
	6	281	NA	31
	37	110	2	2
	35	112	4	2
	37	116	NA	NA

Bird	Location	Days since July 7	Days between successive sightings*	Distance between successive sightings
16	22	131	75	49
	71	206	NA	39
	32	99	NA	NA
17	44	278	3	39
	5	281	0	1
	6	281	NA	71
	77	78	NA	NA
18	30	131	170	1
	31	301	NA	2
	29	77	35	3
	32	112	NA	NA
19	26	233	48	13
	13	281	NA	20
	33	99	13	1
	32	112	NA	NA
20	28	233	48	16
	12	281	NA	NA
21	37	220	13	1
	38	233	65	1
	37	298	NA	NA
22	31	220	59	10
	21	279	0	1
	20	279	22	8
	28	301	NA	4
	32	77	25	11
	21	102	0	3
	18	102	0	2
	20	102	NA	NA
23	32	131	NA	3
	29	77	33	5
	34	110	2	1
	33	112	NA	NA
24	35	112	37	2
	33	75	NA	NA
25	39	233	NA	18
	21	81	NA	NA

Bird	Location	Days since July 7	Days between successive sightings*	Distance between successive sightings
26	70	206	73	51
	19	279	NA	NA
27	31	301	NA	2
	33	77	25	15
	18	102	10	15
	33	112	NA	NA
28	47	134	144	3
	44	278	NA	5
	39	75	NA	NA
29	70	206	0	3
	67	206	0	6
	61	206	NA	1
	60	119	NA	NA
30	72	206	NA	2
	74	109	10	5
	69	119	0	1
	70	119	NA	NA
31	24	81	0	1
	23	81	NA	NA
32	34	279	0	0
	34	279	22	NA
	34	301	NA	NA
33	59	206	0	1
	58	206	NA	36
	22	81	33	0
	22	114	NA	NA
34	69	78	31	0
	69	109	10	5
	64	119	NA	NA
35	35	220	13	1
	36	233	NA	14
	22	81	29	13
	35	110	NA	NA
36	71	206	NA	39
	32	77	NA	NA

Bird	Location	Days since July 7	Days between successive sightings*	Distance between successive sightings
37	44	134	99	5
	39	233	68	7
	32	301	NA	4
	36	75	NA	NA
38	28	233	68	3
	31	301	NA	NA
39	50	134	72	12
	62	206	0	1
	61	206	19	1
	60	225	54	42
	18	279	NA	0
	18	102	3	4
	14	105	NA	NA
40	8	131	104	0
	8	235	NA	29
	37	75	0	1
	36	75	39	17
	19	114	NA	NA
41	64	136	97	36
	28	233	NA	NA
42	21	81	21	0
	21	102	NA	NA
43	35	220	13	1
	36	233	48	24
	12	281	20	23
	35	301	NA	NA
44	39	233	65	2
	37	298	NA	2
	39	110	6	0
	39	116	NA	NA
45	58	206	0	1
	59	206	19	1
	60	225	9	37
	23	234	NA	15
	38	75	35	1
	37	110	6	0
	37	116	NA	NA

Bird	Location	Days since July 7	Days between successive sightings*	Distance between successive sightings
46	34	110	6	3
	37	116	3	16
	53	119	NA	NA
47	25	81	21	3
	22	102	0	4
	18	102	3	15
	3	105	NA	NA
48	36	75	35	1
	37	110	6	0
	37	116	NA	NA
49	71	206	0	0
	71	206	NA	NA
50	35	75	35	1
	34	110	2	1
	35	112	NA	NA
51	20	279	NA	14
	34	77	NA	NA
52	33	220	14	10
	23	234	NA	7
	30	77	0	3
	33	77	0	4
	29	77	37	5
	24	114	NA	NA
53	31	220	NA	9
	22	81	31	10
	32	112	NA	NA
54	29	131	102	1
	28	233	68	8
	20	301	NA	4
	24	114	NA	NA
55	13	131	NA	9
	4	105	0	1
	3	105	8	5
	8	113	NA	NA

Bird	Location	Days since July 7	Days between successive sightings*	Distance between successive sightings
56	28	131	0	1
	29	131	89	0
	29	220	61	17
	12	281	NA	20
	32	99	15	10
	22	114	NA	NA
57	27	233	46	6
	21	279	NA	0
	21	81	21	1
	20	102	0	2
	18	102	12	1
	19	114	NA	NA
58	31	220	14	12
	19	234	NA	13
	32	99	11	5
	37	110	2	3
	34	112	NA	NA
59	40	131	103	16
	24	234	NA	10
	34	112	NA	NA
60	29	233	68	2
	31	301	NA	5
	26	112	NA	NA
61	10	205	15	20
	30	220	NA	3
	33	99	13	3
	30	112	NA	NA
62	29	131	148	5
	24	279	22	3
	27	301	NA	5
	22	102	0	1
	21	102	0	1
	20	102	10	10
	30	112	2	6
	24	114	NA	NA
63	23	81	18	9
	32	99	NA	NA

Bird	Location	Days since July 7	Days between successive sightings*	Distance between successive sightings
64	34	131	102	3
	31	233	NA	2
	33	77	35	0
	33	112	NA	NA
65	30	131	89	1
	31	220	NA	NA
66	38	233	65	1
	37	298	NA	2
	39	110	6	0
	39	116	NA	NA
67	38	110	6	1
	37	116	NA	NA

*Note: "NA" if sighting is last one of a bird or if sightings are in two different years

APPENDIX C

DISTANCES BETWEEN SUCCESSIVE SIGHTINGS MADE DURING "EQUAL PROBABILITY" SEARCHES

Location	Days since July 7	Days between successive sightings	Distance between successive sightings
4	105	0	1
37	233	0	1
28	131	0	1
20	102	0	2
31	131	0	2
62	206	0	1
18	102	0	3
37	75	0	1
32	220	0	1
31	77	0	1
5	281	0	1
22	102	0	1
21	102	0	1
69	119	0	1
58	206	0	1
22	102	0	4
24	81	0	1
34	279	0	0
59	206	0	1
21	102	0	3
21	279	0	1
18	102	0	2
20	279	0	2
71	206	0	0
67	206	0	6
70	206	0	3
30	77	0	3
33	77	0	4
37	110	2	2
34	110	2	1
37	110	2	3
34	110	2	1
30	112	2	6
34	110	2	0

Location	Days since July 7	Days between successive sightings	Distance between successive sightings
34	110	2	1
38	75	2	4
34	110	2	1
18	102	3	4
44	278	3	39
37	116	3	16
18	102	3	15
35	112	4	2
29	77	4	8
39	110	6	0
37	110	6	0
34	110	6	3
37	110	6	0
39	110	6	0
38	110	6	1
3	105	8	5
21	102	8	13
60	225	9	37
18	102	10	15
20	102	10	10
74	109	10	5
70	109	10	0
69	109	10	5
33	99	11	1
32	99	11	5
33	99	11	1
18	102	12	1
33	99	13	3
35	220	13	1
34	220	13	2
33	99	13	1
37	220	13	1
32	99	13	0
35	220	13	1
31	220	14	12
33	220	14	10
32	99	15	10
10	205	15	20
31	83	16	2
23	81	18	9
61	206	19	1
59	206	19	1
18	279	19	15
44	278	20	8
12	281	20	23
21	81	21	3
21	81	21	1

Location	Days since July 7	Days between successive sightings	Distance between successive sightings
21	81	21	0
25	81	21	3
24	279	22	3
34	279	22	0
20	279	22	8
31	77	22	1
34	77	25	16
33	77	25	15
30	77	25	12
32	77	25	11
22	81	29	13
69	78	31	0
22	81	31	10
34	77	32	26
34	77	33	0
21	81	33	2
22	81	33	0
29	77	33	5
29	77	35	3
33	77	35	0
38	75	35	1
36	75	35	1
35	75	35	1
35	112	37	2
29	77	37	5
36	75	39	17
32	77	39	5
29	233	45	15
27	233	46	6
38	233	48	32
36	233	48	24
26	233	48	13
28	233	48	16
60	225	54	42
31	220	59	10
29	220	61	17
31	220	61	18
39	233	65	2
38	233	65	1
38	233	65	1
28	233	68	2
29	233	68	1
50	134	72	12
70	206	73	51
22	131	75	49
29	131	89	0
30	131	89	1

Location	Days since July 7	Days between successive sightings	Distance between successive sightings
64	136	97	36
44	134	99	5
29	131	102	1
34	131	102	3
40	131	103	16
8	131	104	0
47	134	144	3
29	131	148	5
32	131	167	4
30	131	170	1
10	131	170	25
39	233	68	7
28	233	68	3

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