MIGRATION CHRONOLOGY, ROUTES, AND DISTRIBUTION OF PACIFIC FLYWAY POPULATION LESSER SANDHILL CRANES

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Abstract: Managers of migratory game birds require accurate information about bird movements to delineate populations, protect important habitats, and regulate harvest. Data describing movements of sandhill cranes (*Grus canadensis*) belonging to the Pacific Flyway Population (PFP) are lacking. We used satellite telemetry to monitor movements of PFP lesser sandhill cranes (*Grus c. canadensis*) captured in the upper Cook Inlet and Bristol Bay regions of Alaska. Satellite transmitters were deployed on 19 flightless young (colts) and 3 adults over 3-years (2000-2002). Chronology, routes, and stopover or staging areas were identified for fall and spring migration periods. On average, cranes (n = 11) took 27 days (range = 13-44 days) to travel from summer areas in Alaska to winter areas in the Central Valley of California (CVC). Winter locations were concentrated in the Sacramento – San Joaquin River Delta and the East Grasslands (Merced County) regions. In spring, cranes (n = 10) took an average of 58 days (range = 45-65 days) to return to Alaska. In spring, most marked cranes (70%) staged at the Potholes Reservoir region in central Washington. PFP cranes that summer in Cook Inlet and Bristol Bay used identical migration routes and winter areas. Only 3 of 9 colts returning to Alaska, as juveniles, revisited their natal site. We found no evidence that PFP cranes monitored with satellite transmitters mixed with cranes from the Mid-Continent Population (MCP) or with “western segment” PFP cranes.

PROCEEDINGS NORTH AMERICAN CRANE WORKSHOP 9:53-67

Key words: Alaska, Bristol Bay, Central Valley of California, colts, Cook Inlet, distribution, *Grus canadensis*, migration, Pacific Flyway Population, route, sandhill crane, satellite telemetry, staging areas.

Sandhill cranes that summer in Alaska belong to either the Pacific Flyway Population or Mid-Continent Population. The MCP is composed of 3 subspecies (lesser, *G.c. canadensis*, Canadian [*G. c. rowani*], and greater [*G. c. tabida]*) based on differences in morphology (Walkinshaw 1973, Johnson and Stewart 1973, Tacha et al. 1984). Recent progress in mitochondrial DNA research, however, has questioned the validity of a separate Canadian subspecies designation (Rhymer et al. 2001, Glenn et al. 2002, Peterson et al. 2003), even though they are intermediate in morphology to lesser and greater subspecies (Walkinshaw 1965). The geographic range of the MCP has been delineated by direct or remote (satellite telemetry) observations of individuals marked on breeding grounds (Boise 1979), wintering (Tacha et al. 1984) and staging areas (Krapu and Brandt, in prep). MCP cranes that summer in Siberia and Alaska stay north of the Alaska Range and east of the continental divide during fall migration (Fig. 1) and winter in Texas, New Mexico, Oklahoma, and northern Mexico (Boise 1979, Kessel 1984, Tacha et al. 1984).

Cranes belonging to the PFP are considered lesser sandhill cranes (Pacific Flyway Council 1983). Cook Inlet and Bristol Bay regions in Alaska are their primary breeding areas (Pacific Flyway Council 1983; Fig. 1). A small number of PFP cranes, however, nest on islands in southeast Alaska and northern British Columbia (Gabrielson and Lincoln 1959). The geographic extent of these island-nesting cranes is currently under investigation (Ivey pers. comm., Littlefield and Ivey 2002). Morphological measurements suggest that they are the Canadian subspecies (Ivey pers. comm., Littlefield and Ivey 2002). The sub-specific composition of the PFP, however, has not been investigated using genetic techniques.

Pacific Flyway Population cranes primarily winter in the Central Valley of California (Littlefield and Thompson 1982) where they mix with the Central Valley Population of greater sandhill cranes (Pogson and Lindstedt 1991, Littlefield and Ivey 2002). There is no evidence indicating that the PFP integrate with the MCP at any time during the year (Pogson et al. 1988, Krapu pers. comm.).

Information describing the geographic extent of PFP lesser sandhill cranes has been acquired through ground (Herter 1982, Littlefield and Thompson 1982) and aerial (Conant et al. 1985) observations of flocks and limited re-sightings of marked individuals (Pogson 1987, Pogson et al. 1988). Migration routes, especially in northern areas, have not been verified. Stopover sites and staging areas have been identified for some locations (Herter 1982, Mickelson 1985, Streveler and Matkin 1983), yet their relative importance to migrating cranes is not known (Pacific Flyway Council 1983). Because few individuals have been marked and subsequent re-sightings have been limited,

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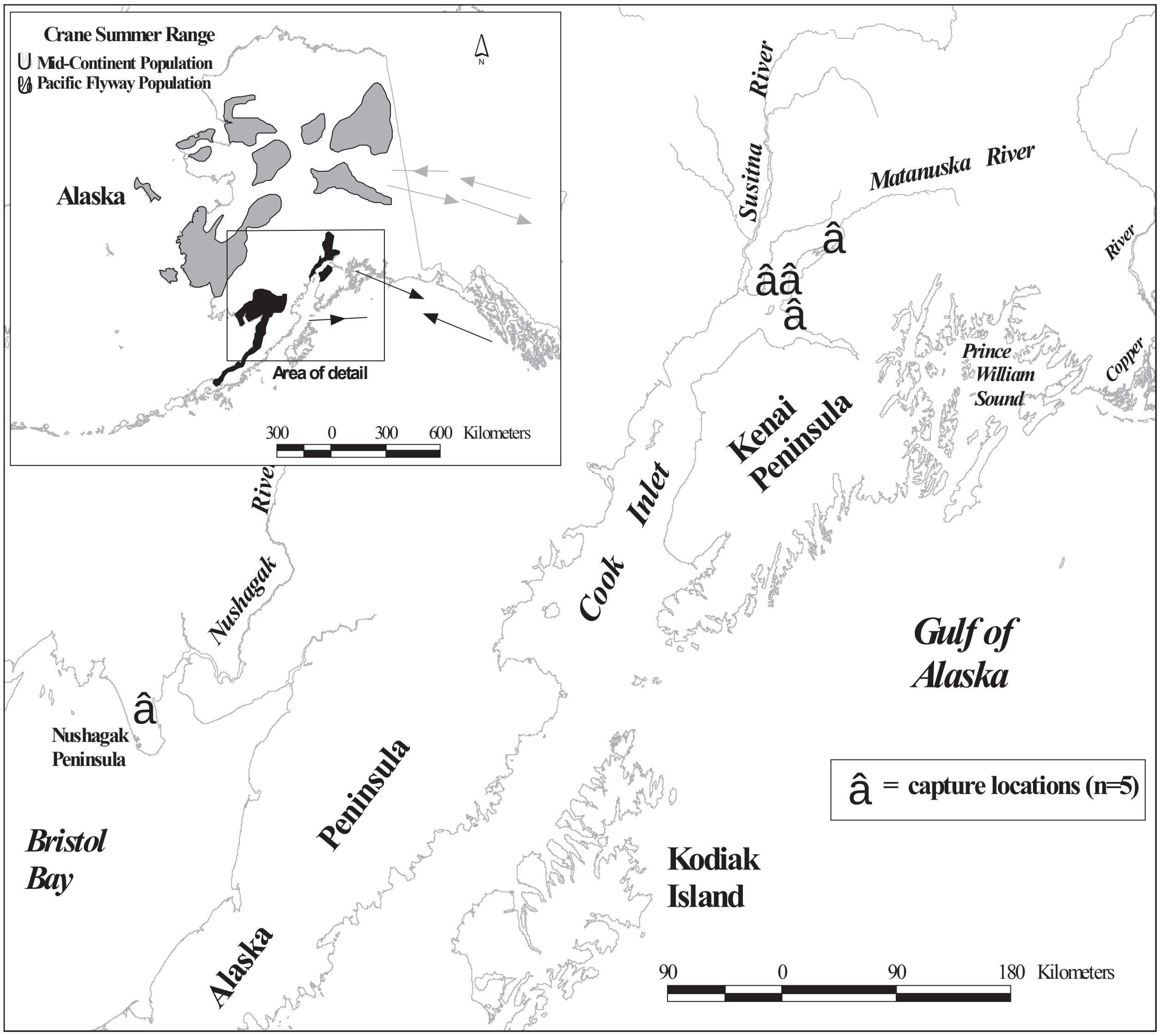

Fig.1. Map of Alaska illustrating primary summer range and general migration paths for the Pacific Flyway and Mid-Continent Populations of sandhill cranes (inset). Locations in the upper Cook Inlet and Bristol Bay regions of Alaska where satellite transmitters were deployed on Pacific Flyway Population lesser sandhill cranes in 2000, 2001 and 2002 (area of detail).

much of the current information delineating the range of PFP lesser sandhill cranes has been speculative. As a result, current hypotheses describing affinities among breeding, staging and wintering areas have gone untested.

Managers of migratory game birds require accurate information about bird movements to delineate populations, protect important habitats, and regulate harvest. This is especially true for PFP cranes because they exhibit isolated distributions during certain periods of the year. Whether gene flow exists among separate breeding areas in Alaska is unknown.

We used satellite telemetry as a tool to identify migration routes, stopover and staging areas, and lengths of stay for PFP sandhill cranes captured in Alaska. We also describe the geographic distribution of PFP cranes during winter and summer months. Delineating affinities among winter, migration, and summer areas is necessary to manage PFP cranes through reliable inventories and appropriate harvest regimes. The need for this information is particularly important for habitat protection as current proposals for development projects throughout the PFP range could have deleterious impacts on habitat quality and quantity. Potential impact on cranes from local developments has generated public concern and the demand for additional information regarding their breeding origin, population estimates and harvest rates.

METHODS AND STUDY AREA

We captured sandhill cranes in the upper Cook Inlet and Bristol Bay regions of Alaska (Fig. 1). Twelve satellite transmitters were deployed on flightless young (colts) at 4 locations in upper Cook Inlet (Palmer Hay Flats, Anchorage Coastal Wildlife Refuge, Susitna Flats, Point McKenzie) in 2000 and 2001, and 7 satellite transmitters were deployed on colts in Bristol Bay (Nushagak Peninsula) in 2002. Colts were captured with the aid of a Robinson 22 helicopter. When a family group was observed from the air, the pilot hovered the aircraft over a colt at approximately 1m above ground level allowing a person to exit the aircraft, capture, and restrain the bird. One colt per family group was captured. At the capture site, we sampled blood for sexing and future genetic analysis. Whole genomic DNA was isolated from blood samples using a salting-out procedure (Medrano et al. 1990). Sex of all individuals was determined using the chromo-helicase-DNA-binding (CHD) avian sex determination primers P2 and P8 (Griffiths et al. 1998).

We attached a satellite transmitter with a leg-band attachment above the tibio-tarsal joint with the stainless steel antenna pointing down (Melvin et al. 1983, Ellis et al. 2001). To the other leg we applied a USFWS metal leg band and a yellow leg band (5cm tall) with a unique alphanumeric code for identification in the field. After release, the colt immediately reunited with adults waiting nearby for all but 2 captures.

Three satellite transmitters were deployed on adult cranes at a spring staging area in upper Cook Inlet (Matanuska Valley) on 27 April 2002. Adult cranes were captured with the use of a rocket net over bait (Urbanek et al. 1991). Marking and processing protocols for adults and colts were otherwise identical.

Each satellite transmitter weighed approximately 55g (with band attachment) and was programmable with up to 5 duty cycles (Microwave Telemetry, Inc.; Table 1). Transmitters contained a battery voltage sensor that was useful in determining the life expectancy of the transmitter. Transmitter signals were received by 4 National Oceanic and Atmospheric Association polar-orbiting satellites. Data were transmitted approximately every 60 seconds during the on-cycle in frames of four, 8-bit messages. Signals were analyzed using Argos Data Collection and Location Systems. Locations were calculated from a Doppler shift in signal frequency (Fancy et al. 1988). We used Argos "standard" and "auxiliary" location data processing services. The accuracy of "standard locations" (class codes 1, 2, and 3) is generally < 1000m and requires that the satellite receives at least 4 messages during a pass over the transmitter (Argos 1996). Location accuracy for "standard locations" with class code 0 is generally > 1000m with no maximum limit (Argos 1996). The accuracy of "auxiliary locations" (class codes A and B) cannot be calculated because the normal system specifications are relaxed to provide locations calculated from 2 or 3 messages. The lack of an estimate for accuracy, however, does not necessarily mean "auxiliary locations" are inaccurate. To distinguish inaccurate locations, we used a program developed by David C. Douglas (USFWS) based on comparing distance, rate, and angle of consecutive locations. Additionally, all usable locations were checked manually for accuracy. Argos locations with class code Z were rejected.

Because satellite transmitters did not transmit continuously

Table 1. Duty cycles used for programming satellite transmitters deployed on Pacific Flyway Population lesser sandhill cranes captured in Alaska (2000-2002).

	Duty Cycle (hours on and off)														
	1			2			3			4			5		
Date deployed	on	off	#cycles	on	off	#cycles	on	off	#cycles	on	off	#cycles	on	off	#cycles
July 17-18, 2000	6	120	9	8	48	39[a]	6	96	21	8	48	to end[b]			
April 27, 2001	6	48	20	6	120	14	8	48	26[a]	6	96	26	8	48	to end[b]
July 27-28, 2001	6	72	10	8	34	27[a]	8	96	24	8	48	to end[b]			
August 02, 2002	8	26	42[a]	6	106	32	8	34	28[b]	6	120	25	6	34	to end

[a] **Indicates duty cycle during fall migration.**

[b] **Indicates duty cycle during spring migration.**

we can only report locations acquired during the transmission cycle. To provide a comprehensive description of the migration route used by PFP cranes while maximizing battery life, we programmed our satellite transmitters to transmit more frequently during migration than other times of the year (Table 1). Nevertheless, stopover sites used by cranes for brief periods (< 2 days) may have gone undetected. Further, the exact route taken during migration may be imprecise for cranes that traveled long distances between transmission cycles. Finally, the number of days reported for cranes while in route and spent at stopover or staging areas was approximated; accuracy being dependent on the number of hours during the off-cycle (Table 1).

To reliably illustrate crane distribution on winter and summer range we used the most accurate location per transmission cycle. Accuracy was based on class code, and in the event of a tie, the number of messages received per satellite pass. All acceptable locations per transmission cycle, however, were used to illustrate migration routes because locations were frequently obtained while birds were flying.

Locations for individual cranes were mapped using a Geographic Information System (ArcView) and posted at http://www.wildlife.alaska.gov/index.cfm?adfg=waterfowl.crane.

RESULTS

We deployed 22 satellite transmitters on PFP cranes (Table 2). Sex ratios were ca. 50:50 (11 males, 10 females and 1 unknown; Table 2). We received little information from 5 transmitters because the birds were depredated and the transmitters were recovered soon after capture (n = 3), shot during the hunting season (n = 1), or the transmitter failed for unknown reasons soon after release (n = 1). Seventeen satellite transmitters provided ample location data (Table 2). Of these, however, 3 went off-line prior to the expected life of the transmitter, and 5 were deployed on cranes that either shed the transmitter or died before returning to Alaska.

Fall Migration

Coastal route. - PFP cranes began their southerly migration in early September (mean = 11 September; Table 3). Cranes captured in Bristol Bay during 2002 began fall migration approximately 8 days later than cranes captured in upper Cook Inlet (Table 3). Since cranes were not captured at Cook Inlet and Bristol Bay during the same year, ascribing a biological meaning to the difference in departure dates between the two nesting areas was not possible.

PFP cranes departed Bristol Bay and traveled east directly to the Kenai Peninsula where they potentially mix with Cook Inlet cranes (Fig. 2). We suspect Bristol Bay cranes entered Cook Inlet through passes in the Aleutian Range south of Iliamna Lake. Bristol Bay cranes continued east and accessed the Gulf Coast of Alaska by flying directly over the Kenai Peninsula and through Prince William Sound. PFP cranes captured in upper Cook Inlet accessed the Gulf Coast by traveling southeast over the Chugach Range. We believe Portage Pass and the Knik Glacier are two primary access corridors to Prince William Sound. Once reaching the Gulf coast in south central Alaska, upper Cook Inlet and Bristol Bay cranes flew southeast along the coast. At Pt. Spencer, PFP cranes left the outer coast and continued migration through the islands and straits of the Alaska panhandle. In contrast to the low-lying areas used by cranes along the outer coast, cranes commonly stopped at higher elevations while traveling through the panhandle. We suspect berry production in perched muskegs and alpine meadows provided foraging habitat at these locations.

Five stopover sites were frequently used by cranes during fall migration in Alaska (Table 4). Twelve of 15 cranes (80%) stopped near the Yakutat Forelands, 40% in the vicinity of the Bering Glacier lowlands and on the Stikine River Delta, and 27% stopped on the Copper River Delta and near Gustavus (Fig. 2). Cranes remained at Gustavus for the longest duration followed by the Yakutat Forelands (Table 4).

On average, PFP cranes left Alaska and entered British Columbia 12 days after beginning fall migration (range = 5–19 days; Table 3). Cranes captured in Bristol Bay spent less time traveling through Alaska (mean = 8 days) than did cranes captured in upper Cook Inlet (mean = 14 days) even though Bristol Bay birds traveled a longer distance. Again, because birds of different nesting areas were marked in different years, inferring biological meaning to this difference is not possible.

Interior route. - Near the Stikine River Delta, PFP cranes migrated inland and entered central British Columbia near Stewart (Fig. 2). They continued south through the Fraser River and Okanogan Valleys. PFP cranes traveled through British Columbia quickly (mean = 5 days, range = 1-18 days; Table 2). With such rapid movement through the province, only a few stopover sites could be reliably identified in British Columbia (Table 4). Locations near Smithers, and Kamloops were used most frequently (Fig. 2), although one crane spent 14 days near Prince George (Table 4).

PFP cranes continued south staying west of the Selkirk Mountains and entered north central Washington near Oroville (Fig. 2). The primary stopover site was in central Washington in the vicinity of the Potholes Reservoir (Fig. 4) where 71% of marked cranes spent, on average, 5.5 days (range = 1-13; Table 4). Two cranes, however, stopped for a brief period east of Monse, Washington (Okanogan County) north of the Columbia River (Fig. 2). Though five stopping areas were identified (Table 4) PFP cranes moved south through central Oregon quickly before entering California, making it difficult to obtain many locations (Table 2). A portion of the population appeared to enter California by crossing the northwest corner of Nevada (Fig. 2). Once in California, cranes traveled directly to winter areas (Table 3). On average, it took 27 days (range = 13-44 days) for PFP cranes to complete the ca. 3,600-km migration from summer range in Alaska to winter range in California (Table 3).

Table 2. Satellite transmitter identification, date and location deployed, age, sex and fate of bird, number of days active, and number and quality of locations received for satellite transmitters deployed on Pacific Flyway Population lesser sandhill cranes captured in Alaska in 2000, 2001 and 2002.

ID	Date deployed	Capture location	Age	Sex	Days active[a]	Fate[b]	Number of locations/class code[c] 3	2	1	0	A	B	Total[d] locations
29302	7/18/00	Palmer Hay Flats	Colt	F	417	off-line	15	27	71	163	57	77	418
29303	7/18/00	Palmer Hay Flats	Colt	M	77	unknown	3	6	13	28	29	24	104
29304	7/17/00	Anchorage Coastal Refuge	Colt	F	46	shot	2	0	2	16	4	10	47
29501	7/18/00	Palmer Hay Flats	Colt	M	55	depredated	4	5	23	30	36	38	137
29502	7/17/00	Anchorage Coastal Refuge	Colt	F	51	depredated	0	1	5	2	12	15	36
29503	7/18/00	Palmer Hay Flats	Colt	M	425	off-line	8	36	79	318	142	170	793
33090	4/27/01	Matanuska Valley	Adult	M	96	unknown	2	8	30	67	32	35	177
33091	4/27/01	Matanuska Valley	Adult	U	131	unknown	2	11	49	62	42	50	218
33092	4/27/01	Matanuska Valley	Adult	M	487	off-line	18	59	151	300	175	189	916
13381	7/28/01	Point McKenzie	Colt	F	373	off-line	9	47	161	338	139	175	890
13385	7/28/01	Susitna Flats	Colt	M	38	depredated	1	5	20	43	22	23	116
13386	7/27/01	Anchorage Coastal Refuge	Colt	M	380	off-line	13	28	88	167	98	131	546
13387	7/28/01	Palmer Hay Flats	Colt	F	401	off-line	14	48	125	283	144	174	811
29501b	7/27/01	Anchorage Coastal Refuge	Colt	F	420	off-line	11	34	107	265	151	183	770
29502b	7/27/01	Palmer Hay Flats	Colt	M	295	off-line	8	24	82	154	60	82	417
13380	8/02/02	Nushagak Peninsula	Colt	F	61	unknown	5	16	50	103	63	76	315
13382	8/02/02	Nushagak Peninsula	Colt	M	361	off-line	2	8	30	181	75	98	460
13385b	8/02/02	Nushagak Peninsula	Colt	M	261	off-line	17	41	124	247	140	151	736
29304b	8/02/02	Nushagak Peninsula	Colt	M	87	unknown	1	12	54	141	67	87	363

[a] **Number of days from transmitter deployment to date when fate determined.**

[b] **Sandhill cranes with unknown fates either carried a defective transmitter, shed the transmitter, or died. Cranes carrying satellite transmitters that went off-line did so at the anticipated end of battery life. Depredated cranes were recovered.**

[c] **See methods for description of class codes.**

[d] **Class code Z locations included in total.**

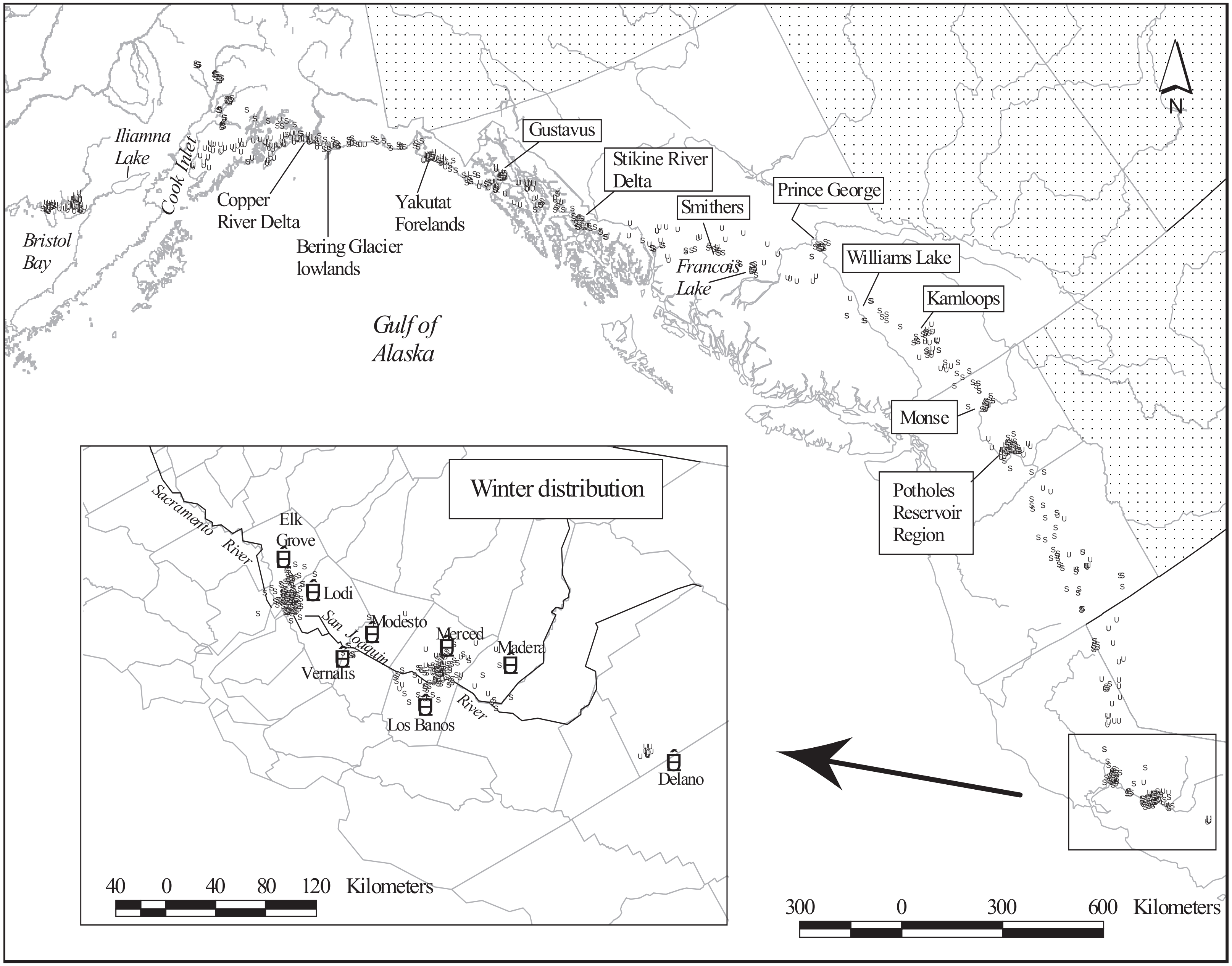

Fig. 2. Locations acquired with satellite telemetry for Pacific Flyway Population lesser sandhill cranes during fall migration and while on wintering areas in the Central Valley of California in 2000, 2001 and 2002. Circles depict cranes captured in upper Cook Inlet and squares depict cranes captured in Bristol Bay.

Table 3. Migration chronology for Pacific Flyway Population lesser sandhill cranes captured in upper Cook Inlet (2000 and 2001) and Bristol Bay (2002) regions of Alaska. X indicates where the satellite transmitter either failed; the bird died; or shed the transmitter.

	Fall migration								Spring migration							
		Approximate no. days in:					Arrive winter	Total trip		Approximate no. days in:					Arrive summer	Total trip
Year/ID[a]	Begin	Alas.	B.C.	Wash.	Oreg.	Calif.	range	length	Begin	Calif.	Oreg.	Wash.	B. C.	Alas.	range	length
2000																
29302	9/6	16	2	11	2	2	10/8	33 days	3/7	3	39[b]	3	4	3	4/28	52 days
29303	9/7	14	2	1	X											
29503	9/7	14	1	9	2	1	10/3	27 days	3/4	5	1	46	4	3	5/1	59 days
2001																
33092	9/7	17	6	3	2	2	10/6	30 days	3/4	10	37[b]	2	5	4	4/30	58 days
13381	9/7	19	6	13	4	2	10/20	44 days	3/6	1	5	43	3	5	5/1	57 days
13386	9/8	15	8	4	2	1	10/7	30 days	3/20	1	4	32	3	5	5/3	45 days
13387	9/5	5	5	12	2	2	9/30	26 days	3/4	4	19	26	5	5	5/1	59 days
29501b	9/12	15	18	1	2	1	10/18	37 days	3/5	1	13	41	3	6	5/7	64 days
29502b	9/7	unk	unk	unk	unk	3	9/19	13 days	2/28	4	49	19	5	X		
2002																
13380	9/11	9	2	4	1	X										
13382	9/18	9	3	2	1	1	10/3	16 days	3/19	1	43	3	3	10	5/18	60 days
13385b	9/19	10	2	2	1	4	10/7	19 days	3/20	1	2	38	12	4	5/24	65 days
29304b	9/19	6	1	13	3	1	10/12	24 days	X							
35667	9/8	6	4	1	1	X										
35669	9/16	9	X													
Average	9/11	12	5	6	2	2	10/7	27 days	3/9	3	21	25	5	5	5/6	58 days

a All cranes were marked as flightless colts except 33092 which was an adult.
b Oregon-Idaho border.

Table 4. Principal stopover sites used by Pacific Flyway Population lesser sandhill cranes during fall migration in 2000, 2001 and 2002 identified with satellite telemetry.

Stopover site	Proportion of cranes detected	Number of cranes per origin of capture[a] BB	UCI	Average number of days spent
Alaska[b]				
Kenai Peninsula	20%	3	0	1.0
Prince William Sound	13%	1	1	1.0
Copper River Delta	27%	2	2	2.3
Bering Glacier lowlands	40%	1	5	1.5
Cape Yakataga	13%	1	1	1.0
Yakutat Forelands	80%	5	7	3.8
Icy Bay	20%	0	3	1.0
Lituya Bay	13%	1	1	1.0
Gustavus	27%	0	4	7.0
Stikine River Delta	40%	2	4	2.2
British Columbia[b]				
near Smithers	27%	1	3	1.5
François Lake	13%	1	1	1.5
near Prince George	7%	0	1	14.0
near Williams Lake	13%	0	2	2.0
near Kamloops	27%	2	2	2.3
Washington[c]				
near Monse	14%	0	2	5.0
Potholes Reservoir region	71%	4	6	5.5
Oregon[c]				
Harney Valley	14%	1	1	2.0
Rabbit Valley	7%	0	1	1.0
Coyote Lake	7%	0	1	2.0
Warner Valley	14%	0	2	1.5
Twelve Mile Table	7%	0	1	1.0

a BB=Bristol Bay; UCI=upper Cook Inlet.
b Data for 14 colts and 1 adult sandhill cranes.
c Data for 13 colts and 1 adult sandhill cranes.

Winter Range

The average arrival date on wintering grounds in the CVC for PFP cranes was 7 October (range = 19 Sep.-20 Oct.). We obtained location data for 11 cranes in the CVC; 10 cranes were monitored throughout the winter and 1 crane went off-line in late October. In winter, location data were obtained for 438 of 455 possible transmission cycles (n = 11 cranes). The best locations for each duty cycle were mostly class codes 1-3 (74%), 24% were class code 0, and 1% were class code A.

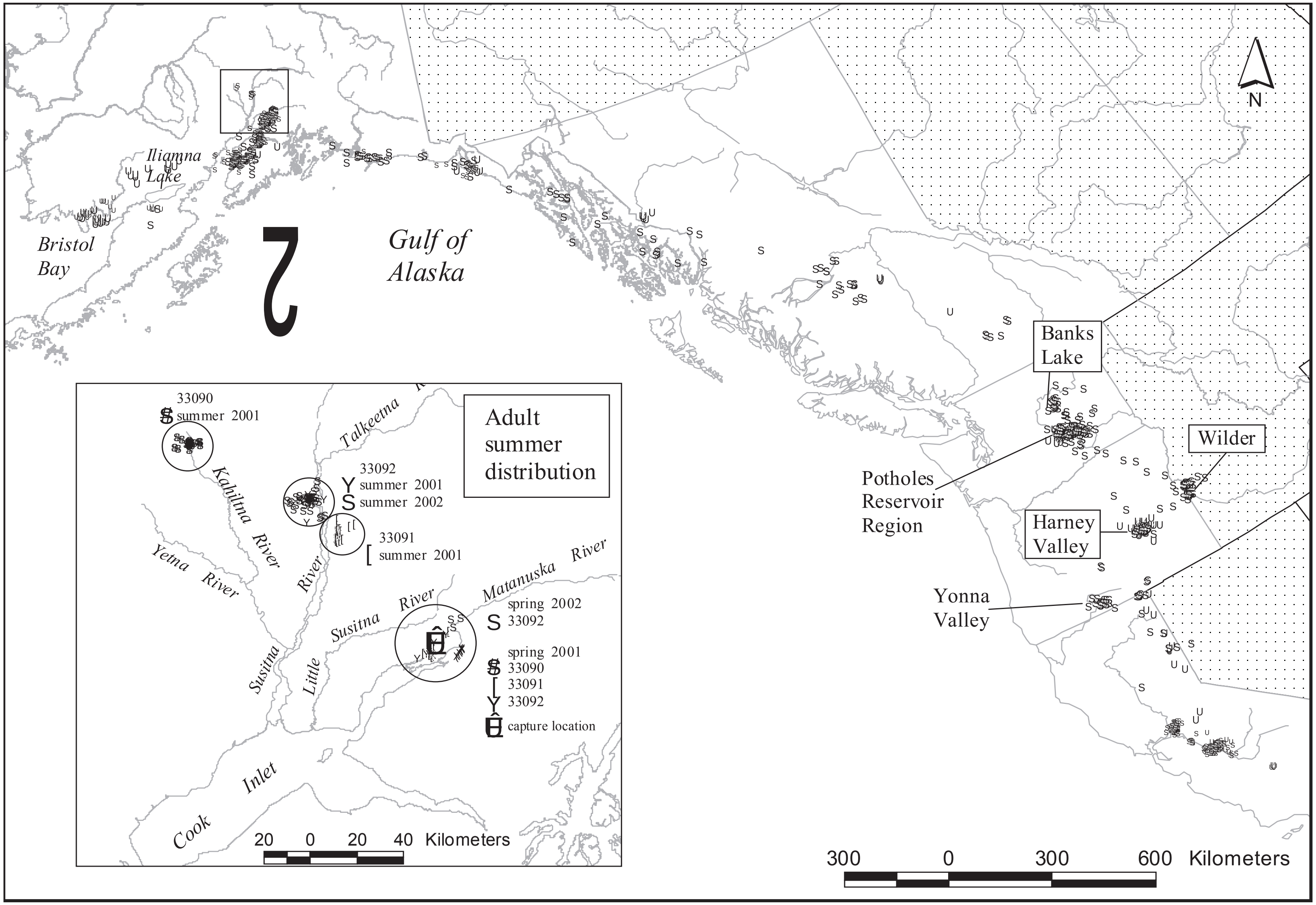

Fig. 3. Locations acquired with satellite telemetry for Pacific Flyway Population lesser sandhill cranes during spring migration in 2000, 2001 and 2002, and for adult cranes while in Alaska during the spring and summer in 2000 and 2001. For migration locations, circles depict cranes captured in upper Cook Inlet and squares depict cranes captured in Bristol Bay.

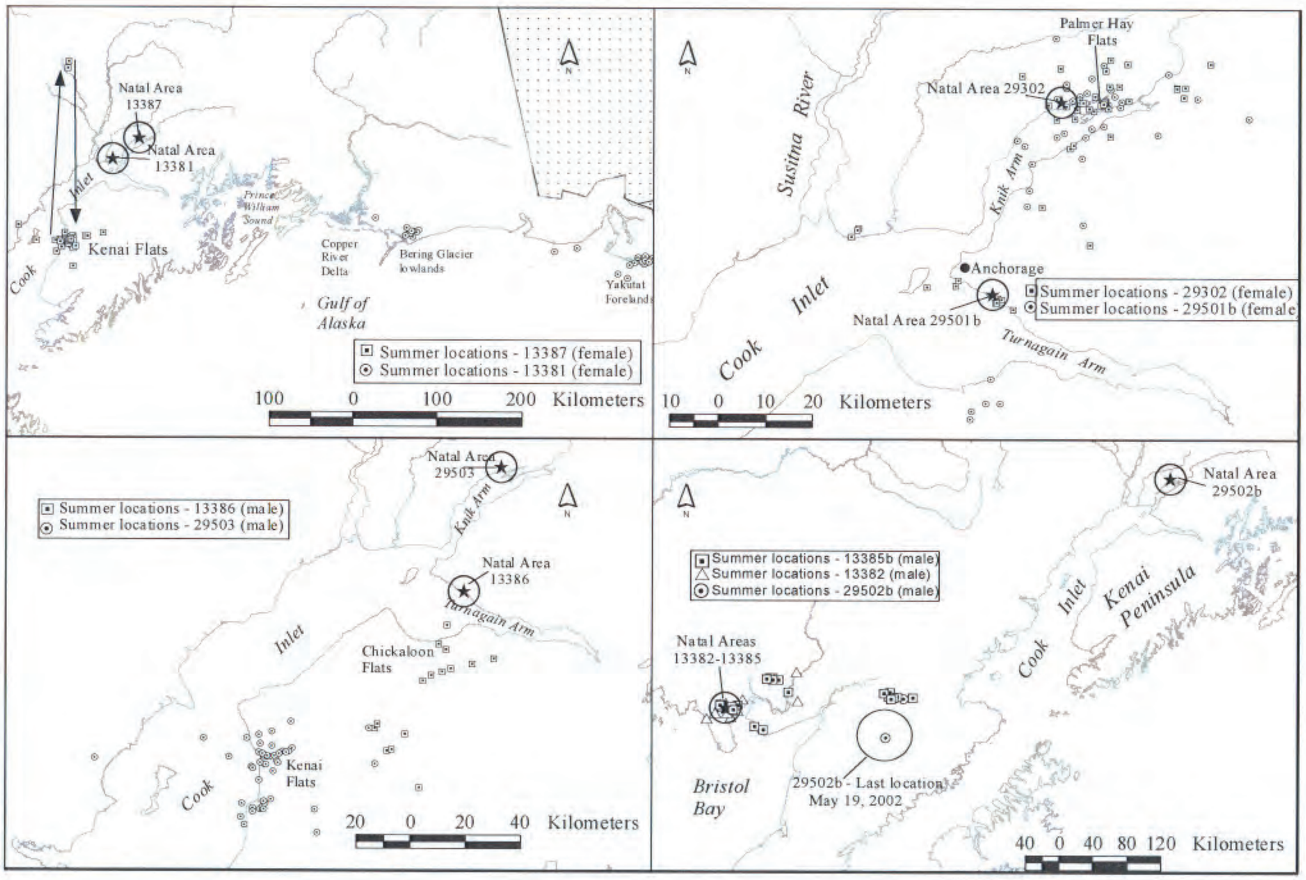

Fig 4. Natal areas and summer locations acquired with satellite telemetry for Pacific Flyway Population lesser sandhill cranes captured as flightless young in upper Cook Inlet and Bristol Bay, Alaska in 2000, 2001 and 2002.

Winter crane locations concentrated in 2 primary areas (Fig. 2): the Sacramento – San Joaquin River Delta (Delta) where 56% of all locations (n = 8 marked cranes) occurred and in Merced County (130 km to the south) where 35% of all locations (n = 6 marked cranes) occurred (Table 5). Within the Delta, 63% of the locations were concentrated on Staten Island, Tyler Island, Canal Ranch, Brack Tract, Terminous Tract, and New Hope Tract. Ninety-four percent of locations in the Delta region were within ca. 425 km2. In Merced County 94% of the crane locations were within 1473 km^2 and included Sandy Mush Country; Kesterson, San Luis and Merced National Wildlife Refuges (NWRs); and the Los Banos and Volta State Wildlife Areas. Only 9% (n = 4 marked cranes) of all locations occurred outside the Delta and Merced County (Table 5). Two cranes were located in these peripheral areas for only a few days (i.e. 1 duty cycle). Crane 33092 stayed near Vernalis for approximately 30 days and crane 13385b stayed north of Delano at the Pixley NWR (Fig. 2) for 83 days.

Though the overall winter range in the Delta and in Merced County for all cranes was relatively large, locations obtained for individual PFP cranes were generally localized. Home ranges of individual cranes averaged 168 km2 (SD = 132 km^2) in the Delta (range = 7-371 km^2) and 1,021 km2 (SD = 942 km^2) in Merced County (range = 67-2,332 km^2; Table 5).

Spring Migration

We obtained location data for 10 cranes during spring migration (Fig. 3). PFP cranes began their spring migration 9 March (range: Feb 28 to Mar 24; Table 3). The travel route north in spring was similar to fall (Fig. 2) but took approximately twice as long to complete (mean = 58 days; Table 3). Unlike fall migration, PFP cranes stopped for an average of 42 days at staging areas in the Pacific Northwest before continuing north. The Harney Valley in Oregon, and the Potholes Reservoir and Banks Lake regions in Washington were the most frequently used staging areas in those states (Table 6). Two cranes traveled further east than the fall migration route and spent ≥ 35 days in the vicinity of Fruitland and Wilder, Idaho before entering Washington (Fig 3). Spring and fall stopover sites in British Columbia and Alaska were similar but relatively less time was spent traveling through Alaska in the spring (Table 3).

Table 5. Number of duty cyclesa present and approximate area (km2) of home range for individual Pacific Flyway lesser sandhill cranes at specific locations in the Central Valley of California during the winter in 2000, 2001 and 2002.

	Delta region		near Vernalis		near Merced		near Delano	
Crane ID	Home range	No. of cycles	Home range	No. of cycles	Home range	No. of cycles	Home range	No. of cycles
13381	124	36	0	2	0	0	0	0
13382	0	0	0	1	2,060	39	0	0
13385b	7	12	0	0	369	9	40	27
13386	0	0	0	0	2,332	48	0	0
13387	119	40	0	0	758	10	0	0
29302	239	30	0	0	67	6	0	0
29501b	329	40	0	1	0	0	0	0
29502b	46	8	0	0	539	43	0	0
29503	371	44	0	0	0	0	0	0
33092	106	29	45	8	0	0	0	0

[a] Satellite transmitters cycled on for 6-8 hrs every 96-106 hrs during the winter.

Table 6. Approximate number of days spent at spring stopover and staging areas in the Pacific Northwest by Pacific Flyway Population lesser sandhill cranes in 2000, 2001 and 2002 estimated with satellite telemetry.

	Crane identification number										
Staging area	29302	29503	13381	13382	13385b	13386	13387	29501b	29502b	33092	Total days
Warner Valley, Oreg.	3	0	0	0	0	0	0	0	0	0	3
Harney Valley, Oreg.	0	0	3	43	2	0	10	12	1	1	72
Yonna Valley, Oreg.	0	0	0	0	0	0	0	0	42	0	42
near Wilder, Id.	35	0	0	0	0	0	0	0	0	34	69
Potholes Reservoir region, Wash.	0	42	34	0	38	10	13	40	15	0	192
Banks Lake, Wash.	1	1	8	0	0	20	7	0	0	0	37

PFP cranes arrived on their summer range during the first week of May (mean = 6 May).

Summer Range

Adults. - Three adult cranes captured during late April at a spring staging area in the Matanuska Valley, AK remained near the capture site for approximately 10 days before dispersing to summer areas in the Susitna and Kahiltna river drainages (Fig. 3). Summer locations were generally localized in this boreal forest, muskeg habitat suggesting that breeding territories were established. Greater than 82% of summer locations for each adult crane were within a 16 km^2 area in 2001. Transmitters on 2 adults subsequently failed just prior to anticipated fall migration. In addition to migration data, 33092 visited the capture location (staging area) the following spring and then returned to summer in the same general location (Susitna River Valley) as the previous year (Fig. 3). The core area, however, used by

33092 during the summer in 2002 was larger (67 km^2 vs. 14 km^2). Relatively less accurate location data during the summer in 2002 may have been responsible for the larger area making it difficult to predict breeding status of 33092 that year.

Colts. - Between fledging and fall migration PFP cranes captured as flightless young in upper Cook Inlet remained within 27 km (mean = 10.3 km, SD = 9.8 km) of their natal site. After arriving in upper Cook Inlet the following spring (late April-early May), juvenile cranes did not return to the vicinity of the natal site. Only one crane (female 29302) revisited the natal site, but in late May, and 2 cranes (female 29501b and male 11386) came within 25 km of their natal site (Fig. 4). Two juvenile cranes (female 13387 and male 29503) returned to upper Cook Inlet but not within 110 km of their natal location (Fig. 4). Brief visits to natal sites may have gone undetected because our transmitters were programmed to transmit for 8 hours every 2 days during this period (Table 1).

Two juvenile cranes returned to Alaska but not Cook Inlet. Female 13381 spent the summer on the Gulf Coast of Alaska between Cape Suckling and the Yakutat Forelands, over 360 km east of Cook Inlet (Fig. 4). The last location for a male 29052b was obtained on the Alaska Peninsula (May 19) indicating the bird had traveled through Cook Inlet and was possibly heading to Bristol Bay (Fig. 4).

Of the 5 juveniles returning to upper Cook Inlet, 2 summered on the Kenai Flats, two near the Palmer Hay Flats, and one on Chickaloon Flats (Fig. 4). One juvenile, who summered on the Kenai Flats, made a brief foray to the upper Kahiltna drainage (a breeding area).

Colts captured in Bristol Bay staged ca. 80 km east of the capture site soon after fledging and prior to fall migration (Fig. 2). Both juveniles (males) that returned the following year visited the immediate vicinity of the natal site in early spring then dispersed to outlying areas (Fig. 4). The extensive movements of some juveniles during the summer, the lack of accurate location data from mid-late summer for others, and the 5-day duty cycle for Bristol Bay cranes precluded meaningful calculation of summer range (km^2) for juvenile cranes.

DISCUSSION

Using satellite telemetry we were able to describe the movements of individual PFP lesser sandhill cranes on summer range in Alaska, winter range in California, and through fall and spring migration. The majority of our satellite transmitters were deployed on colts and may not accurately reflect movements and distribution of other age and social classes in the population. Colts, however, remain with their parents at least through their first migration and winter (Tacha 1988) and likely reflect movements of breeding adults during those periods. We believe non-breeding adults were not represented in this study. Though our sample size was small to fully compare migratory pathways of birds nesting in Cook Inlet and Bristol Bay, all cranes captured in both locations followed the same migratory path and wintered in small, well defined areas of the CVC (Fig. 2).

We do not know the degree of fidelity to breeding sites for adult PFP cranes. The only adult monitored through two consecutive summers returned to the same area (Fig. 3). Most juveniles, however, did not return to their natal sites the first year following hatch (Fig. 4). If fidelity to breeding areas by adults is strong, then it appears that juveniles did not accompany their parents, at least during the later stages of spring migration. Tacha (1988) reported that juvenile cranes remain with their parents until April, approximately 10 months after hatch. The average date of arrival on summer areas for our birds was May 6. Some cranes arrive in upper Cook Inlet up to a week earlier than our marked birds (unpubl. data). Consequently, migration chronology and path exhibited by our radioed juveniles in the spring is more difficult to extrapolate to other segments (age and social status) of the population. Nevertheless, we saw little variation in spring movements through the Pacific Northwest and British Columbia among 9 juveniles and 1 adult monitored during the study.

Stopover, Staging and Winter Areas

Though our satellite transmitters were programmed to transmit more frequently during migration (8 hours on and 26-48 hours off; Table 1) we could not identify stopover sites used for short durations (≤ 2 days). Locations used for longer durations, however, were easily identified. Additionally, lengths of stay at stopover and staging areas should be regarded in relative terms, as we could not precisely quantify their duration.

PFP lesser sandhill cranes completed migration from summer range in Alaska to winter range in the CVC in 13 to 40 days (Table 3). Both the minimum and maximum transit times were from individuals monitored during the fall in 2001 indicating that either cranes exhibit different migration strategies, or experienced different weather conditions.

The migration route for PFP cranes in Alaska is narrow and restricted to the coast by a series of glaciated mountain ranges (Chugach, St. Elias, Wrangell and Coastal Mountains). During fall migration, more time was spent in Alaska than in other states or provinces (Table 3), partly because Alaska makes up the largest proportion of the travel route. Stopover sites in Alaska were used for relatively short durations, especially in the spring, with longer stopovers occurring during the fall at Gustavus and the Yakutat Forelands (Table 4). That 80% of radioed cranes stopped at the Yakutat Forelands during fall migration indicates that the area provides a desirable resource. The relatively high use of the Bering Glacier lowlands, Stikine and Copper River Deltas, and Gustavus indicates their importance to migrating cranes. Only Gustavus and the Copper River Delta have been previously described as stopover sites for PFP cranes. Streveler and Matkin (1983) reported a minimum of 12,899 cranes passed through Gustavus during the fall in 1981, 6,870 of which landed on the Dude Creek State Critical Habitat Area. Herter (1982) indicated similar numbers of cranes migrating through and stopping briefly on the Copper River Delta.

British Columbia also comprises a large proportion of the total migration route but most cranes spent relatively little time (≤ 5 days) in this province during fall and spring migration (62% and 100% of marked cranes, respectively; Table 3), making stopping areas difficult to determine. As was the case in Oregon, a large proportion of locations obtained during the fall were of flying cranes. Most cranes migrated through these regions during the short duration of the transmitters off-cycle, and were located a considerable distance along the migration route during the next transmission period.

The Pothole Reservoir region (Grant County), including Columbia River NWR in central Washington, received more use by radioed cranes than other locations along the migration corridor. This was more apparent in the spring when 70% of radioed birds used the area for 10–42 days (Table 6). Cranes also frequently used the Banks Lake area (north of the Potholes Reservoir region, in the spring) but cranes were not detected there in the fall. These staging areas in Washington, plus locations used for long periods in Oregon and Idaho (Table 6), are important to cranes because they undoubtedly provide a large proportion of the nutritional resources used for the energetic demands of migration (Krapu 1987). Infrequent stops by cranes in British Columbia and Alaska during the spring suggest that foraging opportunities may be limited along this portion of the migration route.

The geographic extent of PFP lesser sandhill cranes monitored during the winter was restricted to 2 primary locations within the CVC with little interchange between areas (Fig 2). With exception of the federal wildlife refuges and state wildlife areas in Merced County, most of the winter locations appear to be on private lands. This is especially true for cranes using lands in the Delta region. Future development of these wintering areas should be monitored closely because traditionally important roost and foraging areas may be limited (Pogson 1990).

Affinities Among Breeding and Wintering Areas

The western boundaries separating the breeding ranges of the PFP and the MCP are in close proximity (Fig. 1) yet we, as did others (Pogson et al. 1988, Krapu and Brandt in prep), found no evidence of overlap between the two populations anywhere during their annual cycle.

Our data suggest that, though geographically distant, the upper Cook Inlet and Bristol Bay breeding populations are genetically linked. PFP cranes breeding in these areas utilize the same migration routes, staging and wintering areas. During the summer, however, juvenile cranes captured in upper Cook Inlet as colts exhibited a broader geographic distribution the subsequent summer than expected based on the close proximity of their natal sites. While 5/7 juveniles returned to the upper Cook Inlet region only one returned to its natal site (Fig. 4). The large dispersal distances of these juvenile cranes can provide gene flow between the two breeding areas.

Littlefield and Thompson (1982) previously described the geographic range of PFP lesser sandhill cranes. They separated the population into two segments based on differences in migration corridor and winter distribution. The migration route for the "western segment" included the Willamette Valley, Oregon, the Washington coast through Puget Sound, and the coast of British Columbia and Alaska. Cranes following this migration route staged at Sauvie Island, Oregon and Ridgefield NWR, Washington during the spring and fall (Littlefield and Thompson 1982, Cooper 1996, Littlefield and Ivey 2002) and wintered near Red Bluff, California. Red Bluff is north of wintering areas used by cranes monitored during this study. Some cranes remain on Sauvie Island over winter (Littlefield and Ivey 2002, Ivey et al. 2005). In recent years, however, sandhill cranes have not used the Red Bluff area during winter, and their current wintering location is unknown (Ivey pers. comm.). The migration route and winter areas described by Littlefield and Thompson (1982) for the "eastern segment" of PFP lesser sandhill cranes was nearly identical to that used by cranes during this study. We found no evidence that PFP lesser sandhill cranes breeding in Cook Inlet and Bristol Bay use an all-coastal route along British Columbia and Washington during migration. During the fall, all marked cranes left the coast near the Stikine River Delta in Alaska and used an interior route through central British Columbia, Washington and Oregon to wintering areas in the CVC. A reverse route was taken in the spring.

Cranes of the PFP nesting on islands in southeast Alaska and along the coast of northern British Columbia are believed to be Canadian subspecies (Littlefield and Ivey 2002, Ivey et al. 2005). Preliminary evidence suggests that they follow a migration route, stage, and winter in areas similar to that described for the "western segment" of the PFP lesser sandhill cranes. It is likely that this coastal, component of the Canadian subspecies explains the geographical differences in range described by Littlefield and Thompson (1982) for the "western" segment of the PFP. No overlap appears to exist in the breeding range of PFP cranes captured in Bristol Bay and Cook Inlet (this study) with cranes breeding to the south along the Pacific Coast (Ivey et al. 2005), suggesting that the coastal group is not part of the PFP lesser sandhill cranes. The possibility of gene flow between these populations, however, warrants further study.

ACKNOWLEDGMENTS

We thank H. J. Griese, D. D. Hill, D. H. Rosenberg and R. J. Sinnott for their assistance during captures of adult cranes. We are grateful to D. O'Hare and E. Hill (Anchorage Daily News) for the public attention their local news story gave to our project and for use of photographs taken during captures.

We thank S. L. Talbot and the staff at the USGS-BRD genetics lab (Region 7, Anchorage, Alaska) for determining the sex of our radioed cranes. We're extremely grateful for the diligent effort by helicopter pilots T. L. Cambier and L. Larrivee. We thank G. L. Krapu and D. H. Ellis for technical assistance with crane marking. We thank D. Douglas for use of his location-filtering program. We appreciate assistance from J. Woolington (ADF&G), P. Walsh and G. Collins (Togiak NWR). We thank the Webless Migratory Game Bird Research Program and the U.S.F.W.S. Migratory Bird Management (Region 7) for partially funding this project. We thank J. A. Barzen, G. L. Krapu and M. G. Spalding for comments that greatly benefited the manuscript.

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PROCEEDINGS OF THE
NINTH NORTH AMERICAN CRANE WORKSHOP

17 - 20 JANUARY 2003
SACRAMENTO, CALIFORNIA, USA

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