

AN ABSTRACT OF THE THESIS OF

Peter M. Sanzenbacher for the degree of Master of Science in Wildlife Science
presented on July 19, 2001. Title: Spatial and Temporal Movement Patterns of
Wintering Dunlin (*Calidris alpina*) and Killdeer (*Charadrius vociferus*) in the
Willamette Valley, Oregon

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Abstract approved: _____

Susan M. Haig

Avian movement behavior provides insight on patterns of regional and local fidelity, habitat and resource requirements, the scale at which individuals perceive the landscape, and the relative influence of the spatial array of resources.

Shorebirds (suborder: Charadrii) are a diverse and mobile group of wetland associated species. Large numbers of shorebirds utilize seasonally flooded wetland habitats in the Willamette Valley of northwest Oregon; however, there is little information on fidelity and movements of birds in the region or at other inland sites. Thus, we quantified winter fidelity and movement patterns of radio-tagged Dunlin (*Calidris alpina*) and Killdeer (*Charadrius vociferus*) in the Willamette Valley in 1998-1999 and 1999-2000.

Prior to field telemetry, we evaluated use of a leg-loop harness design for attachment of radio-transmitters. Comparisons between captive Western Sandpipers (*Calidris mauri*) fitted with a harness package and a control group indicated no significant differences in behavior. In addition, observations of wild Killdeer and Dunlin indicated prolonged harness retention and no adverse effects on behavior. Therefore, we determined that the modified harness design was a suitable method for attachment of transmitters to shorebirds.

Monitoring of radio-tagged Dunlin and Killdeer indicated interspecific differences in regional fidelity and residency patterns. Dunlin exhibited a high degree of regional fidelity and in most cases remained within the Valley for the duration of the winter. In contrast, Killdeer departed the study area throughout the winter and the population segment monitored was composed of winter residents (63%), winter transients (26%) and year-round resident breeders (11%).

Dunlin were highly mobile with frequent movements up to 30 km from roost sites. Among seasons, Dunlin differed significantly in distance traveled, mean distance from capture site, and home range size. All were greatest during late winter. In comparison, the scale of Killdeer movements was much smaller, with no seasonal differences in movements. Results also suggested that resident Killdeer were more sedentary than migrants during the winter months. At a local scale, individuals of both species occurred predominantly in agricultural habitats and exhibited low degrees of fidelity to specific fields, with the exception that Dunlin

frequently returned to certain roost sites. On a daily basis, movements of both Dunlin and Killdeer were most pronounced during crepuscular periods.

Findings provide insight on the fidelity and winter movements of shorebirds, as well provide insight as to the functional connectivity of shorebird habitats in the Willamette Valley.

Spatial and Temporal Movement Patterns of Wintering Dunlin (*Calidris alpina*)
and Killdeer (*Charadrius vociferus*) in the Willamette Valley, Oregon.

by
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Contribution of Authors

Dr. Susan Haig was involved in the design, analysis, and writing of each manuscript. Dr. Lewis Oring assisted with studies of captive Western Sandpipers for the design and evaluation of a harness to attach radio-transmitters to shorebirds.

Table of Contents

<u>Chapter</u>	<u>Page</u>
1. Introduction.....	1
2. Application of a Modified Harness Design for Attachment of Radio Transmitters to Shorebirds.....	5
3. Spatial and Temporal Movement Patterns of Wintering Dunlin (<i>Calidris alpina</i>) in the Willamette Valley, Oregon.....	24
4. Spatial and Temporal Movement Patterns of Killdeer (<i>Charadrius vociferus</i>) Wintering in the Willamette Valley, Oregon.....	61
5. Conclusions.....	94
Bibliography.....	98

List of Figures

<u>Figure</u>		<u>Page</u>
2.1	Attachment of a figure-eight leg-loop harness to a radio transmitter...	11
2.2	Proper alignment of figure-eight leg-loop harness and transmitter on shorebird.....	13
3.1	The Willamette Valley ecoregion and area surveyed during telemetry efforts. Dunlin were captured and radio-marked at a single site in the central region of the study area. Telemetry locations of all radio-marked birds tracked during the study are indicated.....	29
4.1	The Willamette Valley ecoregion and areas covered during ground and aerial telemetry surveys of Killdeer. Capture sites and all detections of radio-marked birds are indicated.....	65
4.2	Proportion of radio-marked birds remaining in the Willamette Valley (solid circles) and total numbers of Killdeer tallied across all shorebird census blocks (empty circles) at various dates during winter of 1999-2000. The primary axis (left) corresponds to proportion of radio-marked birds and the secondary axis (right) corresponds to Killdeer count totals. Mean date of departure of radio-marked birds is indicated by vertical bar on plotted line.....	74
4.3	Comparison of sites visited, minimum total distance traveled, mean distance located from capture site, and maximum distance located from capture site for winter resident and year-round resident Killdeer during the winter months of 1999-2000 in the Willamette Valley, Oregon.....	78

List of Tables

<u>Table</u>		<u>Page</u>
2.1	Behavioral observations of captive Western Sandpipers. Activity categories expressed as proportions of each behavior observed, with flock cohesiveness measured as mean number of individuals within 0.61 m of focal birds.....	16
3.1	Capture and tracking efforts for radio-marked Dunlin in the Willamette Valley, Oregon USA (1998-1999 and 1999-2000).....	38
3.2	Movements of wintering Dunlin in the Willamette Valley, Oregon USA. Means presented with associated standard errors (\pm SE).....	42
3.3	Mean (\pm SE) home range area (100% minimum convex polygons) encompassed by movements of wintering Dunlin in the Willamette Valley, Oregon USA.....	44
4.1	Winter movements of Killdeer in the Willamette Valley of Oregon, USA (1999-2000). Data presented are means with associated standard errors (\pm SE)	77
4.2	Area encompassed by movements (100% minimum convex polygons), home range size (95% kernel), and core use areas (50% kernel) of migrant and resident Killdeer in the Willamette Valley during the winter months of 1999-2000. Results were calculated for all birds with \geq 20 locations.....	81

**Spatial and Temporal Movement Patterns of Wintering
Dunlin (*Calidris alpina*) and Killdeer (*Charadrius vociferus*)
in the Willamette Valley of Oregon**

Chapter 1. Introduction

Studies of animal movement behavior provide fundamental information pertaining to species life histories, population dynamics, habitat use, and other ecological processes (Hansson et al. 1995; Haig et al. 1998; Webster et al., in press). In particular, the movement behavior of an individual defines the scale at which it perceives the landscape and the threshold at which the spatial array of habitat patches impacts functional connectivity of the landscape and movements. As a result, movement data represent an important tool for management and conservation efforts. However, there is a lack of empirical data on avian movement behavior for most taxa and landscapes, particularly for mobile species that operate at large spatial scales (Wiens 1994, Tischendorf and Fahrig 2000). In addition, most research has focused on between season movements (e.g., migration), with fewer studies of within season movements of breeding and wintering birds (Haig et al. 1998).

In the Willamette Valley of northwest Oregon, vast areas of seasonally flooded agricultural wetlands, moist-soil managed impoundments, and sewage ponds attract large numbers of nonbreeding shorebirds and other waterbirds (Gabrielson and Jewett 1940, Budeau 1992). The Willamette Valley accounts for

the majority of urban, industrial, and agricultural activities in the state and surrounding region and has experienced extensive alteration of native vegetation and landforms (Froggat 1984, Boyd 1986, Hulse 1998). In particular, greater than 50% of original wetlands have been lost and less than 1% of wet prairie habitats remain (Conrad and Peterson 2001). With recognition of historical wetland losses and the importance of these habitats for environmental quality and subsistence of plant and animal populations, various governmental agencies and non-profit groups have initiated extensive efforts to protect and restore wetland habitats. To date, these efforts have been opportunistic with regard to the specific location of conservation activities and have targeted select groups of wildlife (i.e., waterfowl). In order to design and implement appropriate regional conservation planning efforts, there is a need for information pertaining to the spatial and temporal scale at which a range of species utilize local and regional wetland resources and the relative importance of the spatial array and distribution of these habitats.

Shorebirds (suborder: Charadrii) represent a diverse and mobile group of wetland associated species. The most abundant species of wintering shorebird in the region is Dunlin (*Calidris alpina*), a medium-sized sandpiper and medium-distance migrant that breeds in Arctic tundra. Previous studies have suggested that the Willamette Valley is of primary importance to migrating Dunlin, and individuals occurring during winter months are likely transients (Strauch 1967). However, sightings of large Dunlin flocks (10,000+ individuals) are not uncommon in winter and there is no empirical data on the status or origin of these birds

(Johnson 1993, 1994). In addition, the region is a major wintering area for Killdeer (*Charadrius vociferus*). This temperate breeding plover is the most common and widely distributed shorebird in North America; however, recent data summaries indicate significant long-term population declines throughout their range (Sanzenbacher and Haig 2001). Further, there is a general lack of information on patterns of residency and various aspects of nonbreeding ecology of Killdeer.

Overall, little is known concerning residency patterns and movements of shorebirds in the Willamette Valley or at other inland sites. Most studies of nonbreeding shorebirds have focused on coastal sites, where habitats are generally predictable and tracking of movements are facilitated by the linear nature of habitats (Warnock and Takekawa 1996, Drake et al. 2001). In contrast, local wetland-associated habitats in the Willamette Valley are extremely dynamic, with significant intra- and inter-annual variation in the relative abundance and spatial configuration of resources.

Research presented in this thesis was designed to determine patterns of regional fidelity and movements of shorebirds wintering in the Willamette Valley, as well as expand knowledge of behavior of nonbreeding shorebirds at inland sites. These data will assist with future conservation planning efforts in the Willamette Valley and other areas. Individual chapters were prepared as manuscripts for submission to peer-reviewed journals and each addresses a different aspect of our studies. Chapter 2 is methodological and represents efforts to develop and evaluate a technique for the attachment of radio-transmitters to shorebirds. Chapter

3 presents results on winter fidelity, movement patterns, and space use of Dunlin in the Willamette Valley during the winters of 1998-1999 and 1999-2000. Chapter 4 deals with similar studies of Killdeer during the winter of 1999-2000.

Chapter 2. Application of a Modified Harness Design for Attachment of Radio Transmitters to Shorebirds

ABSTRACT

Radio transmitter attachment methodology is important to the design of radio telemetry studies. In 1998, we attached 5 transmitters to a captive population of Western Sandpipers (*Calidris mauri*) and 7 transmitters to wild Killdeer (*Charadrius vociferus*) using a modified version of the Rappole and Tipton (1991) figure-8 leg-loop harness. Captive birds fitted with harnesses did not exhibit quantifiable differences in behavior relative to control birds. Based on initial success in using the leg-loop harnesses, we used harnesses to attach transmitters in the wild to 30 Killdeer and 49 Dunlin (*Calidris alpina*) during the winters of 1998-1999 and 1999-2000. This was part of a study on movements of wintering shorebirds in the Willamette Valley of Oregon, USA. Wild birds showed no adverse effects of the harnesses. Thus, the described harness is a practical method for attachment of transmitters to shorebirds. Advantages of this harness method include a reduction in handling time at capture, elimination of the need to clip feathers for attachment, and increased transmitter retention time.

INTRODUCTION

Radio telemetry is an important tool in studies of shorebird biology. Recent applications of the technique include studies of migratory patterns (Iverson et al. 1996, Johnson et al. 1997), within season movements (Warnock et al. 1995; Warnock and Takekawa 1996; Knopf and Rupert 1996; Farmer and Parent 1997; Haig et al. 1998; Powers 1998; Plissner et al., 2000), foraging ecology (Whittingham 1996), mating tactics (Colwell and Oring 1988), and general ecology (Wood 1986, Cresswell and Summers 1988, Gill et al. 1991, Warnock and Oring 1996). Further, a growing recognition of the importance and need for multiple scale landscape studies in ecological research and conservation biology will undoubtedly lead to an increased utilization of radio and satellite telemetry in the future (Haig et al. 1998).

An important consideration in any telemetry study is the method used for attachment of transmitters to the study organism. Primary concerns include potential effects of the attachment method on the behavior of the organism and transmitter retention time (Rappole and Tipton 1991, Warnock and Warnock 1993). Currently, the most common attachment method in shorebird radio telemetry studies involves direct application of the transmitter to the birds' plumage with a glue or waterproof epoxy adhesive (Raim 1978, Warnock and Warnock 1993, Knopf and Rupert 1996). In many cases, this technique is adequate; however there are a number of potentially troublesome issues. Transmitter retention times are

highly variable depending on the study species (e.g., molt schedule, behavior), experience of the researcher, and environmental conditions. Handling time required to process birds is dependent on curing time of adhesives and is greatly influenced by ambient temperatures. In addition, procedures with adhesives sometimes involve clipping an area of feathers at the point of attachment. The thermoregulatory implications of such actions are potentially problematic, particularly during periods of cold weather and precipitation.

In some cases, it is possible to mount a transmitter on a U.S. Fish and Wildlife Service metal identification band, which is subsequently attached to the leg of the study subject (Plissner et al., 2000; Haig and Oring, unpub. data). This technique appears to be well suited for larger, long-legged species, such as the recurvirostrids and some scolopacids; however, issues of leg length and transmitter size prevent application of this method to a broad range of shorebirds. In addition, attachment of transmitters to leg bands does not provide a mechanism for eventual ‘shedding’ of the transmitter.

The attachment of transmitters with harnesses has been used extensively in studies of waterfowl (Conroy et al. 1989, Orthmeyer and Ball 1990), songbirds (Sykes et al. 1990, Rappole and Tipton 1991, Neudorf and Pitcher 1997, Powell et al. 1998), and other avian groups (Godfrey 1970; Hooge 1991; D. Kesler, personal communication). Unfortunately, harness designs often are intrusive, with attachment points at the wings, neck, or bill. Hence, a number of studies have documented adverse effects of harness attachments (Ward and Flint 1995, Dzus and

Clark 1996, Garrettson and Rohwer 1998). In contrast, recent application of a leg-loop harness design for songbirds has proven highly successful (Rappole and Tipton 1991, Neudorf and Pitcher 1997, Powell et al. 1998).

In this paper, we present results on the development and use of a figure-8 leg-loop harness for the attachment of transmitters to captive and wild shorebirds. This method offers a solution to potentially problematic issues associated with other transmitter attachment techniques.

METHODS

In the fall of 1998, we used a modified version of the Rappole and Tipton (1991) harness design to attach 1-gram mock transmitters to a population of Western Sandpipers (*Calidris mauri*) held in a captive facility at the University of Nevada-Reno. Transmitters were crafted with modeling clay to match specifications of those used in field studies of Western Sandpipers (Warnock and Warnock 1993, Warnock and Takekawa 1996; Holohil Systems, Ltd., Canada). All birds also were marked with a unique combination of 1-2 color bands to allow individual identification. Transmitters were harnessed to 5 individuals. A control group of 4 individuals was not harnessed. All harnessed birds were weighed immediately following attachment of the transmitter package, after 10 days, and again after 20 days at the conclusion of the study. Birds also were checked on a

daily basis for obvious signs of discomfort or stress. Over the course of the 20-day study period we conducted behavioral observations on all individuals on 8 different days. On days of observation, all captive birds were randomly ordered and each individual was observed for a 5-minute time period. Activities were recorded every 10 seconds and assigned to the categories: feed, locomotion, preen, rest, and wing movement. In addition, we recorded the number of birds within 0.61 m (2 ft) of the focal bird every 60 seconds in order to assess flock cohesiveness. Two-sided t-tests were used to analyze behavioral data.

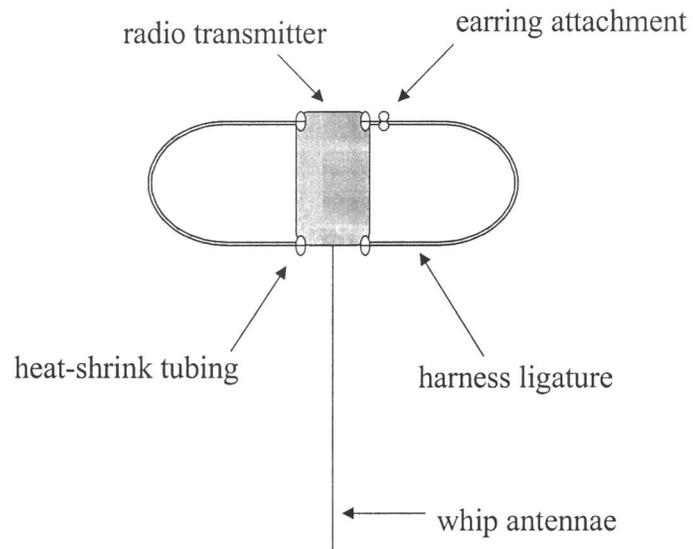
In the spring of 1999, we attached 13 transmitters (2.5 gram, model PD-2; Holohil Systems Ltd., Canada) to a wild population of Killdeer (*Charadrius vociferus*) during the course of a study on winter shorebird movements and wetland connectivity in the Willamette Valley of Oregon, USA. All birds were captured using leg-noose traps (G. Page, personal communication) and banded with unique color band combinations. Of the 13 transmitters deployed, 7 were attached with harnesses and 6 with the epoxy method of Warnock and Warnock (1993; Titan Corporation, Lynwood, Washington, USA). Birds were tracked daily using radio-trucks and aerial telemetry for the duration that they remained in the study area (mean = 10.8 days). Visual observations of study birds were recorded when possible. Observations consisted of recording activity of the radio-tagged individual every 15 seconds over a 10-minute period. The process was then repeated for a randomly selected control individual in the same flock. Behaviors were assigned to the categories feed, locomotion, preen, rest, and wing movement.

Following initial results of the captive and field study, we also used harnesses to attach transmitters to 23 Killdeer and 59 Dunlin (*Calidris alpina*) in the wild during the winter of 1999-2000, as part of ongoing shorebird studies in the Willamette Valley of Oregon, USA.

DESCRIPTION OF HARNESS AND ATTACHMENT

The harness used in this study was a modification of the leg loop figure-8 harness described by Rappole and Tipton (1991; Figure 2.1). It consisted of two loops that slide over each leg of the bird, allowing the transmitter to rest over the lower back/synsacrum area anterior to the uropygial gland. Time required for harness attachment was approximately 2-5 minutes, depending on experience of the researcher. Modifications to the original design included use of heat-shrink hollow tubing set at the front and rear end of the transmitter at time of construction (Holohil Systems Ltd.). The harness material was threaded through the tubing, eliminating the need to glue or tie the harness to the transmitter. Tubing added only 0.1 g weight and 4.5 mm length to the original transmitter dimensions. In addition, an earring backing was used to fasten the harness to the bird. Free ends of the harness material were threaded through the eyelets of the backing and then the eyelets crimped when the harness was of proper length. As a result, the harness

Figure 2.1. Attachment of a figure-eight leg-loop harness to a radio transmitter.



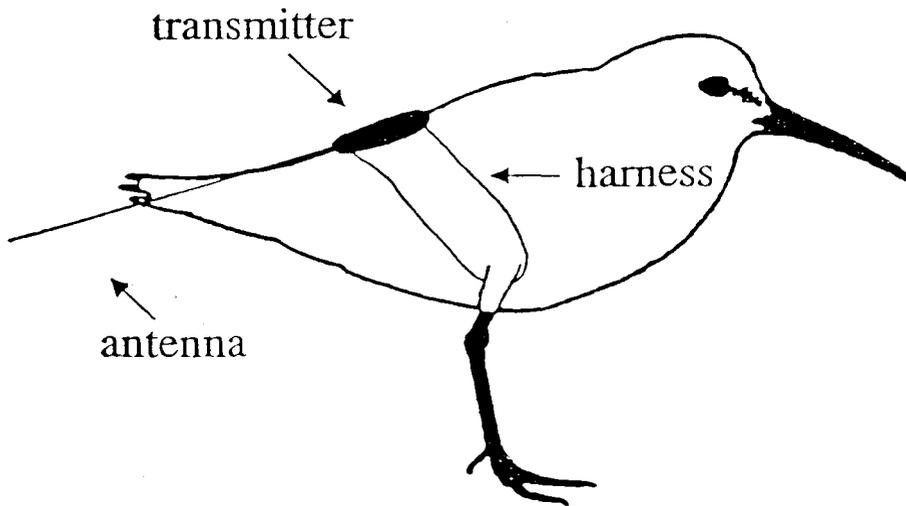
was fitted to each individual bird and there was no need to tie potentially troublesome knots. The earring backing added 0.09 g weight to the transmitter package.

Harness ligature should be a non-abrasive material with a diameter 1 mm or greater in order to prevent irritation (Rappole and Tipton 1991). In our trials, we used a 2-mm diameter silk cord. Harness ligature must be of a diameter equal to or less than that of the transmitter tubing and earring backing.

ATTACHMENT PROCEDURE: SEE FIGURE 2.2.

1. Prior to a birds' capture, string a 30-cm length of ligature through the front and rear tubing of the transmitter. Thread each end of the ligature through the earring backing and crimp one eyelet. This results in two loops of material on either side of the transmitter (Figure 2.1).
2. With bird in hand, slip the left leg of the bird through the left harness loop. Maneuver the loop up the leg as far as possible, such that the ligature rests against the birds's body. The loop must be situated above the tibia/femur attachment point, otherwise the legs will be immobilized when the harness is pulled taut.
3. Holding the left leg loop in place, lay the transmitter across the birds' back with the transmitter resting over the lower back/synsacrum, anterior to the uropygial gland.

Figure 2.2. Proper alignment of figure-eight leg-loop harness and transmitter on shorebird.



4. Slide the remaining leg loop over the free leg of the bird, as previously described.
5. With the transmitter in place, slowly pull the free end of the ligature through the eyelet of the earring backing until the harness is taut. The transmitter should have 2 to 3-mm of play and the ligature should be tight enough that the leg loops cannot slip down beyond the tibia/femur joint. As an example, Killdeer harness ligature after proper fitting was 16.5 cm in length and each leg loop measured approximately 2.95 cm from the edge of the transmitter to the end of the stretched loop.
6. With the harness properly aligned, crimp the remaining eyelet of the earring backing with pliers and trim off excess ligature. The earring backing should rest against the transmitter so it does not contact the birds' body and cause irritation. A drop of quick drying superglue at one end of the front and rear transmitter tubes will prevent the transmitter from sliding on the birds' back.
7. Feathers pinned underneath the ligature and/or transmitter on the birds' back should be carefully freed so that they lay over the transmitter. This will allow the bird to preen the transmitter into the plumage, reduce transmitter visibility, prevent alteration of thermoregulatory processes, and reduce the aerodynamic drag of the transmitter (Caccamise and Hedin 1985).
8. Following harness attachment, place the bird in a holding box (e.g., covered laundry basket) for 1-5 minutes in order to check for immediate signs of immobilization or discomfort.

RESULTS

Captive Western Sandpipers were observed for 20 days and showed no signs of irritation or abrasion where the harness and transmitter contacted the bird. However, all birds with harnesses preened out a 5 mm swath of feathers in the distal region of the tibia. All harnessed birds gained weight during the study (mean = 1.58 ± 0.33 g), presumably to compensate for the added weight of the transmitter. We neglected, however, to weigh control birds as a comparison. Analyses of over 1,800 behavioral observations collected in 360 minutes of observation time did not suggest significant differences in time-activity budgets between harnessed and control birds (Table 2.1; two-sided t-tests, $p > 0.05$).

There was an insufficient number of behavioral observation sessions of wild Killdeer ($n = 13$) to carry out statistical analyses. However, based on 6 harnessed bird observation sessions, average time-activity budget was as follows: 48.15% rest, 12.59% preen, 22.96% forage, 16.30% locomotion. In 7 observation sessions of control birds, we observed the following time-activity budget: 71.05% rest, 13.16% preen, 11.58% forage, 3.68% locomotion, 0.53% wing movement.

Table 2.1. Behavioral observations of captive Western Sandpipers. Activity categories expressed as proportion of each behavior observed with flock cohesiveness measured as mean # of individuals within 2 feet of focal birds.

		Behavior (mean proportion \pm SE)						
	Total						Wing	Flock
Birds (<i>n</i>)	obs. (<i>n</i>)	Rest	Preen	Forage	Locomotion	movement	cohesiveness	
Control group	4 806	34.01 \pm 1.85	2.36 \pm 2.20	20.01 \pm 2.99	40.62 \pm 4.96	2.98 \pm 0.68	4.60 \pm 0.43	
Harness group	5 1003	31.46 \pm 5.69	4.57 \pm 2.49	14.57 \pm 2.74	47.48 \pm 3.75	2.32 \pm 0.41	4.48 \pm 0.29	

Additional resightings of radio-tagged birds ($n = 37$) did not indicate differences in behavior among harnessed birds, epoxy birds, or birds without transmitters attached. In one case, the harness was not properly secured (earing backing not crimped) and within 24 hours following release the bird shed the transmitter. Within 2 weeks of capture, all radio-tagged birds, except for one harnessed individual, migrated out of the study area. These movements coincided with the departure of large numbers of winter resident Killdeer. The harnessed bird that remained was a male that we observed copulating numerous times following harness attachment and was presumed to be nesting in the area.

During the course of the winter of 1999-2000 there were 18 direct visual sightings of 12 different Killdeer with harness packages. Additionally, we recorded 4 sightings of 4 different Dunlin with transmitter harnesses. In all cases birds were observed with conspecifics and did not exhibit any behaviors indicative of discomfort or stress. Activities observed included foraging, walking, flying, and preening. Furthermore, we collected extensive numbers of locations of radio-marked birds. Over the course of 10 weeks we recorded 493 locations of 20 marked Killdeer and 294 locations of 29 marked Dunlin. Harness packages did not appear to inhibit flight capabilities of study subjects as marked Dunlin were detected making non-stop flights of up to 30 km.

DISCUSSION

Findings indicate that our modified harness attachment did not significantly alter the behavior of study subjects and is a viable method of transmitter attachment for shorebird studies. The issue of feather loss in the captive Western Sandpipers is a concern. It is noteworthy, however, that birds preened out feathers on their tibia, not an area contacted by the harness. It is possible that initial inexperience of the researcher resulted in attachment of harnesses too tightly or altered arrangement of feathers such that birds were irritated. Another potential explanation is that feather loss was a by-product of the captive setting whereby birds had more time for comfort movements and tended to fall into fixed-action patterns. In addition, all captive birds preened intensively immediately after their facility was cleaned. This extra stimulus may have heightened awareness of birds to the presence of the harness. Finally, early removal of harnesses prevented an evaluation of whether birds replaced lost feathers following initial stages of harness wear.

Use of the harness method eliminates a number of potential problems associated with other attachment techniques. For example, previous shorebird telemetry studies have reported short retention times and/or premature loss of transmitters with use of adhesives (Rappole and Tipton 1991; Whittingham 1996; Powers 1998; S. Haig, unpublished data). This is a serious concern given the time and resources required to conduct radio telemetry studies. While we were not able to quantify retention time of our transmitter harnesses due to the onset of migration,

use of the same harness material and design on a tropical kingfisher (*Halcyon cinnamomina*) indicated a retention span of well over four months (D. Kesler and S. Haig, unpublished data). Further, studies of a migratory songbird reported that individuals successfully migrated with harnesses and showed no adverse effect from the attachment method after 21 months (Powell et al. 1998). Previous studies found that use of a 5-kg test, braided Dacron line resulted in a retention time of 4-9 months (Powell et al. 1998). Ideally, there is the need for a ligature material that will degrade following the expected lifespan of the radio transmitters used. Additional studies will likely provide insight on retention qualities of different harness materials.

Other benefits of the harness technique include a reduction in handling time during transmitter attachment and elimination of the need to clip feathers. Attachment of our leg-loop harness required 2-5 minutes. In contrast, the curing time of a commonly used bird epoxy (Titan Corporation) ranged from 4-15 minutes and was highly dependent on ambient temperatures (Warnock and Warnock 1993; P. Sanzenbacher, personal observation). Furthermore, Warnock and Takekawa (1996) reported an increased mortality of radio-tagged birds associated with increased handling time. These are potentially important issues, particularly if researchers need to process multiple individuals at a time or during adverse weather conditions.

In summary, our findings indicate that the harness method reported is a viable technique for the attachment of radio transmitters to shorebirds of all sizes.

These harnesses will not alter behavior but will provide a safe, long-lasting, and simple method of transmitter attachment. As the use of radio-telemetry in avian studies progresses there is the need for further studies of the effects of different attachment techniques on all aspects of behavior, including flight capabilities and breeding activities.

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Chapter 3. Spatial and Temporal Movement Patterns of Wintering Dunlin (*Calidris alpina*) in the Willamette Valley, Oregon

ABSTRACT

Knowledge of avian movement provides a means to assess regional and local fidelity, space use of individuals, and functional connectivity of habitat patches. The complex wetland landscape of the Willamette Valley of Oregon attracts large numbers of nonbreeding waterbirds; however, patterns of shorebird (suborder: Charadrii) use in the region and at other inland areas are not well understood. During the winters of 1998-1999 and 1999-2000, we tracked movements of 67 radio-marked Dunlin (*Calidris alpina*) throughout the Willamette Valley. Individual birds were tracked across multiple weeks and exhibited a high degree of regional fidelity. Distances traveled within the region were extensive and greatest during late winter ($P < 0.05$). Females ranged farther from capture sites than males ($P < 0.05$) and movements from capture site for all birds were greatest during the late winter period ($P < 0.05$). Mean home range size (minimum convex polygons) of birds was $301.43 \pm \text{SE of } 50.26 \text{ km}^2$ and was greatest during the late winter period ($P < 0.01$). Birds exhibited varied degrees of fidelity to specific wetland sites and were detected at an average of 9.10 ± 0.41 different sites. Diurnal roost sites were identified as a center of daily activities and daily movements were most pronounced during crepuscular periods. Data represent the

most extensive documentation of winter movements for a shorebird at an inland site. Findings indicate Dunlin were winter residents in the Willamette Valley and extensive local movements suggest a high degree of functional connectivity of shorebird habitats within the Valley.

INTRODUCTION

Studies of avian movement provide fundamental information pertaining to species life histories, population dynamics, habitat use, and other ecological processes (Hansson et al. 1995, Haig et al. 1998, Walters 2000). Further, movement data can assist in the identification of important sites for breeding and migrating birds, assessment of potential impacts of landscape alteration (e.g., habitat fragmentation), and other critical aspects of conservation planning (Myers et al. 1987, Hagan and Johnston 1992, Wiens 1994, Petit 2000).

Movement behavior is a function of the stage of the annual cycle and physiological condition of the individual. Movements are further influenced by the interaction of numerous other factors, such as intra- and interspecific interactions, resource patterns and availability, and weather. Thus, selection of appropriate spatial and temporal scales is a critical component of movement studies and depends on the species, landscape, and ecological processes under investigation (Ims 1995, Bissonette 1997, Huston 1999). Recent innovations in geographic

information science (Merrill et al. 1999, Corsi et al. 2000), radio and satellite telemetry (Cohn 1999, Nichols and Kaiser 1999), genetic techniques (Haig 1998, Waits and Leberg 1999), and isotope tracking (Marra et al. 1998, Hobson 1999) have facilitated expansion of scales examined in movement studies. While there is increasing recognition of the need to consider ecological processes at multiple scales (Christensen et al. 1996, Bissonette 1997, Haig et al. 1998, Poiani et al. 2000), there is a lack of empirical data on avian movement behavior for most taxa (Wiens 1994; Tischendorf and Fahrig 2000; Webster et al., in press). Further, most efforts have been conducted in landscapes that facilitate tracking of movements, such as coastal areas with linear habitats (Warnock and Takekawa 1996, Drake et al. 2001) or inland sites with isolated habitat patches (King et al. 1995, Plissner et al. 1999).

Investigations of within-season movements of birds have most often focused on breeding individuals, in part due to the direct implications of reproductive behavior on population dynamics (Hagan and Johnston 1992, Hohman et al. 1992). Also, behavior during this period facilitates tracking efforts, as movements are more restricted and activities generally focused at nest sites (Plissner et al. 2000). However, for most species the winter period encompasses the greater part of the annual cycle and is a major source of annual mortality (Fretwell 1972, Weller and Batt 1988, Hagan and Johnston 1992). In particular, resident and migrant populations that winter at northern latitudes (temperate regions) must deal with the energetic costs of thermoregulation and potential risk of

severe winter storms (Dugan et al. 1981, Castro et al. 1992, Carey and Dawson 1999). Furthermore, nonbreeding birds must regulate body mass to balance the survival benefits of energy reserves with the negative aspects of fattening. For example, extended foraging time and reduced flight capabilities associated with fattening increase the risk of predation (Whitfield et al. 1988). Also, shorter daylight periods during winter may limit foraging time. Compounding these factors, migrants may arrive at winter areas in poor physical condition due to the energetic demands of fall migration. Finally, individual condition at the conclusion of winter may impact other stages of the annual cycle, including migratory behavior (Dugger 1997) and, potentially, reproductive performance (Heitmeyer and Frederickson 1981, Krapu 1981, Myers 1981).

The Willamette Valley of Oregon is an agricultural landscape with a complex array of local wetland habitats and significant intra- and inter-annual variation in the abundance and spatial configuration of resources. During winter months, large numbers of waterbirds utilize permanent and ephemeral wetland resources across the region (Gabrielson and Jewett 1940, Gullion 1951, Clark and Jarvis 1978). In particular, avian surveys and anecdotal observations suggest the Willamette Valley is an important inland area for several species of nonbreeding shorebirds (suborder: Charadrii; Gabrielson and Jewett 1940, Budeau 1992). Dunlin (*Calidris alpina*) are a mobile shorebird species that occur in large numbers in the region, with sightings of winter flocks of $\geq 15,000$ individuals (Johnson 1993, 1994). However, relatively little is known about habitat use and movements

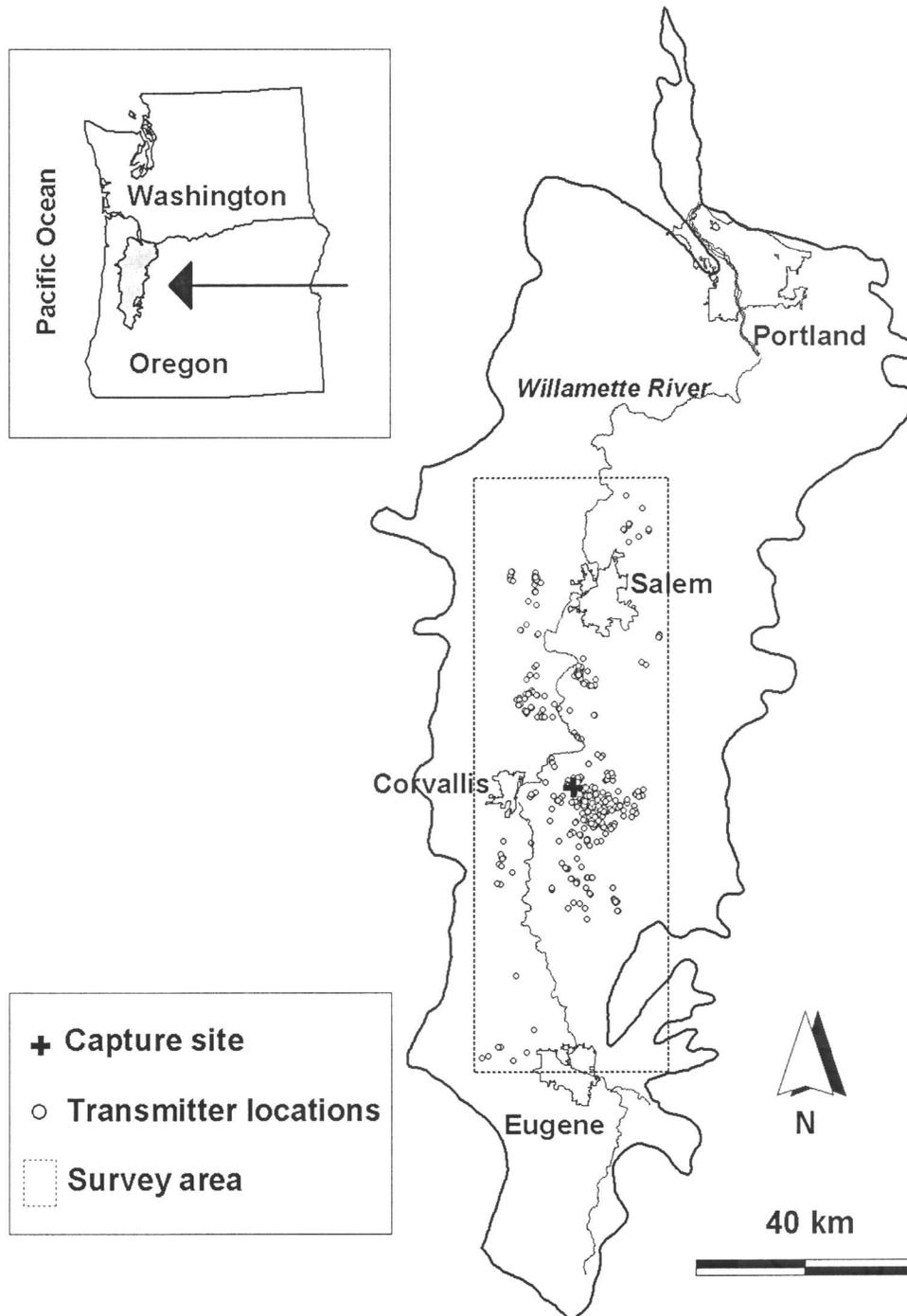
within the Willamette Valley or other inland sites. Strauch (1967) speculated that individuals observed in the region during the winter months were transients and previous studies have documented the role of inland sites as refugia for Dunlin during adverse conditions at coastal sites (Warnock et al. 1995). Thus, our objectives were to quantify fidelity, movement patterns, and space use of Dunlin across the Willamette Valley throughout the winter period.

METHODS

STUDY AREA

The Willamette Valley ecoregion (Figure 3.1) is an extensive lowland formation within the Willamette River Basin of northwest Oregon (45°N, 123°W). The region encompasses an area of approximately 7000 km² and is bounded by the Coast Range to the west, and the Cascade Mountains to the east. Other major physical features include the Willamette River that flows 273-km south to north along the valley floor and its numerous associated tributaries. Regional climate is characterized by warm, dry summers and cool, wet winters. Mean winter temperatures range from 3-5°C and greater than 50% of the annual precipitation (30-year mean = 104.8 cm) occurs from December through February (Taylor 2000).

Figure 3.1. The Willamette Valley ecoregion and area surveyed during telemetry efforts. Dunlin were captured and radio-marked at a single site in the central region of the study area. Telemetry locations of all radio-marked birds tracked during the study are indicated.



The Willamette Valley has been subjected to extensive alteration of native vegetation and landforms (Sedell and Froggatt 1984, Boyd 1986, Hulse 1998). Agriculture is the dominant land use and grass seed is the most widespread crop in terms of acreage. Due to climate, geomorphology, and land use patterns, winter waterbird habitats are a shifting mosaic of saturated soils with frequent ponding and formation of sheet water, as well as a diversity of vegetation types and growth stages. Other more permanent waterbird habitats include scattered managed wetland impoundments and sewage ponds.

CAPTURE AND MARKING

We captured Dunlin at a single site in the central Willamette Valley (Figure 3.1) in January 1999, December 1999, and February 2000. These sampling periods are hereafter referred to as *mid-winter*, *early winter*, and *late winter* respectively. The capture site was an agricultural field with areas of sheep pasture, corn stubble, and a 2.5 ha pond. Counts as high as 20,000 individual Dunlin identified the site as a major roosting and feeding area. Initially, all birds were captured at night with multiple mist-nets strung across sections of the field. During later efforts, birds were captured at dusk with noose-traps (G. Page, pers. comm.) placed in known feeding and bathing areas. Birds were aged and sexed based on plumage characteristics and length of exposed culmen (males ≤ 37.8 mm, females ≥ 39.8 mm, unknown sex ≥ 37.9 to ≤ 39.7 mm; Page 1974). Each individual was fitted

with a metal U.S. Fish and Wildlife Service band and given a unique combination of ultraviolet-resistant color rings (A.C. Hughes, England). Green flags were placed above the tibiotarsal joint to indicate a United States banding origin. Finally, birds were fitted with 1.6-gram radio-transmitters with individual frequencies and an estimated battery lifespan of 8 weeks (Model BD-2, Holohil Systems Ltd., Canada). Transmitters were attached to the lower dorsal region with an epoxy adhesive (Warnock and Warnock 1993) during the mid-winter period, whereas a leg-loop harness was later used in the early winter and late winter periods (Sanzenbacher et al. 2000). The weight of the combined markers and harness package ranged from 1.86 to 1.96 g and averaged $3.68 \pm 0.03\%$ of the body mass of captured Dunlin.

RADIO-TRACKING

Following transmitter deployment, we tracked movements of individuals throughout the Willamette Valley for the duration of transmitter lifespan. Sampling efforts involved intensive daily ground surveys and periodic aerial surveys that extended from areas as far south as Eugene and Fern Ridge Reservoir, north to the Gervais and Lake Labish region (Figure 3.1). All known sites with major Dunlin activity were visited at least once per week and blocks of habitat that connected sites were searched as well. In addition, we conducted weekly exploratory searches throughout the region. Most tracking occurred during

daylight hours (approx. 0800-1600 hrs); however, we also conducted night surveys and attempted to track movements of individuals from diurnal sites to nocturnal sites a minimum of twice weekly.

Ground telemetry efforts utilized two trucks outfitted with dual-Yagi, 4-element, null-peak antenna systems. Tracking protocol was to scan for all transmitter frequencies at two-second intervals in each of four cardinal directions. This process was repeated every 1.6 to 3.2 km to insure complete coverage of areas and maximize probability of transmitter detection. To determine the location of radio-marked birds, observers recorded bird azimuth, truck azimuth, and exact location of the telemetry vehicle (geographical positioning system [GPS]; Trimble Navigation, Sunnyvale, California, USA) at two or more locations. All location data were collected within a 10-min period in order to reduce the probability that a focal bird had moved. This information was later input into program LOAS (Ecological Software Solutions, <http://www.ecostats.com>) to produce estimates of individual locations and associated error (error polygons, error ellipses). In some cases, visual observations of radio-marked birds or associated flocks were plotted on USGS topographic maps or determined with a GPS. Other data collected with location information included flock size, general behaviors (e.g., flying, resting, foraging), and habitat characteristics.

As weather permitted, we conducted bi-weekly aerial surveys to locate radio-marked birds and identify areas of potential shorebird habitat. Flights were completed in a Cessna 182RG with two-element 'H' antennas attached to each

wing strut and a switch box system to isolate signal location. Survey protocol was to fly east-west transects spaced 4 to 6 km apart at an altitude of 457 m and air speed of 222 km/h. During flights, locations of radio-marked birds were plotted on topographic maps (1:150,000 scale, DeLorme) and later transferred to USGS topographic maps (1:24,000 scale).

We conducted annual trials to assess range of transmitter detection and accuracy of estimated locations. Two observers listened for test transmitters ($n = 8$) at various distance intervals across level terrain to determine transmitter range from telemetry trucks. Accuracy of telemetry locations from ground surveys was assessed by two observers that each located three test transmitters at different distances (mean = 0.50 km). Location estimates and bearing information were then compared to actual locations of transmitters recorded with a GPS. In addition, we compared location estimates of test transmitters and mortalities of radio-tagged birds to actual locations of transmitters to ascertain the accuracy and range of aerial surveys.

DATA ANALYSES

Prior to calculation of movement parameters, all data were checked for potential biases. We determined that a minimum of 30 minutes must separate successive locations of an individual to reduce effects of autocorrelation. This interval was deemed sufficient to allow a bird to traverse the extent of its home

range and was based on our observations of Dunlin movements in the Willamette Valley (Swihart and Slade 1997, De Solla et al. 1999, Otis and White 1999). An exception to this rule was when observers tracked direct movements of birds between sites. Furthermore, no more than three locations were permitted for an individual in a single day. For cases that violated these criteria, a subset of locations was randomly selected for inclusion in calculations. Also, data for individuals that shed transmitters prematurely or were found depredated were omitted from all analyses. To determine minimum sample sizes required for summaries we examined scatterplots of data and conducted regression analyses with the parameter estimate as the dependent variable and sample size as the independent variable.

We used multiple approaches to examine fidelity, movement patterns, and space use of Dunlin. Fidelity of wintering Dunlin to the Willamette Valley was quantified as the proportion of radio-marked birds relocated following capture, as well as the number of days from transmitter deployment to final detection for each individual. The assumption was that individuals tracked for extensive periods in the region exhibited a high degree of fidelity and were likely winter residents in the Willamette Valley. Cases where individuals were not detected for extended periods and thus may have visited other regions were identified. In addition, we conducted a comprehensive telemetry flight of the Oregon coast during the early winter period.

We calculated a range of parameter estimates to quantify movements of birds across the landscape. Individual mobility was described as the total sum of linear distances between successive locations. This measurement represented the minimum total distance a bird moved during a seasonal period, because birds moved to some extent between relocations. Distance estimates were not presented as a rate (e.g., km/d) because time between relocations varied and movements were often focused around roost sites. Estimates were calculated for all birds with ≥ 10 locations and two birds were excluded from analyses as outliers based on Studentized residuals (> 2.5) and relative leverage values. Whereas studies of breeding individuals often utilize the nest site as a point of reference for movement estimates, we calculated the mean and maximum distance at which wintering radio-marked birds were detected from the capture site. All birds with ≥ 1 location were included in calculations and estimates of mean distance were log transformed for analyses to meet assumptions of normality and variance.

A final approach to estimate seasonal movements and space use was to quantify home range sizes. We considered a number of methods including fixed kernels, bivariate ellipses, and minimum convex polygons (MCPs). Based on sample size constraints and distribution of the data, we determined that MCPs were the most conservative and appropriate home range estimator (Samuel and Garton 1985, White and Garrot 1990, Seaman et al. 1999). This method quantifies the area encompassed by movements of each individual; however, estimates do not imply actual utilization of entire areas due to the inclusion of large tracts separating

detection locations. We calculated home ranges using ArcView GIS software and the Animal Movement extension (Hooge and Eichenlaub 1997). Previous work has shown a positive bias in MCP area with increased numbers of locations (White and Garrot 1990, Mazur et al. 1998). In contrast, our data indicated a non-significant but slight negative trend in area bias and suggested that it adequately described areas traversed for sample sizes of ≥ 15 locations. Home range estimates were log transformed prior to analyses.

Finally, we quantified the number of sites (e.g., agricultural fields, managed wetlands, sewage ponds) at which radio-marked birds were detected throughout a season. Using a geographical information system (GIS; ArcView, ESRI Inc.), bird locations were plotted on map layers with habitats classified and roads delineated. Functional sites were differentiated based on physical borders (e.g., roads, hedgerows), vegetation characteristics, and substrate moisture levels. As a rule, locations greater than 1 km apart were defined as distinct sites. Results were calculated for all birds with ≥ 10 locations and data were log transformed prior to analyses.

We utilized analysis of variance (ANOVA) tests to examine differences in parameters for sample groups (SAS/ASSIST/INSIGHT, SAS Institute Inc. 1997). For each parameter, a two-way ANOVA was used to test for effects of winter sample period, sex, and the interaction term. Enriched models used a subset of data that excluded individuals of unknown sex that might confound analyses. When coefficients were determined significant ($P < 0.05$), Fisher's least-significant-

difference (LSD) multiple comparison tests were used to examine differences between groups. In cases where seasonal period was identified as the only significant coefficient, a one-way ANOVA, including individuals of unknown sex, was used to further test for seasonal differences. Means are reported throughout with associated standard error (\pm SE).

RESULTS

We radio-marked 67 Dunlin: 29 in early winter, 18 in mid-winter, and 20 in late winter (Table 3.1). Sex ratios of all known sex birds captured, based on culmen length, were slightly male biased in early winter (57% male) and late winter (55% male) and heavily male biased in mid-winter (71% male). Following deployment, 10 transmitters were recovered as a result of predation events ($n = 6$), attachment failure ($n = 2$), and unknown causes ($n = 2$). Approximately 1316 hrs of tracking resulted in 1211 locations of radio-marked birds, with an average of 21.25 ± 1.39 locations per individual across all sampling periods. The overall area searched during regular telemetry surveys exceeded the area in which radio-marked birds were observed to an extent that suggested a high degree of coverage (Figure 3.1).

Table 3.1. Capture and tracking efforts for radio-marked Dunlin in the Willamette Valley, Oregon, USA.

	Radio-marked birds				Locations per individual			Ground	Aerial survey
	Male	Female	Unknown	Total	n^a	Mean	SE	survey (hrs)	(hrs)
Early Winter	11	10	8	29	23	19.83	1.57	535.40	21.00
Mid-winter	9	4	5	18	16	27.63	3.51	329.00	11.30
Late winter	7	8	5	20	18	17.39	1.80	400.65	18.65
Total	27	22	18	67	57	21.25	1.39	1265.05	50.95

^a Excludes mortalities, dropped transmitters, and autocorrelated locations.

Based on field trials, transmitter range from the ground averaged 1.35 ± 0.12 km (range 0.85 – 1.82 km). Additional observations revealed that searching from high points (e.g., road overpasses, hills) increased range of transmitter detection. The average distance between estimated and actual locations of test transmitters was 33.02 ± 3.22 m. The mean standard bearing error (azimuth error) was $2.12 \pm 0.17^\circ$. For location estimates of radio-marked birds, the mean error polygon size was 0.83 ± 0.19 ha ($n = 543$) and the mean error ellipse was 2.20 ± 0.51 ha ($n = 80$).

During aerial surveys, test transmitters were detected at an average range of 2.4 km. However, the activity of radio-marked birds greatly influenced detection range. For example, birds in flight were detected from a distance of up to 16 km. Accuracy of aerial locations was estimated at 0.48 ± 0.14 km ($n = 4$ transmitters); however, many bird locations were known with greater accuracy because individuals repeatedly used sites with known geographic coordinates.

Following capture, all radio-marked birds were relocated in the study area (67/67; 100%). An exception was a single radio-marked bird that was detected at a coastal estuary of Oregon during early winter, approximately 60 km from the Willamette Valley. This individual returned to the Valley within 10 days and remained for the duration of the sampling period. Study birds were tracked over an average span of 41.46 ± 1.36 days, or 74.04% of predicted transmitter lifespan (Table 3.2). The number of days birds were tracked did not differ by sex ($F_{5,23} = 1.17$, n.s.) and there was no significant interaction of season and sex ($F_{5,23} = 0.31$,

n.s.). However, individuals captured in late winter were tracked for a shorter duration than other periods ($F_{2,36} = 4.81, P = 0.014$). The mean spring departure date of radio-marked birds from the region during the second winter of study was March 22nd ± 1.80 days ($n = 17$ birds). Departure date was unknown for two individuals that remained past April 4th, when tracking efforts were terminated.

Dunlin traveled extensive distances within the study area. The average minimum total distance birds traveled in a seasonal period was 167.75 ± 11.30 km (Table 3.2). Sex ($F_{5,37} = 0.07$) and the interaction of sex and season ($F_{5,37} = 0.34$) were both non-significant factors in analyses ($P > 0.05$); however, individuals did exhibit seasonal differences in movements ($F_{2,51} = 4.50, P < 0.05$). Birds in late winter covered greater distances than birds during early winter or mid-winter periods ($P < 0.05$). In addition, there was considerable variation among individuals within all sample groups, as some birds were relatively sedentary and others more mobile (range 23.24 – 455.01 km).

The mean distance that individuals were detected from the capture site was 14.92 ± 1.48 km. Estimates differed with respect to sex ($F_{5,38} = 6.12, P < 0.02$) and season ($F_{5,38} = 10.89, P < 0.01$), with no interaction effect ($F_{5,38} = 2.30, n.s.$). Females were found at greater distances from the capture site than males and in late winter birds ranged farther than during other sample periods (Table 3.2). In comparison, estimates of the maximum distance that individuals traveled from the capture site indicated extensive exploratory movements throughout the study area.

Table 3.2. Movements of nonbreeding Dunlin in the Willamette Valley, Oregon, USA. Means presented with associated standard errors (\pm SE).

	Days tracked		Minimum total distance traveled (km)		Distance from capture site (km)		
	<i>n</i> radios ^a	<i>n</i> obs.	Mean	<i>n</i> obs. ^b	Mean	<i>n</i> obs.	Mean
Sex							
Male	26	614	41.69 (2.41)	611	174.11 (15.96)	614	12.35 (1.89)
Female	18	316	40.89 (1.96)	322	178.13 (21.92)	316	20.17 (2.32)
Unknown	13	281	41.77 (2.13)	222	132.66 (20.02)	281	12.17 (3.89)
Season							
Early winter	23	454	47.04 (4.42)	430	148.44 (16.14)	454	10.50 (1.51)
Mid-winter	16	443	41.31 (3.38)	413	141.78 (19.13)	443	8.03 (2.07)
Late winter	18	314	34.44 (1.94)	312	213.83 (20.24)	314	26.69 (1.86)
Total	57	1211	41.46 (1.36)	1155	167.65 (11.30)	1211	14.92 (1.48)

^a Excludes mortalities and dropped transmitters.

^b Number of individuals and observations reduced due to sample size constraints or outliers as described in methods.

Table 3.2. Movements of nonbreeding Dunlin in the Willamette Valley, Oregon, USA. Means presented with associated standard errors (\pm SE). (Continued).

	<i>n</i> radios ^a	Max. distance from capture site (km)		Sites visited	
		<i>n</i> obs.	Mean	<i>n</i> obs. ^b	Mean
Sex					
Male	26	614	31.00 (2.73)	606	9.58 (0.68)
Female	18	316	37.96 (3.44)	288	8.79 (0.60)
Unknown	13	281	33.41 (4.65)	274	8.50 (0.75)
Season					
Early winter	23	454	32.89 (3.47)	439	8.76 (0.63)
Mid-winter	16	443	23.67 (2.91)	431	7.43 (0.52)
Late winter	18	314	43.80 (1.59)	298	8.47 (0.62)
Total	57	1211	33.75 (1.97)	1168	9.10 (0.41)

^a Excludes mortalities and dropped transmitters.

^b Number of individuals and observations reduced due to sample size constraints or outliers as described in methods.

For all sample groups, the maximum distance estimate was two to three times the mean distance that individuals were located from the capture site. Maximum distances did not vary with respect to sex ($F_{5,38} = 2.05$, n.s.) or the interaction term ($F_{5,38} = 2.65$, n.s.), but were different among seasons ($F_{2,54} = 10.51$, $P < 0.01$).

Results from multiple comparison tests indicated differences across all seasons ($P < 0.05$); birds were found the greatest distance from the capture site in late winter (43.80 ± 1.59 km), followed by early winter (32.89 ± 3.47 km), and mid-winter (23.67 ± 2.91 km).

As further evidence of Dunlin mobility, average home range (MCPs) size was 301.43 ± 50.26 km² (range = 10.14 – 1378.79 km²; Table 3.3). There was no sex effect ($F_{5,24} = 1.86$ n.s.) or interaction of sex and season ($F_{5,24} = 1.39$ n.s.), but in general females tended to travel over larger areas than males. Estimates differed significantly by season ($F_{2,37} = 17.66$, $P < 0.01$), with birds in late winter (mean = 621.05 km²) traversing larger areas than individuals during either early winter (mean = 202.92 km²) or mid-winter (mean = 120.06 km²).

Radio-marked birds were detected at numerous agricultural fields, managed wetlands, and artificial impoundments within the Willamette Valley. Birds were detected at a total of 213 distinct sites during the study; however, the mean number of sites visited per individual calculated across all periods was 9.10 ± 0.41 (range = 4 - 18; Table 3.2). Birds were detected at a similar number of sites regardless of sex ($F_{5,32} = 0.67$, n.s.) or season ($F_{2,47} = 1.36$, n.s.), with no interaction effect ($F_{5,32} = 0.41$, n.s.).

Table 3.3. Mean (\pm SE) home range area (100% minimum convex polygons) encompassed by movements of nonbreeding Dunlin in the Willamette Valley, Oregon, USA.

	Home range (km ²)		
	<i>n</i> birds	<i>n</i> locations	Mean
Sex			
Male	20	556	300.18 (69.20)
Female	10	241	356.15 (123.48)
Unknown	10	250	249.22 (87.70)
Season			
Early winter	15	365	202.92 (56.17)
Mid- winter	13	420	120.06 (14.74)
Late winter	12	262	621.06 (104.67)
Total	40	1047	301.43 (50.27)

Daily movement patterns indicated diurnal roost sites were centers of activity and surveys revealed six major roost sites located throughout the study area that accounted for 56.75% (689/1214) of all telemetry locations. These sites included sewage ponds, flooded rice fields, and managed wetland impoundments. A common characteristic of all six sites was the presence of impounded water. Average flock size at these roosts was $6,274 \pm 408$ birds (range = 30 to 20,000 birds). The dominant flock activity recorded during 113 visits to diurnal roosts was flying (61.95% of visits), roosting (27.43%), and foraging (10.62%). Sites were used at all times of day; however, numbers frequently peaked in afternoon hours with the gradual arrival of flocks of 5-400 birds from surrounding areas. In addition, 76.56% (127 observations of 39 birds) of radio-marked birds present at diurnal roost sites during afternoon hours departed at dusk to surrounding agricultural fields. Crepuscular movements were typical at sites throughout the study area, as radio-marked birds located 1-2 hrs prior to dusk and then relocated at night traveled an average of 8.54 ± 1.55 km ($n = 47$) between sites. In some cases, birds were tracked on direct crepuscular flights of greater than 30 km. Fluctuation of transmitter signals at nocturnal sites suggested foraging was a common activity.

DISCUSSION

Shorebirds are a group of highly mobile wetland-associated species for which information on winter movements and space use is limited. Few studies have been conducted at a scale sufficient to quantify the extent of individual movements across a landscape and efforts have focused almost exclusively on coastal habitats (Ruiz et al. 1989, Warnock et al. 1995, Warnock and Takekawa 1996, Drake et al. 2001). Our study represents the most extensive data on winter fidelity and movements of a shorebird species at an inland landscape.

Previous efforts have established that inland sites support significant numbers of wintering shorebirds (Lane 1987, Shuford et al. 1998); however, prior to our study there was scarce information on winter shorebird use of the Willamette Valley. Published reports include sightings of large Dunlin flocks (15,000+ individuals) and documented use of local habitats by nonbreeding shorebirds (Budeau 1992, Johnson 1994). Based on limited local surveys and information from Pacific Coast wintering areas, Strauch (1967) asserted that Dunlin were rare winter visitors to the Willamette Valley and that the region was of primary importance for migrating shorebirds, not over-wintering shorebirds. In contrast, we consistently encountered large groups of Dunlin and tracked individuals for extended periods among numerous sites within the study area. Simultaneous surveys at multiple roost sites resulted in counts over 30,000 birds and suggests greater numbers within the extended Willamette Valley region. Our findings

indicate that Dunlin encountered during winter months (December-March) were residents during the nonbreeding period and exhibited a high degree of regional fidelity within a given year.

Observations of movements and daily activity patterns provide insights to the selective pressures affecting behavior of wintering shorebirds. The movement behavior of an individual determines the scale at which it perceives the landscape and the threshold at which the spatial array of habitat patches impacts connectivity and movements. For example, observations of migrating Pectoral Sandpipers (*Calidris melanotos*) at an interior stopover site in North America revealed localized movements with few inter-wetland exchanges (Farmer and Parent 1997). However, as the distance between wetland patches decreased, birds exhibited a greater frequency of movements between patches. Conversely, we found that Dunlin in the Willamette Valley traveled extensive distances with larger home ranges than previously reported for any wintering shorebird species (Warnock and Takekawa 1996, Drake 2001). The extent of these movements and use of multiple sites suggests that individuals perceived large segments of the landscape as functionally connected.

Other factors affecting movement behaviors of nonbreeding shorebirds include daily and seasonal metabolic demands. Radio-marked Dunlin in the Willamette Valley traveled greater distances and exhibited larger home ranges during the late winter sampling period. Studies at coastal habitats of Western Sandpipers (*Calidris mauri*) and Piping Plovers (*Charadrius melodus*) did not

reveal similar patterns (Warnock and Takekawa 1996, Drake et al. 2001); however, Ruiz et al. (1989) observed a general increase in movements of Dunlin at later winter dates. These seasonal differences in movements are potentially a response to increased energetic demands of pre-migratory restlessness (i.e., Zugunruhe), molt, and fat deposition associated with the onset of spring migration (Gill 1990). For example, alternate molt in Pacific Coast Dunlin occurs from late February to early May (Holmes 1966, Warnock and Gill 1996). However, reported body masses of Dunlin in California and Washington are at annual lows during the months of February and March, with major pre-migration fattening not occurring until mid-April (Buchanan et al. 1996, Warnock and Gill 1996). Therefore, based on this information and departure dates of Dunlin from the study area, timing of energetic costs related to molt and migration are variable and incurred to some degree while in the Willamette Valley. In addition, observed differences in seasonal movements may be partly an artifact of tracking efforts, as our knowledge of sites used by Dunlin increased as the study progressed. However, we reject this explanation due to relatively equal tracking effort among sampling periods and the extensive coverage of the region during aerial surveys.

Seasonal differences in movement patterns of Dunlin in the Willamette Valley may also reflect the spatial and temporal variability of regional wetland resources. In particular, increased mobility was potentially a result of lower precipitation levels during the late winter period (Taylor 2000) and thus a decrease in the abundance and density of agricultural wetlands. Also, seasonal growth of

grass fields in the Willamette Valley may approach a threshold that limits use of some sites by wintering birds. For example, Colwell and Dodd (1997) reported that pasture use by nonbreeding Dunlin and other shorebirds at coastal sites in California was associated with short vegetation.

Differential movements in response to resource availability are consistent with the findings of other avian studies in areas with dynamic habitats. For example, Skagen and Knopf (1994) documented use of shifting and variable wetland habitats by migrating shorebirds at inland sites of North America. They proposed that birds dependent on ephemeral and unpredictable resources exhibited flexible and opportunistic movements. Similarly, Dunlin in the Willamette Valley utilized multiple agricultural wetland sites within a season and exhibited a relatively low degree of fidelity to specific habitat patches. A notable exception was that birds frequently returned to a select group of traditional sites used for roosting and foraging (e.g., sewage lagoons, managed wetlands, permanent impoundments). Regardless, use of multiple sites and extensive exploratory movements may have resulted in an increased knowledge of regional resources and facilitated the rapid response of individuals to the emergence of sites as seasonal rains charged ephemeral wetlands and late winter drawdowns at managed wetlands exposed shorebird habitats. This evidence suggests that greater late winter movements of radio-marked Dunlin was a response to an increasingly fragmented landscape as well as seasonal hormonal changes (i.e., Zugunruhe) associated with spring migration.

Sex ratios of birds captured was similar to that observed by Sheppard et al. (2001) at sites in British Columbia and California. Our studies suggest sex-related differences in the scale of movements, with females ranging over larger areas. Potential resource partitioning based on sexual dimorphism (i.e., culmen length, body size) was not evident but warrants further attention (Warnock and Gill 1996).

Previous studies have reported large-scale winter movements of shorebirds and other waterbirds in response to weather conditions (Laubahn and Metzner 1999, Cox and Afton 2000). In particular, Warnock et al. (1995) documented movements of Dunlin up to 140 km from coastal sites to inland areas during periods of heavy rains. Presumably, winter storms at coastal areas resulted in deterioration of local feeding conditions and potentially increased availability of flooded habitats at inland sites (Warnock et al. 1995). Similarly, we found that a radio-marked Dunlin traveled approximately 60 km from the Willamette Valley to a coastal estuary of Oregon. The departure of this individual coincided with an isolated 10-day period when minimum daily temperatures were below freezing (0°C) throughout the study area. During this time, substrate and standing water were frozen for extended periods, thus limiting foraging opportunities at a time of increased metabolic demands for thermoregulation. Furthermore, after approximately 10 days the individual was relocated within the Willamette Valley and remained for the duration of the sampling period. These findings link the Willamette Valley to coastal areas, as well as further substantiate the influence of adverse weather conditions on movements of shorebirds in winter. Moreover,

return of an individual from a coastal site and the fact that a majority of radio-marked Dunlin remained in the study area during severe weather conditions provide additional evidence of the high degree of regional fidelity of wintering Dunlin to the Willamette Valley.

As has been observed in other shorebird studies, we found that Dunlin congregated on a daily basis at diurnal roost sites (Ruiz et al. 1989, Warnock and Takekawa 1996). Timing of roost formation and departure were variable and occurred at all times of day. However, dawn and dusk were consistent periods of activity. Factors associated with roost formation at coastal sites include tidal cycles, time of day, and lunar cycles (Handel and Gill 1992). In particular, tidal effects dictate availability of foraging habitat and thus are closely associated with movements between feeding areas and roost sites (Handel and Gill 1992). In the absence of tidal effects, formation of large flocks at roost sites in the Willamette Valley and other inland areas may promote “information sharing” that facilitates knowledge of regional resources and increases foraging opportunities of individuals (Brooke 1972, Sparling and Krapu 1994). Furthermore, it is well established that flocking behavior enhances predator avoidance (Cresswell 1994, Barbosa 1997), and numerous studies have shown that raptor predation is a major source of mortality for wintering shorebirds (Cresswell and Whitfield 1994, Warnock and Gill 1996, Barbosa 1997). For example, Page and Whitacre (1975) estimated 21% mortality in a winter population of Dunlin as a result of raptor predation. Aerial predators were common at roost sites in the Willamette Valley and we observed

predation of Dunlin by Peregrine Falcons (*Falco peregrinus*), Merlin (*F. columbarius*), and Cooper's Hawks (*Accipiter cooperii*). In addition, unidentified predators depredated six radio-marked birds. Furthermore, we found that Dunlin flocks at major roost sites engaged in extended periods of flight over flooded impoundments. Recent studies at coastal sites have associated this aerial flocking with a lack of unvegetated roost sites and the presence of raptors (Dekker 1998, Hötker 2000).

In conclusion, findings of this investigation indicate Dunlin are winter residents of the Willamette Valley that exhibit a high degree of regional fidelity during the wintering period. Individuals utilize numerous sites within the region and are capable of opportunistic movements to exploit the dynamic temporal and spatial nature of local resources. Furthermore, results highlight the importance of scale in studies of mobile species and complex landscapes. Information from this study provides a basis to further evaluate the distribution and connectivity of wetland resources within the region. Finally, recognition of the importance of farmed wetlands and roost sites to local shorebird populations indicates the need to consider these habitats in future conservation planning efforts.

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**Chapter 4. Regional Fidelity and Movement Patterns
of Killdeer (*Charadrius vociferus*)
Wintering in the Willamette Valley, Oregon**

ABSTRACT

Killdeer (*Charadrius vociferus*) are a common species with a range that extends throughout North America. However, data from large-scale surveys indicate long-term declines in many regions. There are few studies of this species and little information on residency patterns and nonbreeding movements across the species' range. Thus, we quantified fidelity and movement patterns of 24 radio-tagged Killdeer in the Willamette Valley of Oregon during the winter of 1999-2000. Results from telemetry surveys and census efforts revealed that the population segment monitored was composed of winter residents (63%), early winter migrants (26%), and year-round resident breeders (11%). Movements were localized with birds detected at an average distance of 5.15 ± 0.91 (SE) km from site of capture. Mean home range size (95% kernel) was 7.73 ± 3.19 km². However, results also indicated periodic exploratory movements, with some birds detected up to 30 km from banding sites. Overall, individuals exhibited a low degree of fidelity to specific sites and were detected at an average of 11.91 ± 1.14 sites. Analyses found no differences in monthly movement patterns; however, there was a tendency for birds to range farther from capture sites as the winter

progressed. In most cases, movements of resident breeders were smaller in scale than those of winter residents.

INTRODUCTION

Killdeer (*Charadrius vociferus*) are one of the most common and widespread shorebird (suborder: Charadrii) species in North America. The range of this predominantly temperate breeding species extends from the southern edge of the Arctic Circle to the Caribbean and northern areas of South America (Bent 1929, Jackson and Jackson 2000). Recent data summaries from large-scale avian surveys indicate significant long-term declines in Killdeer throughout segments of their range, with the most severe declines occurring in regions of Canada and the western United States (Page and Gill 1994, Sanzenbacher and Haig 2001). However, there has been a general lack of concern regarding their status, presumably because they are a visible species that often occur in altered and degraded habitats (e.g., urban and industrial developments). Efforts to determine potential causes of decline and identify populations at risk are further complicated by a general lack of information on basic Killdeer ecology.

Most Killdeer research has focused on breeding behavior (Mace 1971; Nol 1980; Schardien 1981; Mundahl 1982; Nol and Lambert 1984; Brunton 1988a,b,c, 1990; Powers 1998; Plissner et al. 2000). The few nonbreeding studies have been

limited to aspects of social organization (Myers et al. 1979, Heck 1985) and habitat use (Brush 1995, Colwell and Dodd 1997). In fact, the nonbreeding period represents the largest segment of the annual cycle for shorebirds and has a major impact on population dynamics (Evans and Pienkowski 1984). Killdeer winter in large numbers in temperate regions; thus major segments of the population are exposed to pressures associated with adverse weather conditions, such as increased costs of thermoregulation (Castro et al. 1992), decreased foraging opportunities (Dugan et al. 1981), and enhanced risk of predation (Whitfield et al. 1988).

Killdeer occur in a range of open wetland and upland habitats; however, these habitats are some of the most threatened in North America. As a result of the conversion of native habitats to urban and agricultural areas, less than half of the wetlands that existed prior to European settlement remain today (Dahl 1990) and losses of upland habitats, such as native prairies, are even more extensive (Samson and Knopf 1994). Furthermore, the continued degradation and alteration of these habitats have been implicated in widespread declines of numerous avian species, including shorebirds (Haig 1992; Knopf 1994, 1996; Page et al. 1995; Brown et al. 2000).

The Willamette Valley in western Oregon is a heavily altered landscape in which most native upland and wetland habitats have been converted for agricultural purposes (Hulse 1998). Regardless, vast areas of seasonally flooded agricultural fields attract large numbers of nonbreeding shorebirds and other waterbird species (Gabrielson and Jewett 1940, Budeau 1992). The region is an important area for

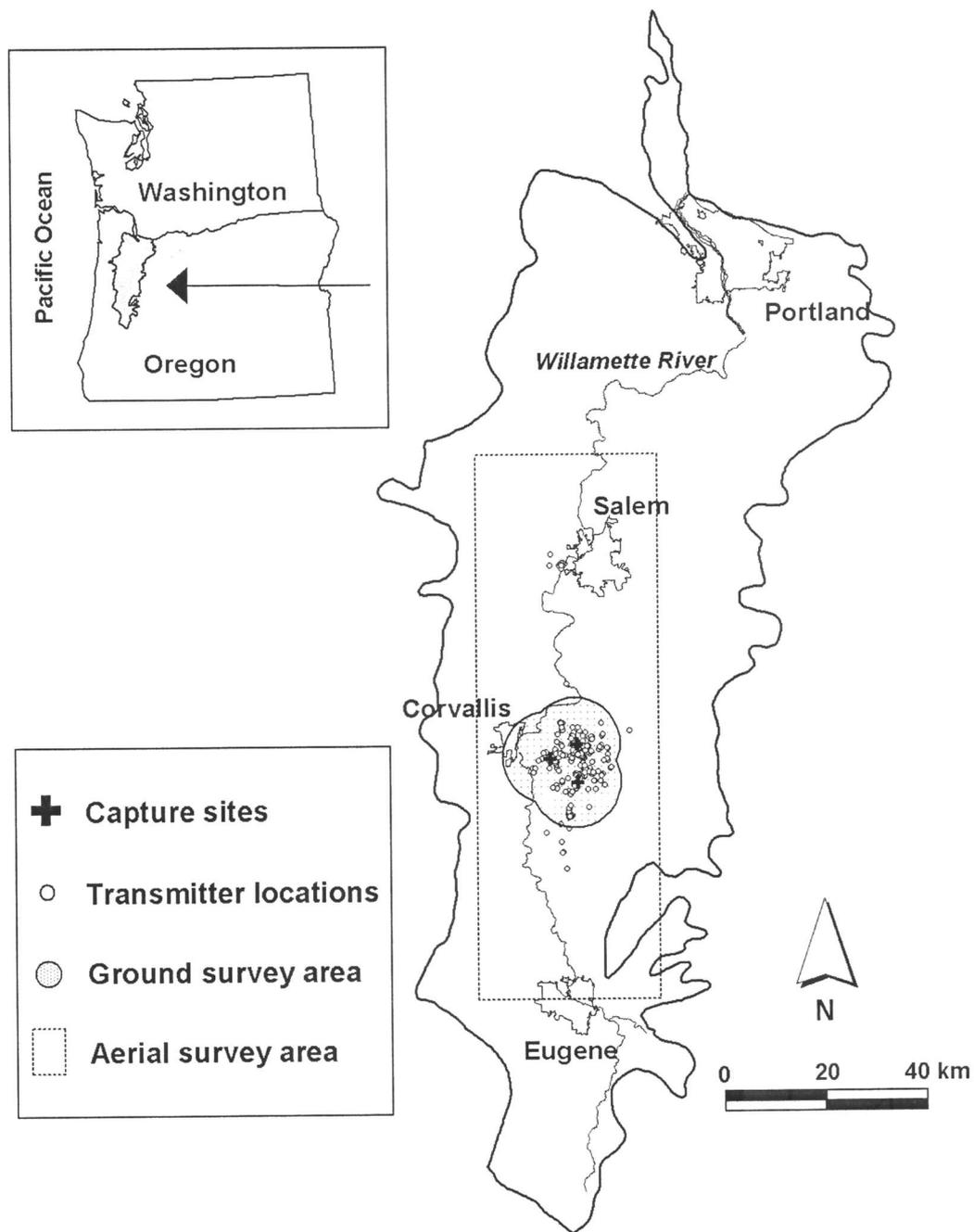
Killdeer that winter at northern latitudes and supports some of the highest densities of nonbreeding individuals (Sauer et al. 1996). In some cases, Killdeer occur in single loose flocks of up to 1000 birds or more. Previous studies of Killdeer have suggested a latitudinal gradient in the proportion of migrant versus resident segments of populations (Jackson and Jackson 2000). Further, information suggests differences in winter movements of migrants versus year-round residents (Schardien 1981, Heck 1985). However, there is little quantitative information on residency patterns or seasonal movements across the species range. Thus, we radio-tracked Killdeer wintering in the Willamette Valley to determine fidelity, movement patterns, and space use of birds.

METHODS

STUDY AREA

We studied Killdeer during the winter months (December-March) of 1999-2000 in the Willamette Valley of Oregon (45°N, 123°W; Figure 4.1). The Willamette Valley is a 7000 km² lowland area of northwest Oregon, located approximately 60-km inland from the Pacific Coast and bordered by the Coast Range to the west and Cascade Mountains to the east. Winter climate is characterized by average temperatures of 3-5°C and extensive rains.

Figure 4.1. The Willamette Valley ecoregion and areas covered during ground and aerial telemetry surveys of Killdeer. Capture sites and all detections of radio-marked birds are indicated.



The majority of annual precipitation (30-year mean = 104.8 cm) occurs from December through February (Taylor 2000). Regional land cover consists of large tracts of cultivated grass seed fields interspersed with various row crops, pasture, and areas of urban and industrial development (Hulse 1998). As a result of land use practices, precipitation levels, and occurrence of hydric soils, the dominant waterbird habitats during winter months are a dynamic assemblage of farmed wetlands with a high degree of annual and seasonal variation in distribution and site characteristics. Vegetation at sites varies with crop type as well as stage of the winter growing season and there is frequent formation of sheet water and ponding. However, drainage practices such as construction of artificial waterways and tiling are widespread. The result is a complex and shifting mosaic of saturated soils and flooded agricultural fields during winter months. In addition, there are numerous moist-soil managed wetland refuges and hunt clubs located throughout the region.

KILLDEER SURVEYS

Weekly roadside shorebird censuses were conducted as part of associated studies of shorebirds in the Willamette Valley. Census efforts covered 10 focal areas that were approximately 15 km² each and were selected as representative of the distribution and spatial array of local habitats (O. Taft, pers. comm.). Census protocol was to drive all roads within designated areas on a weekly basis.

Observers used binoculars and spotting scopes to scan all sites with potential

shorebird habitat and count numbers of all shorebird species. For each census period, total counts were summed across all focal areas. These counts represent an index of relative shorebird numbers within a representative segment of the Willamette Valley and provide information on temporal changes of winter Killdeer numbers.

CAPTURE AND MARKING

We radio-marked 20 Killdeer from 29 November to 3 December 1999, and an additional four birds on 2 February 2000. Killdeer were captured with leg-noose traps (G. Page, pers. comm.) during daylight hours at three agricultural sites, located approximately 8 km apart (Figure 4.1; Sanzenbacher and Haig, in review). Birds were fitted with 2.75-g radio-transmitters with individual frequencies and an estimated lifespan of 16 weeks (model PD-2, 2.75 g, Holohil Systems, Canada). Transmitters were attached using a leg-loop harness (Rappole and Tipton 1996, Sanzenbacher et al. 2000) and rested approximately 1-2 cm anterior to the uropygial gland. In addition, birds were banded both above and below the tibiotarsal joint with a U.S. Fish and Wildlife Service aluminum band and a unique combination of ultra-violet resistant DarvicTM color bands (A.C. Hughes, England). A green flag was attached to indicate a United States banding origin. Total weight of transmitters and auxiliary markers averaged 3.93 g and did not exceed 4% of a bird's body weight. Sexing and aging of birds at time of capture was not possible

due to a lack of reliable morphological characteristics to differentiate groups (Jackson and Jackson 2000).

TELEMETRY SURVEYS

We conducted surveys for radio-marked birds for the duration of the 16-week transmitter lifespan, approximately December through March. Tracking efforts included daily ground surveys that each week covered all areas within a 10-km radius of trap sites. Sites with large flocks of Killdeer and areas with previous detections of radio-marked birds were visited with greater frequency. In addition, bi-weekly aerial surveys and periodic exploratory ground surveys covered extensive areas of the Willamette Valley (Figure 4.1). Most tracking efforts occurred during daylight hours (approx. 0800-1800 hrs); however, night ground surveys were conducted a minimum of once per week.

Ground telemetry was conducted with two trucks outfitted with dual 4-element Yagi antennas and null-peak systems. Survey protocol was to scan for all frequencies at 2-second intervals in each of four cardinal directions. This process was repeated every 1.6-3.2 km in order to insure complete coverage of areas. Following detection of a transmitter, observers determined the location of the radio-marked bird based on intersection of signal bearings taken from two or more points. All location information was collected within a 10-min period in order to reduce probability of a bird moving during data collection. Program LOAS

(Ecological Software Solutions, <http://www.ecostats.com>) was used to derive location estimates and associated error (error polygons, error ellipses). In some cases, it was possible to get visual sightings of radio-marked birds or associated flocks and plot locations on USGS topographic maps. With visual sightings we recorded information on flock size, activities (e.g., foraging, resting, flying), habitat type (e.g., crop type), and vegetation characteristics (e.g., height, density). As weather permitted, bi-weekly aerial surveys were conducted in a Cessna 182-RG with H-element antennas attached to each wing strut. Survey protocol was to fly latitudinal transects at 2 to 4 km intervals and at an altitude of approximately 457 m (1500 feet). Locations of radio-marked birds were plotted on topographic maps. Field trials were conducted with test transmitters to determine range of transmitter detection and accuracy of estimated locations for both ground and aerial surveys.

STATISTICAL ANALYSES

We used multiple approaches to examine fidelity, movement patterns, and space use of Killdeer. Data were evaluated for potential biases prior to calculation of parameter estimate. We estimated that a minimum of 45 mins was required between locations for a given individual to reduce effects of autocorrelation. This interval was determined as a sufficient time for an individual to traverse the extent of its home range (Swihart and Slade 1997, De Solla et al. 1999, Otis and White 1999) and was based on observations of Killdeer movements within the study area.

An exception to this rule was when observers tracked direct movements of birds between sites. In addition, no more than three locations were permitted for an individual in a single day. For cases that violated these criteria, a random subset of data were selected for inclusion in calculations.

To determine the regional fidelity of Killdeer during the wintering period, we calculated the departure date of each radio-marked bird from the study area. Departure was estimated as the last date each radio-marked bird was detected. Fidelity of birds to local areas was evaluated based on the number of sites at which individuals were detected. We used a geographic information system (GIS; ArcView, ESRI Inc.) to determine the number of sites each bird visited and plotted bird locations on digital map layers of road systems and general habitat classes (O. Taft and S. Haig, unpubl. data). Sites were differentiated based on physical borders (e.g., roads) and habitat types.

Killdeer movements were quantified as the sum of linear distances an individual traveled between successive locations. In addition, we calculated the mean and maximum distance each bird was detected from its capture site. Finally, we calculated home ranges based on two different methods. Home range has been defined as the area utilized by an individual during normal activities for a given period of its life cycle (Burt 1943). However, there are numerous different estimators and software packages used to calculate home ranges that complicate comparisons between studies and often represent different aspects of movements and space use. Therefore, we calculated minimum convex polygons (MCPs), using

ArcView GIS software and the Animal Movement extension (Hooge and Eichenlaub 1997), to estimate the total area encompassed by movements of each individual (White and Garrot 1990). These estimates do not imply actual utilization of space due to the inclusion of large areas that separate bird locations. We determined actual space use of winter home ranges with a non-parametric fixed kernel method (Worton 1989). Previous work has established that fixed kernel estimators result in less bias relative to other home range procedures (Seaman and Powell 1996). Estimates were calculated with KERNELHR software (Seaman et al. 1998) using least squares cross-validation to determine smoothing parameters and automatic selection of grid cell size (Worton 1995). We selected contour levels to represent home ranges with 95% of an individual's locations and derived core use areas based on 50% of locations for an individual.

Estimates of local fidelity, movements, and home ranges were summarized across the entire winter and for each monthly period. Sample size requirements of individuals for inclusion in summaries were based on visual assessments of scatterplots and simple regression analyses of each parameter versus sample size. Estimates of number of sites visited, total distance traveled, mean distance detected from capture site, and maximum distance located from capture site were calculated for birds with ≥ 10 locations across the entire winter. Monthly estimates were derived for birds with ≥ 5 locations within a given period. Winter home ranges and core use areas were summarized for individuals with ≥ 20 locations; however,

sample size constraints prevented calculation of monthly estimates (Seaman et al. 1999).

We used one-way analysis of variance (ANOVA) tests to investigate potential monthly differences in sites visited and movements of wintering Killdeer (SAS/ASSIST/INSIGHT, SAS Institute Inc. 1997). In models with a significant overall F -statistic ($P < 0.05$), Fisher's least-significant-difference (LSD) tests were used to determine group differences. Sample size constraints prevented statistical comparisons of migrants versus residents so all birds were lumped for analyses.

Assumptions of independence of observations were violated because some individuals ($n = 11$) were represented in more than one monthly period. However, assuming estimates for individuals in multiple time periods were correlated and thus similar, then tests would provide conservative results for monthly differences. Further, we conducted repeated measure ANOVAs, using an unstructured covariance structure, for birds with data across all monthly periods ($n = 9$). Results of these tests did not differ from the outcome of previous ANOVAs that included all data. Estimates of average and maximum distances from band sites were log transformed for analyses to meet assumptions of normality and homogenous variance. All values were reported as means with associated standard errors (\pm SE).

RESULTS

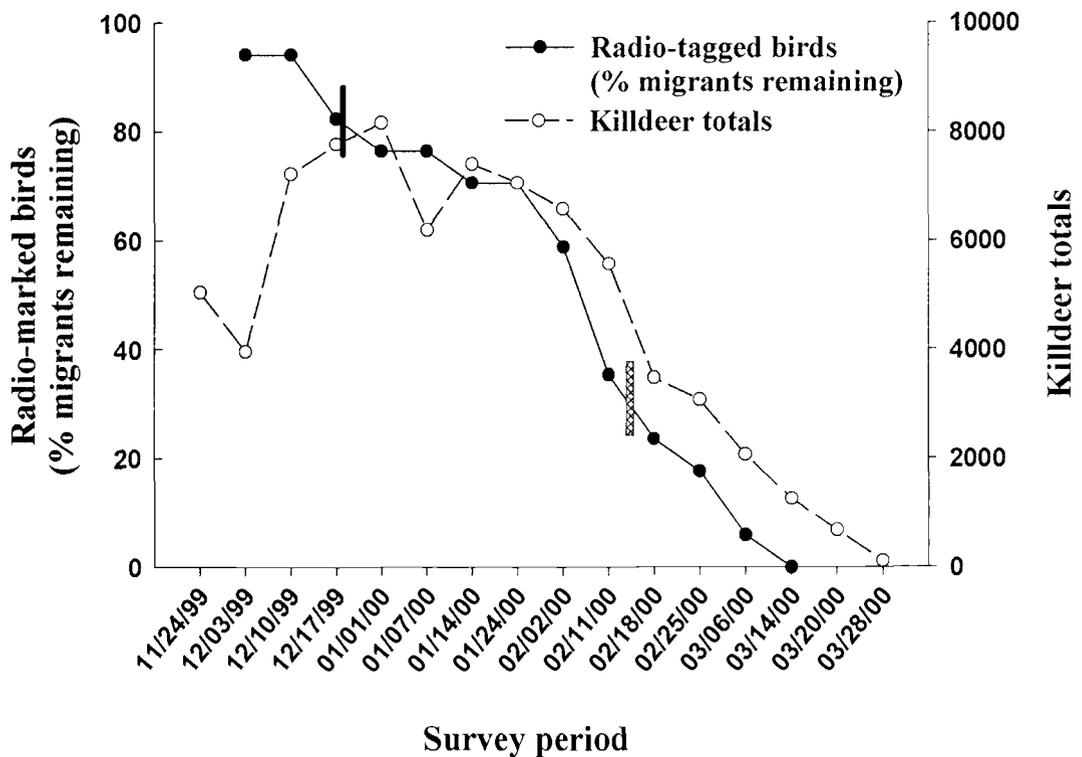
KILLDEER SURVEYS

Sixteen shorebird surveys were conducted from 24 November 1999 to 28 March 2000 (Figure 4.2). Killdeer totals summed across all census areas ranged from 119 to 8162 birds per survey period. Numbers fluctuated in early winter, with an overall increase throughout December and peak winter counts occurring in the final two weeks of the month. A decline in numbers was observed in the latter part of January and continued for the duration of surveys.

TRACKING EFFORT

Tracking efforts initiated immediately after deployment of radios and continued until transmitters ceased operation or individuals departed the study area. Approximately 932 hrs of ground surveys and 29 hrs of aerial surveys resulted in 453 locations of radio-marked birds (mean 18.88 ± 2.91 locations per bird). Whereas the majority of radio-marked birds were located in areas of intensive ground surveys, scattered detections of Killdeer outside focal areas (Figure 4.1), aerial survey efforts, and results from concurrent studies of radio-marked Dunlin (*Calidris alpina*; Sanzenbacher and Haig, in review) suggested a high degree of coverage across the study area.

Figure 4.2. Proportion of radio-marked birds, excluding resident breeders and birds marked in late winter, remaining in the Willamette Valley (solid circles) and total numbers of Killdeer tallied across all shorebird census blocks (empty circles) throughout the winter of 1999-2000. The primary axis (left) corresponds to proportion of radio-marked birds and the secondary axis (right) corresponds to Killdeer count totals. Mean departure date of radio-marked winter residents is indicated by hatched vertical bar and mean departure date of winter transients is signified by solid vertical bar.



Field trials indicated average transmitter detection range from telemetry trucks was 1.59 ± 0.06 km with a standard bearing error of $1.70 \pm 0.22^\circ$. The mean distance from estimated locations of test transmitters ($n = 8$ transmitters) to actual locations was 24.20 ± 2.70 m. Detection range during aerial surveys was approximately 1.6-3.2 km and the accuracy of location estimates was 0.48 ± 0.14 km ($n = 4$ transmitters).

REGIONAL FIDELITY

Most radio-marked birds were relocated in the study area following initial capture (23/24, 95.83%); however, individuals exhibited varying degrees of fidelity to the Willamette Valley over the winter. A majority of the study population, monitored from the beginning of the winter sampling period, was composed of *winter residents* (63% of radio-marked birds, 12/19) that were detected in the study area for extended periods prior to departing the region in February and March. In contrast, several radio-marked birds (26%, 5/19) departed the region earlier in winter during December and mid-January, and hereafter are referred to as *winter transients*. Fluctuations in Killdeer survey numbers over the same period support the contention that a segment of the population departed the region (Figure 4.2). Overall, the mean departure date of winter residents was 15 February and for winter transients was 18 December. Based on date of final detection and observations of nesting activities, we determined that two radio-marked Killdeer (11%, 2/19) were

year-round *resident breeders*. An individual radio-marked during February trapping sessions also remained to breed in the study area.

LOCAL MOVEMENTS

Radio-marked birds were detected at 139 distinct sites and individuals were detected at an average of 12.15 ± 1.00 sites (Table 4.1). There were no differences in the number of sites individuals visited each month ($F_{2,27} = 1.43$, n.s.). Similar numbers of sites were used by winter residents ($n = 10$ birds, mean = 12.40 ± 1.14 sites) and resident breeders ($n = 2$ birds, mean = 13.50 ± 1.50 sites; Figure 4.3). In some cases, birds exhibited greater site tenacity and used specific sites over extended periods. For example, winter resident #151.391 was detected at the same site on 11 different days.

The minimum total distance radio-marked birds traveled during the winter period averaged 52.41 ± 7.16 km. Estimates did not differ with respect to month ($F_{2,27} = 0.01$, n.s.), but there was considerable individual variation for both winter residents ($n = 10$ birds, mean = 58.13 ± 8.02 km), as well as resident breeders ($n = 2$ birds, mean = 41.81 ± 13.41 km). Whereas sample size constraints prevented statistical comparisons of winter residents with resident breeders, there were apparent differences between groups as resident breeders were more sedentary than winter residents (Figure 4.3).

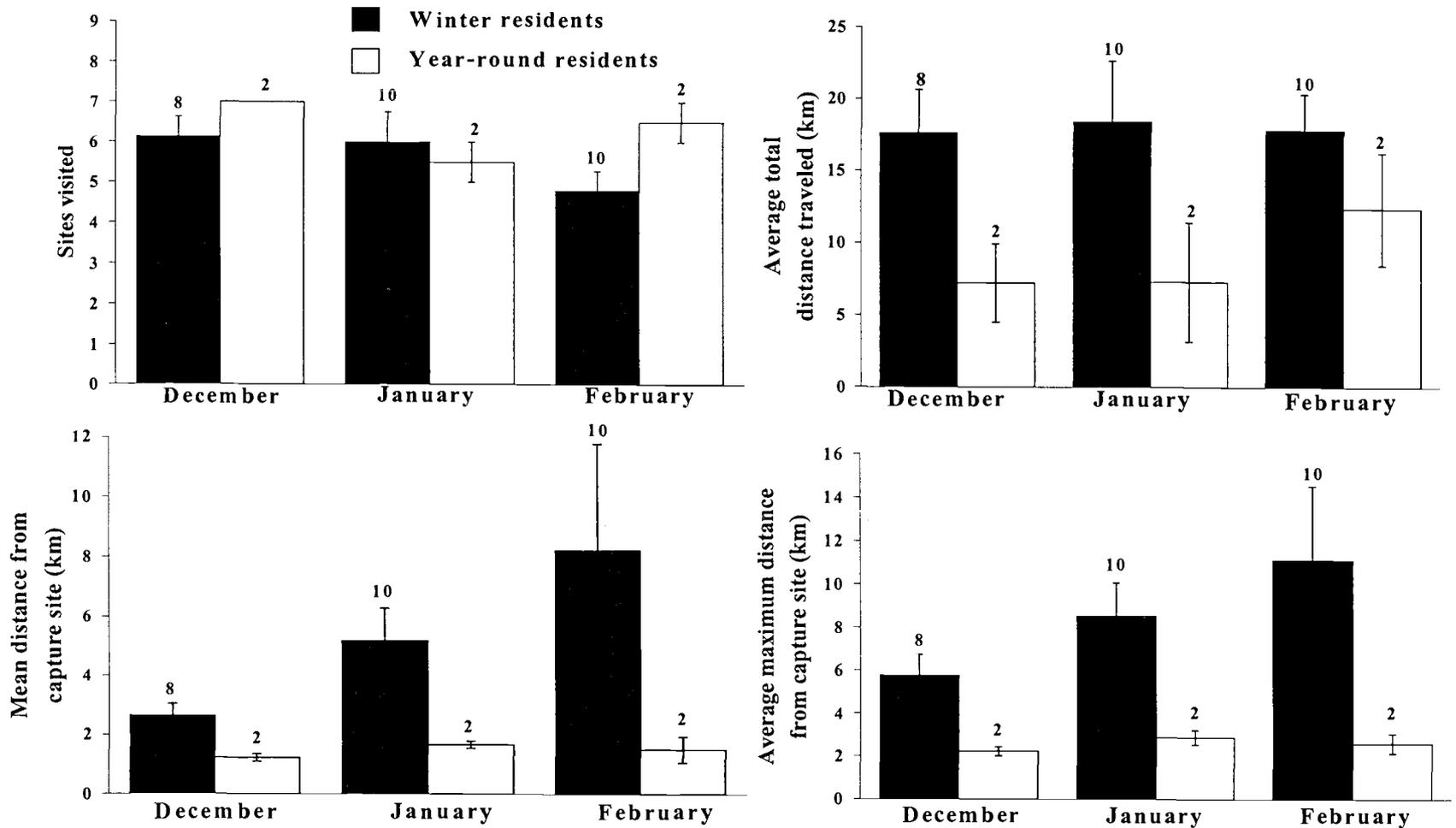
Table 4.1. Movements of wintering Killdeer in the Willamette Valley of Oregon, USA (1999-2000). Data presented are means with associated standard errors (\pm SE).

	<i>n</i> birds	<i>n</i> obs.	Sites visited	Total distance traveled (km)	Mean distance from capture site (km)	Max. distance from capture site (km)
Month ^a						
December	11	102	6.10 (0.57)	14.52 (2.73)	2.57 (0.38)	4.87 (0.84)
January	13	117	5.85 (0.59)	16.00 (3.50)	5.03 (1.00)	7.87 (1.32)
February	14	150	4.79 (0.43)	15.86 (2.28)	3.87 (0.78)	8.86 (2.61)
Total ^b	13	375	12.15 (1.00)	52.41 (7.16)	4.61 (0.85)	8.58 (1.29)

^a Calculated based on individuals with ≥ 5 locations within a monthly tracking period.

^b Calculated based on individuals with ≥ 10 locations across entire tracking period.

Figure 4.3. Comparison of sites visited, average total distance traveled, mean distance located from capture site, and maximum distance located from capture site for winter resident and year-round resident Killdeer during the winter months of 1999-2000 in the Willamette Valley, Oregon.



In general, movements of birds occurred within discrete areas, as the mean distance of locations from respective capture sites averaged 4.61 ± 0.85 km. Exceptions were two winter residents that shifted to more distant areas shortly after capture (see Figure 4.1). Monthly period was not a significant factor in distance from capture site analyses ($F_{2,27} = 1.23$, n.s.), even though distances winter residents were observed from capture site gradually increased as the winter progressed. In contrast, resident breeders exhibited more confined movements over time. Overall, winter residents ranged farther than resident breeders with mean distances located from capture site of 4.62 ± 0.83 km ($n = 10$ birds) and 1.64 ± 0.18 km ($n = 2$ birds) respectively (Figure 4.3). Estimates of maximum distances that birds were detected from the capture site were up to 2 times greater than the average distance for all sample groups and indicate the occurrence of exploratory movements during the tracking period. The average maximum distance across all periods was 8.58 ± 1.29 km. These distances did not differ by month ($F_{2,27} = 1.91$, n.s.); however, there was a trend for increased maximum distances from capture sites as winter progressed. Results suggest winter residents moved greater distances ($n = 10$ birds, mean = 9.45 ± 1.51 km) than resident breeders ($n = 2$ birds, mean = 5.23 ± 3.15 km; Figure 4.3).

Winter movements of Killdeer encompassed a mean area of 34.29 ± 8.00 km² (MCP home range). In contrast, average kernel home range estimates (95% kernel) were considerably smaller, with a mean utilization area of 6.65 ± 2.64 km². Similarly, core use areas (50% kernel) averaged 1.65 ± 0.70 km². In all cases,

results indicated considerable individual variation and were suggestive of differences between winter residents and resident breeders (Table 4.2).

DAILY ACTIVITY PATTERNS

All locations of radio-marked Killdeer were in agricultural habitats, with greater than 50% of habitat observations ($n = 191$ total observations) occurring in fields actively farmed for grass seed. Other crop types used by Killdeer included clover, peas, and sugar beets, as well as fallow fields and pasture. Killdeer showed a tendency to congregate in relatively large, loose flocks as average flock size associated with radio-marked birds was 81.67 ± 9.73 individuals ($n = 149$ observations). Movements were detected at all times of day; however, birds were relatively sedentary during diurnal and nocturnal periods. In contrast, dawn and dusk were periods of major movement activity, as birds located in afternoon hours and then relocated at night moved an average distance of 1.47 ± 0.25 km between sites (range = 0.34 to 3.54 km, $n = 46$ observations). For some individuals, use of specific diurnal and nocturnal sites was predictable over time, with crepuscular movements between particular diurnal and nocturnal sites.

Table 4.2. Areas encompassed by movements (minimum convex polygon), home range size (95% kernel), and core use areas (50% kernel) of winter residents and year-round resident Killdeer in the Willamette Valley during the winter months of 1999-2000. Results were calculated for all birds with ≥ 20 locations.

	<i>n</i> radios	<i>n</i> obs.	Area encompassed					
			by movements (km ²)		Home range size (km ²)		Core use area (km ²)	
			Mean	SE	Mean	SE	Mean	SE
Winter resident	8	249	39.18	8.99	7.73	3.19	1.92	0.84
Year-round resident	2	86	14.73	11.70	2.28	2.05	0.58	0.54

DISCUSSION

Knowledge of avian movement behavior provides insight into various aspects of species life histories and an array of ecological processes, yet difficulties associated with detecting and quantifying movements have resulted in limited studies of movement behavior (Hansson et al. 1995; Haig et al. 1998; Webster et al., in press). Killdeer exhibit complex and variable patterns of residency and timing of migration across the species range; however, knowledge of population structure is limited for most geographical areas and phases of the annual cycle. This information is most often derived from scattered observations of marked individuals or indirect methods such as census data (except see Plissner et al. 2000). Our results from tracking of radio-marked individuals and concurrent shorebird surveys indicate considerable variation in residency status, timing of departure, and local movements of Killdeer in the Willamette Valley during winter.

REGIONAL FIDELITY AND MOVEMENTS

Previous studies of Killdeer reported the occurrence of partial migration, in which a local population consists of both resident and migratory individuals, and suggest a latitudinal gradient in frequency of occurrence (Schardien 1981, Heck 1985). For example, Schardien (1981) determined that a majority of Killdeer at study sites in the southeastern United States were resident breeders. Our findings

indicated that permanent residents accounted for a minority of wintering birds in the Willamette Valley and thus was consistent with the proposed hypothesis that the proportion of migrants in populations increases at more northern latitudes (Jackson and Jackson 2000). However, we observed that year-round resident Killdeer were relatively sedentary and eventually nested within winter home ranges. Thus, the proportion of resident breeders in the population we monitored may reflect the fact that we only trapped birds at three sites.

Whereas we were unable to confirm the status of transient individuals that departed the region in early winter (i.e., December and January), there are numerous competing, but not mutually exclusive hypotheses to explain the departure of these birds. For instance, it is likely that some of these individuals represent the delayed migration of local breeders and fledged juveniles. For example, in some areas (e.g., Illinois, Nevada) Killdeer remain at breeding sites until forced south by local environmental conditions, such as lack of water or onset of harsh winter weather (Jackson and Jackson 2000, Plissner et al. 2000). In this case, it is possible that juvenile birds constitute the majority of late fall and early winter migrants, because in many shorebird species that breed in temperate regions adults depart breeding grounds prior to juveniles (Haig 1992; Paulson 1995; Nol and Blanken 1999).

Early winter departures of Killdeer may represent a protracted or facultative migration, in which birds annually winter as far north as possible but retain the ability to move further south as environmental conditions deteriorate (Terrill and

Ohmart 1984). Previous reports indicate that numbers of Killdeer overwintering in Oregon are reduced during winters with severe weather (Nehls 1994) and shorebird surveys in the Central Valley of California have detected mid-winter increases in Killdeer numbers (Shuford et al. 1998). The winter climate of the Willamette Valley is generally mild; however, during our study there was a period (approx. 10 days) of freezing temperatures in late December. During this time, the substrate and most standing water were frozen for extended periods. Such harsh conditions increase metabolic costs associated with thermoregulation while reducing foraging opportunities (Blem 1990, Castro et al. 1992, Carey and Dawson 1999). Further, previous studies have documented large-scale movements of wintering shorebirds associated with weather events (Warnock et al. 1995; Sanzenbacher and Haig, in review).

An additional explanation for early winter departure of Killdeer is that a segment of the winter population is composed of wandering individuals or floaters (Matthysen 1993, Reed et al. 1999). In a study of nonbreeding Killdeer in North Carolina, Heck (1985) also suggested the presence of mobile winter visitors. Dispersal patterns of Killdeer are not well understood, but studies suggest that like other shorebirds, Killdeer exhibit low rates of natal philopatry (Lenington and Mace 1975, Colwell and Oring 1989, Powers 1998), yet strong breeding site fidelity (Jackson and Jackson 2000). Also, both sexes will breed at one year of age (Jackson and Jackson 2000). Thus, juvenile birds may represent the major proportion of winter transients as the extended winter movements of these birds

provides a mechanism to prospect for and evaluate potential breeding sites (Reed et al. 1999).

LOCAL FIDELITY AND MOVEMENTS

At a local scale, individual Killdeer visited numerous agricultural fields in the Willamette Valley throughout the winter period, such that the degree of local site fidelity was relatively low. In contrast, other studies of nonbreeding shorebirds reported a high degree of local site fidelity (Warnock and Takekawa 1996, Drake et al. 2001). However, these studies inferred site fidelity based on scale of local movements, not persistence at specific sites as defined in our study. Using a similar scale, Killdeer wintering in the Willamette Valley are quite site faithful. Observed fidelity of nonbreeding shorebirds at coastal sites has been attributed to occurrence of predictable and abundant resources (Skagen and Knopf 1993, Drake et al. 2001). Conversely, agricultural land use practices and variation in winter precipitation at inland sites in the Willamette Valley result in a highly fragmented and changing landscape. For example, crop types, planting regimes, and growing conditions influence the density and height of vegetation at different sites. Therefore, use of multiple agricultural sites within a relatively small home range is likely a response to the complex spatial and temporal variation in the distribution of resources. In addition, Killdeer at inland sites tend to congregate in loose flocks. Whereas flocking behavior has been identified as a strategy that lessens

vulnerability to predators (Creswell 1994, Barbosa 1997), switching sites over time may also prevent predators from cueing in on specific sites where birds congregate.

Estimates of the total distance Killdeer traveled did not indicate seasonal differences in the scale of movements; however, average distances that birds were detected from capture sites suggest that areas of use shifted and expanded as the winter progressed, in particular for winter residents. A similar trend was observed for radio-marked Dunlin over the same period (Sanzenbacher and Haig, in review). These movement patterns likely reflect both physiological factors related to the onset of spring (e.g., premigratory restlessness), as well as changes in the spatial array and distribution of local resources. For example, precipitation levels decrease as spring approaches and wetland mapping conducted concurrent with our studies revealed a reduction in the area of saturated soils that are indicative of shorebird habitats (O. Taft and S.M. Haig, unpub. data).

Seasonal movements and space use suggested differences between winter residents and resident breeders; however, small sample sizes prevented direct statistical comparisons. Regardless, resident breeders exhibited a tendency to remain closer to original sites of capture with smaller home ranges than winter residents. In addition, at least two of three individuals identified as resident breeders nested near the centroid of their respective winter home ranges (100% MCP). Similarly, year-round resident Killdeer in other regions often remain on breeding territories during the winter (Schardien 1981, Heck 1985).

Finally, a comparison of movements and space use from other studies of Killdeer indicate that breeding individuals from other regions exhibit seasonal movements at a much smaller scale than did Killdeer in the Willamette Valley during winter (Schardien 1981, Plissner et al. 2000). For example, our estimates of home ranges (95% kernel) for wintering birds were an order of magnitude greater than that reported for breeding birds (Plissner et al. 2000). Thus, differences in movements among breeding and wintering birds highlight the need to consider seasonal differences in habitat needs and space use requirements.

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Chapter 5. Conclusions

Shorebirds are a group of highly mobile, wetland-associated species for which information on winter movements is limited. Further, few studies have been conducted at a scale sufficient to quantify the extent of individual movements across a landscape and efforts have focused almost exclusively on coastal habitats. This study provides extensive data on winter fidelity and movements of shorebirds at an inland landscape.

On a regional scale individual Dunlin were detected wintering in the Willamette Valley over extended periods. Contrary to previous assertions, results indicated Dunlin were winter residents that exhibited a high degree of persistence in the Valley. An exception was a single individual that traveled to the coast during a period of adverse local weather conditions. The large-scale movements of this individual link the Willamette Valley to coastal areas, as well as highlight the influence of weather on movement behavior. The mean spring departure date of Dunlin from the region was March 22nd \pm 1.80 (SE) days. In contrast, Killdeer exhibited complex and variable patterns of residency over the winter period. The population monitored was composed of winter residents (63%), winter transients (26%), and year-round resident breeders (11%). These findings were consistent with the proposed pattern that migrants occur in greater proportions at more northern latitudes (Jackson and Jackson 2000) and help elucidate issues of population structure. Potential explanations for the occurrence of winter transients

include delayed migration of local breeders and fledged juveniles, facultative migration patterns in response to local environmental conditions, and prospecting by subadults for future breeding sites.

At a local scale, both Dunlin and Killdeer occurred predominantly in agricultural habitats and exhibited a relatively low degree of fidelity to specific fields. The use of multiple agricultural sites was likely a response to spatial and temporal variation in the distribution of local resources, as well as disturbance associated with predators and human activities. Estimates of distances traveled indicated Dunlin were highly mobile and in some cases conducted non-stop flights in excess of 30 km. Further, home range sizes were greater than that previously reported for nonbreeding shorebirds. Dunlin also exhibited significant differences in seasonal movements and space use with increased movements during the late winter period. In comparison, Killdeer were relatively sedentary and exhibited less pronounced seasonal differences in extent of movements. Regardless, estimates of movements and space use were greater than previously reported for Killdeer in other habitats. Results also suggest resident breeders were more sedentary during winter than winter residents. Similarly, studies of resident Killdeer in other regions indicate a tendency for resident breeders to remain on territories throughout the year (Schardien 1981, Heck 1985).

Daily movement data indicated the importance of diurnal roost sites for Dunlin, which frequently congregated at sites in large flocks. Characteristic of all roost sites was the presence of impounded water and unvegetated areas. Extensive

movements among a limited number of roost sites suggest that suitable sites were potentially limited in the region. Observations of extensive aerial flocking at sites suggests a high degree of raptor predation pressure (Dekker 1998, Hötter 2000). Finally, movements of both Dunlin and Killdeer were most pronounced during crepuscular periods and in almost all cases individuals switched sites at these times.

Our findings on regional fidelity and movement patterns of Dunlin and Killdeer in the agricultural landscape of the Willamette Valley will provide guidance for future regional conservation planning efforts and assist in efforts to provide resources for large numbers of wintering shorebirds. However, expanding local human populations and changing agricultural practices will undoubtedly alter the regional landscape in the future. The unknown impact of these changes on shorebird populations and other wildlife species that inhabit the Willamette Valley warrants concern and caution. Increased avian monitoring efforts and refinement of survey techniques are needed to determine the status of local shorebird populations. In addition, future studies should investigate potential threats to Dunlin and Killdeer associated with dependence on agricultural habitats. These threats include exposure to toxins from chemical applications (Fair et al. 1994, Warnock and Schwarzbach 1995), disturbance related to human activities (Smit and Visser 1993, Pfister et al. 1992), and impact of elevated predator populations in altered habitats (Whitfield et al. 1988, Oring et al. 2000). Studies are also warranted to further investigate Killdeer population structure within the region. Comparative investigations of resident and migratory individuals have the potential

to provide important insight on the evolution of avian migration patterns and influence of cross-seasonal interactions on survivorship and breeding success.

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