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BREEDING GROUNDS, WINTER RANGES, AND MIGRATORY ROUTES OF RAPTORS IN THE MOUNTAIN WEST

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Abstract.—We report band-encounter locations accumulated between 1980 and April 2001 for five species of North American raptors (Sharp-shinned Hawk, *Accipiter striatus*; Cooper's Hawk, *A. cooperii*; Northern Goshawk, *A. gentilis*; Red-tailed Hawk, *Buteo jamaicensis*; and American Kestrel, *Falco sparverius*) banded or recaptured during migration in northern Oregon ($N = 14$), northeastern Nevada ($N = 325$), and north-central New Mexico ($N = 136$). Based on a discriminant function analysis of the encounter locations and comparisons of intra- and inter-flyway recapture rates, migrants passing through these areas travel along three distinct regional flyways: Pacific Coast, Intermountain, and Rocky Mountain. Encounter locations of Pacific Coast migrants were generally restricted to west of the Sierra Nevada and Cascade ranges from southern British Columbia through California. Intermountain migrants were encountered from interior Alaska to southwestern Mexico, usually east of the Sierra Nevada–Cascade ranges and west of the Rocky Mountains and Sierra Madre Occidental. Rocky Mountain migrants were found from interior Alaska to southern Mexico, usually within or east of the latter two ranges. Because encounter distributions tended to converge in the far northwest and southern Mexico, the delineation of regional flyways in western North America is probably most relevant for distinguishing subpopulations of birds that originate south of mainland Alaska and winter north of Central America. During summer and migration seasons, most encounters away from the banding sites resulted from death due to collisions with human structures or unknown causes. In contrast, most winter encounters involved birds shot in Mexico. We also examined the Nevada encounter data for evidence of differential migration distances among age and sex classes, and found a consistent but nonsignificant pattern for four species. Mean winter latitude tended to increase with age within sexes and to be higher for males than females within age classes. These patterns are most consistent with predictions of foraging-efficiency and arrival-time hypotheses proposed to explain differential migration.

Key Words: *band encounters; band recoveries; differential migration; migration; flyways; western North America.*

Campos de anidacion, rangos invernales, y rutas migratorias de Las Rapaces en la Montaña Oeste

Resumen.—Reportamos las localidades de encuentros de individuos marcados acumulados entre 1980 y abril de 2001 para cinco especies de rapaces norteamericanas (*Accipiter striatus, A. cooperii, A. gentilis, Buteo jamaicensis,* y *Falco sparverius*) anilladas o recapturadas durante la migración en el norte de Oregon ($N = 14$), noreste de Nevada ($N = 325$), y Nuevo Méjico Norcentral ($N = 136$). Con base en un análisis de función discriminante de las localidades de encuentros y comparaciones de las tasas de recaptura intra- e inter-corredores de vuelo, los migrantes pasan a través de estas áreas de viaje a lo largo de tres distintos corredores regionales de vuelo: costa pacifica, ínter montañoso y por las montañas rocosas. Las localidades de encuentro de los migrantes de la costa pacifica estaban generalmente restringidos al oeste de la Sierra Nevada y Cascade ranges desde el sur de British Columbia hasta California. Los migrantes ínter montanos fueron encontrados desde el interior de Alaska hasta el suroeste de Méjico, usualmente al oriente de la Sierra Nevada y Cascade ranges y el oeste de las montañas rocosas y la Sierra Madre Occidental. Los migrantes de las montañas rocosas fueron encontrados desde el interior de Alaska al sur de Méjico, usualmente dentro o al este de los dos últimos rangos. Debido a que las distribuciones de los encuentros tendían a convergir en el lejano noroeste y sur de Méjico, la delineación de corredores de vuelo regionales en el occidente de Norteamérica es probablemente mas relevante para distinguir subpoblaciones de aves originarias del sur de Alaska continental y que invernan al norte

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de Centroamérica. Durante el verano y las estaciones migratorias, la mayoría de encuentros lejos de los sitios de marcaje fueron resultado de la muerte por colisiones con estructuras humanas o por causas desconocidas. En contraste, la mayoría de encuentros invernales involucraron aves impactadas en México. Examinamos además los datos de encuentros de Nevada buscando evidencia de distancias de migración diferenciales entre edad y clases de sexo, y encontramos un consistente pero no significante patrón para cuatro especies. La latitud media invernal tendió a incrementarse con la edad dentro de sexos y a ser mas alta para los machos que para las hembras dentro de clases de edad. Estos patrones son mas consistentes con las predicciones de eficiencia del forrajeo y la hipótesis del tiempo de arribo propuesta para explicar la migración diferencial.

[Traducción de César Márquez]

Linking summer and winter ranges and migratory or dispersal routes of bird populations is necessary before effective year-round and location-specific conservation strategies can be designed (Myers et al. 1987, Sherry and Holmes 1995). Establishing such linkage, thus defining migration flyways, also ensures the proper geographic context for interpreting trends observed at count sites (Senner and Fuller 1989). Assessing the status of raptor populations is difficult using breeding-season census methods, because most species are secretive, occupy large home ranges, and occur at low breeding densities (Fuller and Mosher 1981). For this reason, researchers have turned to estimating population trends by counting migrating raptors as they pass concentration points (Zalles and Bildstein 2000).

HawkWatch International, Inc. (HWI) and its organizational precursors have been banding raptors at migration sites since 1980 to help identify source populations and migration routes of western raptors (Smith and Hoffman 2000). Herein, we describe the breeding areas, wintering grounds, and migratory routes of raptors encountered as migrants at four long-term monitoring sites in New Mexico, Nevada, and Oregon. Our analyses concern five species (Sharp-shinned Hawk, *Accipiter striatus*; Cooper's Hawk, *A. cooperii*; Northern Goshawk, *A. gentilis*; American Kestrel, *Falco sparverius*; Red-tailed Hawk, *Buteo jamaicensis*) and derive from 475 encounters with previously banded birds recorded between autumn 1980 and April 2001 (Table 1).

With these data, we also examined variation in migration distances among age and sex classes, commonly referred to as differential migration. Several hypotheses have been offered to explain this phenomenon (see Ketterson and Nolan 1983, Kerlinger 1989).

When discussing raptor migration, it is important to recognize that migrants recorded at concentration points may be involved in at least six different types of movements: complete migration, partial migration, natal dispersal, and irruptive, nomadic, and local movements, including altitudinal migration (Dingle 1980, Kerlinger 1989). Worldwide, 70% of all migratory falconiform species are considered partial migrants, which involves seasonal movements between breeding and non-breeding ranges by some but not all members of a population or a seasonal departure from only a portion of the breeding range (Kerlinger 1989). Herein, we consider the migratory movements of five species of partial migrants.

While species such as Sharp-shinned and Cooper's Hawks routinely follow largely north–south migration pathways, other species (e.g., Prairie Falcons, *Falco mexicanus*; Red-tailed Hawks; Ferruginous Hawks, *Buteo regalis*; and Golden Eagles, *Aquila chrysaetos*) often migrate or disperse from natal territories in many directions (Steenhof et al. 1984, Bloom 1985, Watson and Pierce 2000). Moreover, as one moves south, especially along the coast of California (A. Fish pers. comm.), patterns of movement become increasingly complex and populations include permanent residents and wintering birds, as well as actual migrants. Thus, although herein we adopt the classic terminology of "flyways" to describe relatively distinct regional movement corridors, we caution readers to recognize that movements within flyways can be multi-directional and complex and that the model we articulate may not apply to all species or populations.

METHODS

Study Sites. The Goshute banding site (Hoffman 1985) is located on a ridgetop near the southern end of the Goshute Mountains in northeastern Nevada (40°25.46′N, 114°16.26′W; Fig. 1). Annual autumn migration counts, begun in 1983, currently range from about 16 000–25 000 migrants of up to 18 species (Sherrington 1999). From one to six banding stations were operated each year since 1980 ($\bar{x}$ elevation = 2695 m). Annual capture totals average about 2100 raptors of up to 13 species.

Table 1. Banding totals and encounters with previously banded birds through spring 2001 by species and migration site. "Foreign encounters" indicate birds observed elsewhere after banding; "foreign recaptures" indicate birds recaptured after being banded elsewhere; and "recaptures" indicate birds banded and recaptured at the same migration site.

	Nevada (since 1980)				New Mexico (since 1990)				Oregon (since 1995)		
Species	Captured	Foreign Encounters	Foreign Recaptures	Recaptures	Captured	Foreign Encounters	Foreign Recaptures	Recaptures	Captured	Foreign Encounters	Foreign Recaptures
Sharp-shinned Hawk	24 698	87	8	32	6229	19	0	13	643	5	2
Cooper's Hawk	12 050	101	6	32	5964	21	4	64	173	2	0
Northern Goshawk	615	9	3	2	80	1	1	1	27	0	0
Red-tailed Hawk	1201	29	2	0	714	9	0	0	186	5	0
American Kestrel	2797	9	5	0	524	3	0	0	1	0	0
Total	41 361	235	24	66	13 511	53	5	78	1030	12	2

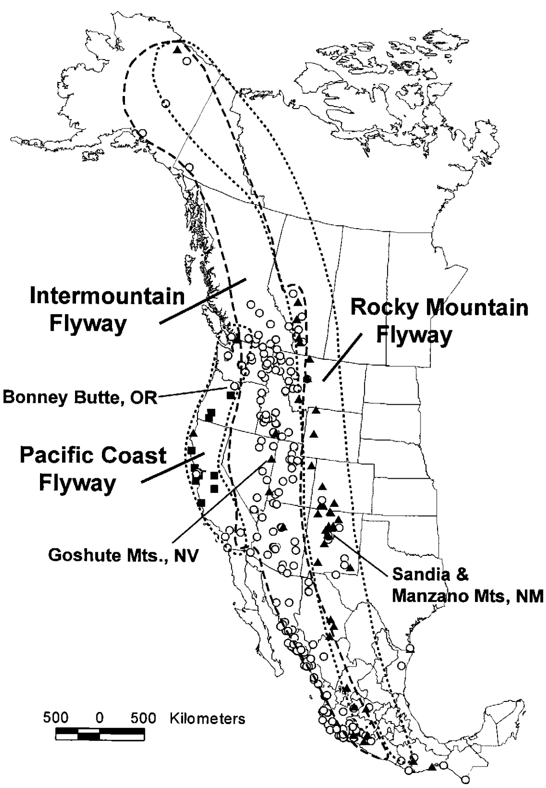

Figure 1. Distribution of foreign encounters and foreign-recapture banding locations associated with raptor migration-banding sites in New Mexico (triangles), Nevada (circles), and Oregon (squares), and the associated regional flyways in western North America.

The Manzano banding site (DeLong and Hoffman 1999) is located on a ridgetop in the Manzano Mountains of central New Mexico (34°42.25′N, 106°24.67′W; Fig. 1). Annual autumn migration counts, begun in 1985, range from about 4500–6000 migrants of up to 19 species (Sherrington 1999). From one to four banding stations were operated each year since 1990 ($\bar{x}$ elevation = 2730 m). Annual capture totals average about 1000 raptors of up to 12 species.

The Sandia banding site is located on a ridgetop near the southern end of the Sandia Mountains (41-km long, north-south range) ca. 34 km north of the Manzano site and 18 km east of Albuquerque, New Mexico (35°05.21′N, 106°25.93′W; Fig. 1). The vegetation around the site is similar to that described for the Manzano site in DeLong and Hoffman (1999), typical of the Upper Sonoran life zone. Annual spring migration counts, begun in 1985, range from about 3700–5500 migrants of up to 20 species (Sherrington 2000). Banding has occurred each year since 1990, except in 1992, mostly at a single station (elevation = 2235 m). Annual capture totals average about 265 raptors of up to 12 species.

The Bonney Butte banding site is located in the eastern Cascade Mountains of north-central Oregon (45°16.08′N, 121°59.72′W; Fig. 1). Bonney Butte is a mostly bald knoll (summit elevation = 1754 m) at the southern terminus of Surveyor's Ridge, which originates near the town of Hood River and terminates southeast of Mt. Hood. With the exception of scattered montane meadows and forest clearcuts, mixed conifer forest covers the immediate area surrounding Bonney Butte. Autumn migration counts, begun in 1994, range from about 2200–2800 migrants of up to 18 species (McDermott 1999). Banding has occurred each year since 1995 at a single station at the north end of Bonney Butte. Annual capture totals currently range from about 150–350 raptors of up to 12 species.

Capture and Processing Methods. Migrant raptors were captured between March and April in the Sandia Mountains and between mid-August and early November at the autumn sites. The number of stations and variety of capture devices used at each site differed, but the basic capture and processing methods used were consistent across all sites. Trappers attracted raptors using live, non-native, avian lures manipulated from camouflaged blinds. Capture devices included bow nets, dho-gaza nets, and mist nets (Bloom 1987). Unless already banded, all birds were fitted with a uniquely-numbered, U.S. Fish and Wildlife Service/U.S. Geological Survey aluminum leg band. Processors identified species, subspecies, sexes, and ages using morphological characteristics described in the U.S. Bird Banding Laboratory (BBL) manual, Wheeler and Clark (1995), and Hoffman et al. (1990).

Data Classification. We considered three types of encounters with banded birds. "Foreign encounters" included birds originally banded as migrants at one of the four banding sites that were subsequently encountered elsewhere. "Foreign recaptures" included birds originally banded by other researchers that we later recaptured as migrants. For analytical purposes, we pooled foreign-encounter locations and foreign-recapture banding locations associated with each migration site. "Recaptures" included individuals banded and later recaptured at the same migration site.

Between 1990 and April 2001, 34 between-site recaptures of banded birds occurred at the Manzano and Sandia sites, which is similar to the number of same-site recaptures that occurred at the two sites during this period (44). We consider this strong confirmation that the two sites lay within the same flyway, which we expected given their proximity and situation along a north–south line of relatively isolated mountain ranges. Hence, we treated data from the two New Mexico sites as representing a single migration site.

We classified foreign encounters/recaptures by season based on dates that foreign encounters occurred or foreign recaptures were originally banded: (1) summer, 15 May–19 August; (2) winter, 15 November–14 March; and (3) migration, 15 March–14 May or 20 August–14 November. We chose these dates based on knowledge of primary passage periods for migrants observed during standardized western counts (HWI unpubl. data). After we classified cases strictly by the reported BBL encounter date, it quickly became apparent that some assignments were not reasonable. Twenty-five cases warranted a change from migration to winter status because the foreign encounter location was in the southern portion of the species' wintering range (i.e., Nayarit, Mexico and farther south). Two cases warranted a change from summer to spring-migration status because the location was in Mexico where breeding was improbable.

Data Analysis. We analyzed the encounter data in two ways to determine if the three migration sites could be classified as located along different flyways. First, we used discriminant function and classification analysis (Afifi and Clark 1996) to determine whether foreign encounters/recaptures could be classified according to migration site based on the latitude and longitude (lat–long) of the encounters (Nichols and Kaiser 1999). For this analysis, we withheld one foreign encounter from Massachusetts, because inclusion of this extreme outlier skewed the bivariate distribution of lat-longs. Discriminant function analysis resulted in a two-way table of predicted versus actual migration-site associations. Second, we compared the number of intra- and inter-site recaptures across the three migration sites.

Table 2. A comparison of actual and predicted migration-site associations based on a discriminant function analysis using latitudes and longitudes of foreign encounters and original banding locations of foreign recaptures.

	PREDICTED			
ACTUAL	OREGON	NEVADA	NEW MEXICO	PERCENT CORRECT
Oregon	13	1	0	93
Nevada	10	202	41	80
New Mexico	1	6	50	88
Total	24	209	91	82

To examine differential migration distances, we conducted one-way or two-way factorial analysis of variance (ANOVA) on the winter latitudes of different sex–age classes of Sharp-shinned, Cooper's, and Red-tailed Hawks associated with the Nevada site. Smaller sample sizes precluded such analyses for other sites and species. We also compared sex ratios at banding and among foreign encounters using G-tests of independence with William's correction (Sokal and Rohlf 1981:737–738). We conducted all statistical analyses using Systat (SPSS 1998).

RESULTS

Flyway Delineation. The discriminant function correctly classified 77% of the Nevada birds, 82% of the New Mexico birds, and 93% of the Oregon birds (Wilks's lambda = 0.65, $F_{4,646} = 39.51$, $P < 0.001$). However, when we eliminated from the analysis several foreign encounters/recaptures from Alaska and the Yukon Territory (Fig. 1), which improved the bivariate normality of the lat-long dataset, our classification efficiency improved to 80% of the Nevada birds, 88% of the New Mexico birds, and 93% of the Oregon birds (Wilks's lambda = 0.53, $F_{4,640} = 59.04$, $P < 0.001$; Table 2).

Recapture data (Table 1) also confirmed that the probability of a same-site recapture (66 Nevada recaptures, 78 New Mexico recaptures, no Oregon recaptures) was much greater than the probability of a flyway crossover (only one Manzano–Goshute crossover encounter since 1990).

Sharp-shinned Hawk. Females comprised 82% of the foreign encounters, which is significantly higher than the proportion of females banded at the three migration sites through 2000 (51%; $G_{adj} = 46.5$, $P < 0.001$).

A two-way incomplete factorial ANOVA with SEX and AGE as the main effects and winter-location latitudes of Nevada migrants as the dependent var-

Table 3. Mean latitude of winter foreign encounters by sex and age for selected species banded in the Goshute Mountains, Nevada. Except for Sharp-shinned Hawks, means were not significantly different based on analysis of variance.

		HATCH-YEAR		SECOND-YEAR		AFTER-SECOND-YEAR	
SPECIES	SEX	MEAN ± SE	(*N*)	MEAN ± SE	(*N*)	MEAN ± SE	(*N*)
Sharp-shinned Hawk	Female	22.61 ± 1.87	(8)	26.11 ± 1.60	(11)	23.64 ± 1.87	(8)
	Male	—		16.33	(1)	39.67 ± 3.74	(2)
Cooper's Hawk	Female	22.28 ± 2.63	(6)	21.56 ± 2.43	(7)	24.21 ± 1.29	(25)
	Male	22.54 ± 3.72	(3)	23.58 ± 3.72	(3)	26.52 ± 2.43	(7)
American Kestrel	Female	18.33 ± 1.33	(2)	18.53 ± 0.07	(2)	19.03	(1)
	Male	19.83	(1)	—		—	
Red-tailed Hawk	Unknown	30.40 ± 3.39	(5)	30.65 ± 3.79	(4)	31.77 ± 2.68	(8)

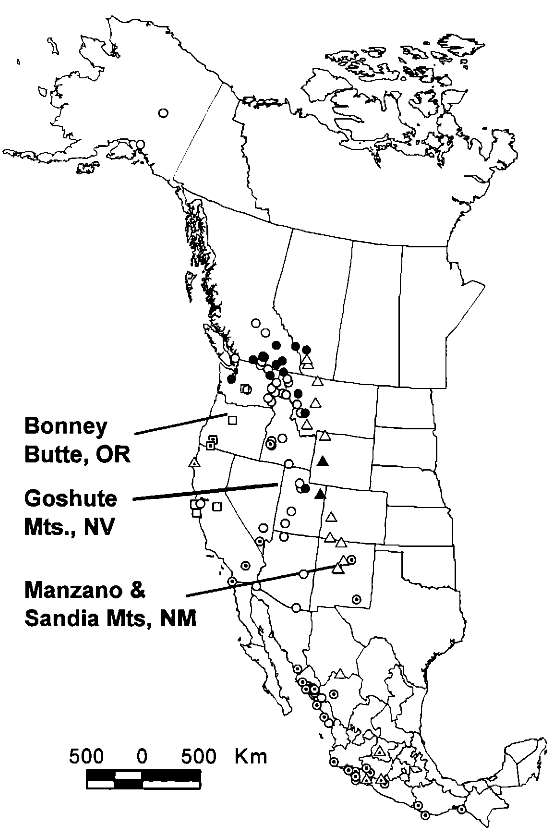

Figure 2. Distribution of foreign encounters and foreign-recapture banding locations for Sharp-shinned Hawks associated with migration-banding sites in New Mexico (triangles), Nevada (circles), and Oregon (squares) during summer (solid fill), winter (filled with a dot), and migration seasons (no fill).

iable revealed a significant overall model ($F_{4,25}$ = 5.43, P = 0.003); however, close examination of group means revealed a complex pattern (Table 3). Planned post-hoc contrasts indicated significant differences ($P < 0.05$) for second-year (SY) versus after-second-year (ASY) males (higher latitudes for ASY birds) and for ASY males versus ASY females (higher latitudes for males). However, due to small sample sizes for males, these results must be considered tentative. There were no significant age-related differences for females. Moreover, although HY females averaged the most southerly winter latitudes, SY females averaged more northerly latitudes than ASY females. Similarly, although two ASY males averaged more northerly latitudes than ASY females, the opposite appeared true for SY birds. Thus, our results are equivocal concerning sex-related differences within age groups, but suggest that older birds generally winter farther north than younger birds, with the difference perhaps less pronounced for females than for males.

Two summer locations of New Mexico migrants were in northeastern Utah and west-central Wyoming (Fig. 2). Six other encounters during late spring migration (late April–mid-May), which may represent summer locations, extended along the eastern Rocky Mountains from western Colorado to western Alberta. Summer locations of Nevada migrants were in the Intermountain West and northwestern Rocky Mountains from northern Utah to central and eastern British Columbia and western Alberta (N = 12). However, two autumn locations were in central Alaska, indicating that the breeding-ground origins of Nevada migrants extend at least that far north. No summer records were available for Oregon migrants.

Table 4. Disposition of foreign encounters by species.

	SPECIES				
DISPOSITION	SHARP-SHINNED HAWK	COOPER'S HAWK	NORTHERN GOSHAWK	RED-TAILED HAWK	AMERICAN KESTREL
Captured and released	6	6	2	2	3
Collision w/ human structure	33	11	2	6	0
Shot	25	47	0	4	3
Held in captivity	2	2	1	1	2
Injured or sick	3	9	0	7	0
Poisoned	1	2	0	1	0
Cat/dog kill	1	0	0	0	1
Electrocuted	0	0	0	1	0
Caught in coyote leg-hold trap	0	0	0	1	0
Starved	1	0	0	0	0
Found dead—cause unknown	33	43	5	17	2
No reported reason	7	3	0	3	1
Total	112	123	10	43	12

Three winter locations of New Mexico migrants were in southwestern Mexico, but another was on the northern California coast (Fig. 2). Nevada migrants wintered primarily from the southwestern U.S. to Oaxaca, with concentrations in Sinaloa and Michoacán (N = 30). The only true winter locations of Oregon migrants were in southern Oregon (N = 2); however, three migration locations were in northern California.

Migration locations of New Mexico migrants were along the eastern Rocky Mountains from Alberta to Chihuahua (N = 13; Fig. 2). Most migration locations of Nevada migrants extended from central Alaska, through the Intermountain West and Great Basin, and down the Sierra Madre Occidental into southwestern Mexico (N = 51). However, one SY female was recovered during September near San Francisco, California, and one adult male was captured and released during October after it landed on a ship from Guyana somewhere at sea. Since 1995, our Goshute project and Idaho Bird Observatory's (IBO) Boise Ridge migration-banding project (340 km north-northwest of the Goshutes) have recorded seven between-site encounters. Migration locations of Oregon migrants (N = 5) were in northern California (3) and the eastern Cascades of Oregon and Washington.

The most common reason for summer and migration foreign encounters was injury or mortality due to collisions with human structures such as windows, buildings, and cars (56% of summer encounters, 38% of migration encounters, 30% overall; Table 4). In contrast, the most common cause of winter encounters was shooting (43%), with 96% of all reported shootings in Mexico.

Cooper's Hawk. Females comprised 71% of the foreign encounters, which was significantly higher than the proportion of females banded at the three migration sites through 2000 (56%; G_{adj} = 10.6, $P < 0.005$).

There were no significant differences in the mean winter latitudes of different sex–age classes of Nevada migrants (two-way factorial ANOVA: Sex—$F_{1,45} = 0.44$, $P = 0.51$; Age—$F_{2,45} = 0.94$, $P = 0.40$; Interaction—$F_{2,45} = 0.08$, $P = 0.93$). However, the mean winter latitudes of males were slightly farther north than for females of the same age group, and within sexes, mean winter latitudes increased with age except for HY versus SY females (Table 3).

Most summer locations of New Mexico migrants were in the southern Rocky Mountains of New Mexico and Colorado (N = 10; Fig. 3). However, one summer location was in southwestern Alberta and another individual, banded as a HY bird in the Manzano Mountains, was reportedly found dead five years later during summer in Massachusetts (extreme outlier; maybe transcription error?). The summer locations of Nevada migrants were concentrated in the Intermountain West from Nevada to western Alberta (N = 8). No summer records were available for Oregon migrants.

Winter locations of New Mexico migrants extended from central New Mexico south through

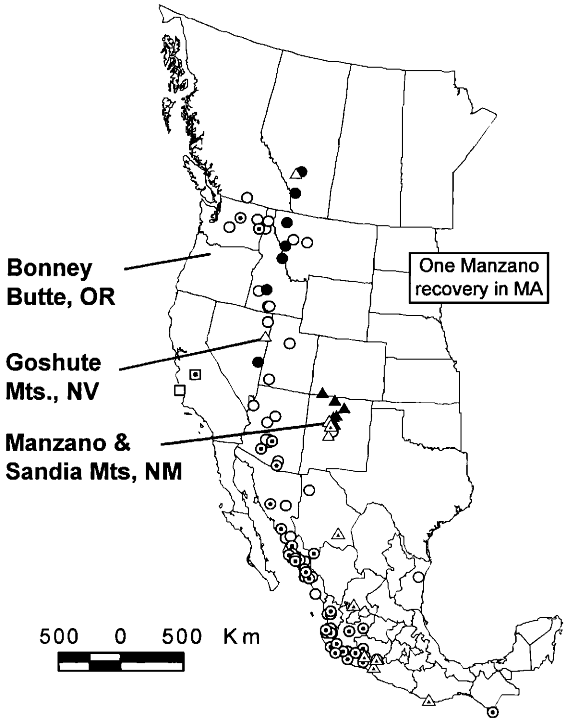

Figure 3. Distribution of foreign encounters and foreign-recapture banding locations for Cooper's Hawks associated with migration-banding sites in New Mexico (triangles), Nevada (circles), and Oregon (squares) during summer (solid fill), winter (filled with a dot), and migration seasons (no fill).

Chihuahua and San Luis Potosí, remaining east of the Sierra Madre Occidental, and along the southwestern coast of Mexico from Michoacán to Oaxaca ($N = 9$; Fig. 3). Most winter locations of Nevada migrants extended from Arizona south along primarily the western flanks of the Sierra Madre Occidental and into the Pacific coastal states of Mexico from Sinaloa to the Guatemala border, with concentrations in Sinaloa and Michoacán ($N = 49$). However, two other Nevada migrants were recovered as adults during January in central and eastern Washington after cars hit them. One Oregon migrant was recovered during winter in the southern Central Valley of California near Fresno.

Three migration locations of New Mexico migrants were in south-central New Mexico, but another was recaptured in the Goshute Mountains (Fig. 3). Migration locations of Nevada migrants extended from central British Columbia through the Great Basin and western Arizona, and south into the Pacific coastal states of Mexico ($N = 46$). This includes four between-site encounters of birds banded in the Goshutes and at IBO's Boise Ridge site. One migration location of an Oregon migrant was along the south coast of California.

Most summer foreign encounters (81%) were birds found dead—cause unknown (35% of all encounters; Table 4). Most winter encounters (56%) were due to shooting (38% overall). During migration, common reasons for encounters included shooting (27%) and collisions with fences and windows (11%).

Northern Goshawk. Females comprised 60% of the foreign encounters, which is only slightly higher than the proportion of females banded at the three migration sites through 2000 (50%; $G_{adj} = 0.3$, $P > 0.50$).

A single New Mexico autumn foreign recapture was banded as a nestling the previous spring in the Jemez Mountains, ca. 105 km northwest of the Manzano site (Fig. 4). A single New Mexico foreign encounter (found dead—cause unknown) occurred 28 km north of the Manzano site the spring after banding as a HY bird. A single New Mexico recapture occurred seven years after banding as a HY bird in the Manzano Mountains. Ten of 12 goshawk foreign encounters/recaptures associated with the Nevada migration site were clustered in the Great Basin or adjacent portions of the northwestern Rocky Mountains in Utah, Nevada, Idaho, and Oregon, most within 300 km of the project site. These include five between-site encounters involving our Goshute site and a long-term nesting study in the Independence Mountains of Nevada (209 km northwest of the Goshutes; M. Bechard pers. comm.). The latter included three birds banded as nestlings and later recaptured in the Goshutes the same year, and two birds banded in the Goshutes (one HY and one SY) that were later resighted as breeding adults (both as 3-yr birds). The two exceptions to the Great Basin/northern Rockies foreign-encounter locations were birds recovered during summer in the Gila Mountains of southeastern Arizona (found dead—cause unknown) and during spring in central Alberta (released after striking unknown object). Three of the remaining five Nevada birds recovered in the Great Basin were found dead—cause unknown; another died when it hit a barbed wire fence; and the last was simply reported as in captivity (Table 4).

Red-tailed Hawk. There were no significant age-

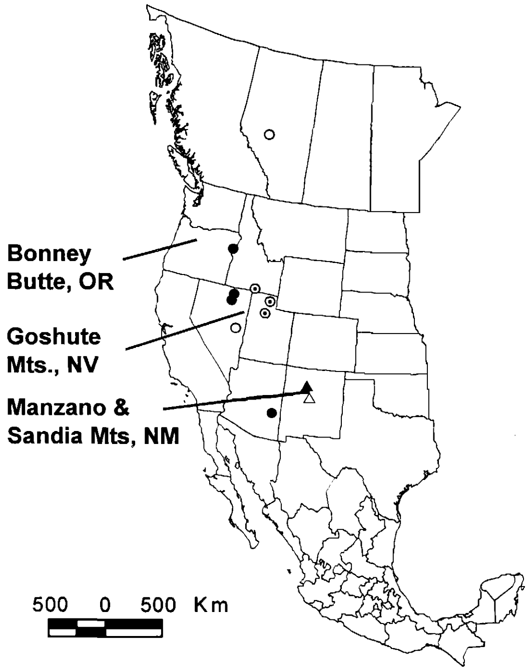

Figure 4. Distribution of foreign encounters and foreign-recapture banding locations for Northern Goshawks associated with migration-banding sites in New Mexico (triangles), Nevada (circles), and Oregon (squares) during summer (solid fill), winter (filled with a dot), and migration seasons (no fill).

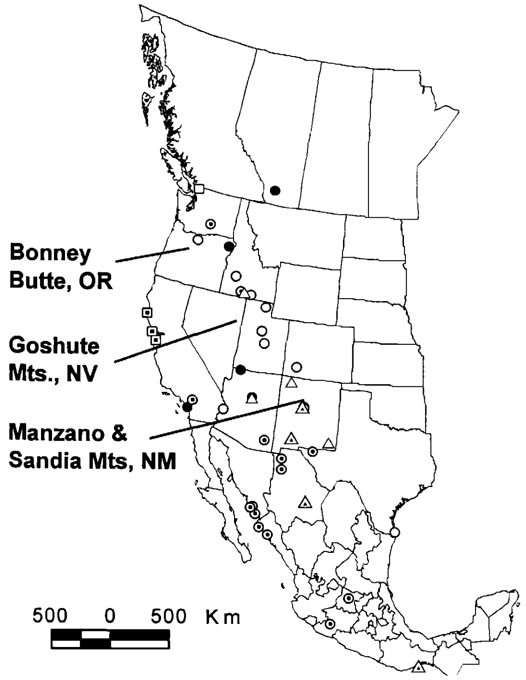

Figure 5. Distribution of foreign encounters and foreign-recapture banding locations for Red-tailed Hawks associated with migration-banding sites in New Mexico (triangles), Nevada (circles), and Oregon (squares) during summer (solid fill), winter (filled with a dot), and migration seasons (no fill).

related differences in the mean winter latitudes of Nevada migrants (ANOVA: $F_{2,14} = 0.06$, $P = 0.942$); however, the means showed a consistent pattern of increasing latitude with increasing age (Table 3).

No summer locations were available for New Mexico or Oregon migrants. Two foreign recaptures in Nevada were originally banded as nestlings in the Wallowa Mountains of northeastern Oregon and in the coastal foothills of southern California (Fig. 5). Two other summer locations of Nevada migrants were in southwestern Alberta and near the Utah–Arizona border. Based on satellite tracking, three other Nevada migrants summered in central British Columbia, northwestern Montana, and southeastern Idaho (HWI unpubl. data).

Winter encounters of New Mexico migrants were in central New Mexico, Chihuahua, and Oaxaca ($N = 4$; Fig. 5). Based on satellite tracking, six other New Mexico migrants wintered from northern Sinaloa and western Tamaulipas south through southern Oaxaca and east-central Veracruz (HWI unpubl. data). Winter encounters of Nevada migrants extended from south-central Washington to Guanajuato and Michoacán, including one in southern California and one near the southern tip of Texas ($N = 17$). Based on satellite tracking, five other Nevada migrants wintered from Baja California and northwestern Chihuahua south to the Nayarit/Jalisco area (HWI unpubl. data). Four winter locations of Oregon migrants were near the coast of northern California.

Migration locations of New Mexico migrants were in northern New Mexico, Arizona, and southern Idaho ($N = 5$; Fig. 5). Migration locations of Nevada migrants extended from the northeastern Cascade Mountains of Oregon, through the western Rocky Mountains of Idaho and Utah, into southwestern Arizona, and as far as coastal Texas ($N = 9$). One migration location of an Oregon migrant was in southwestern British Columbia.

No specific causes of mortality were reported for three Red-tailed Hawks found during summer.

Common reasons for winter encounters included shooting (12%), collisions with cars and human structures (12%), and other unspecified injury or illness (12%; Table 4). Common reasons for migration encounters included unspecified injury or illness (29%) and collisions with human structures (14%).

American Kestrel. Females comprised 92% of the foreign encounters, which is significantly higher than the proportion of females banded at the three migration sites through 2000 (48%; G_{adj} = 10.7, $P < 0.005$).

The sample of winter locations for kestrels was too small to warrant statistical analysis of differential migration distances; however, like for Red-tailed and Cooper's Hawks, consistent patterns emerged. The winter latitudes of females increased with age and the winter latitude of the single male encounter was farther north than for any female (Table 3).

One New Mexico migrant was found dead (cause unknown) during summer in central Alberta (Fig. 6). All summer locations of Nevada migrants reflect encounters with breeding adults (N = 3) or nestlings (N = 5) in artificial nest boxes. Six were birds from two nest-box studies near Boise and Fairfield, Idaho. The other two were banded as nestlings in north-central Washington and the southwestern Yukon Territory.

Winter locations of Nevada (N = 6) and New Mexico (N = 2) migrants were in similar areas in Jalisco, Michoacán, and Oaxaca (Fig. 6). Common reasons for these encounters included shooting (37.5%), died in captivity (25%), and killed by a dog (12.5%; Table 4).

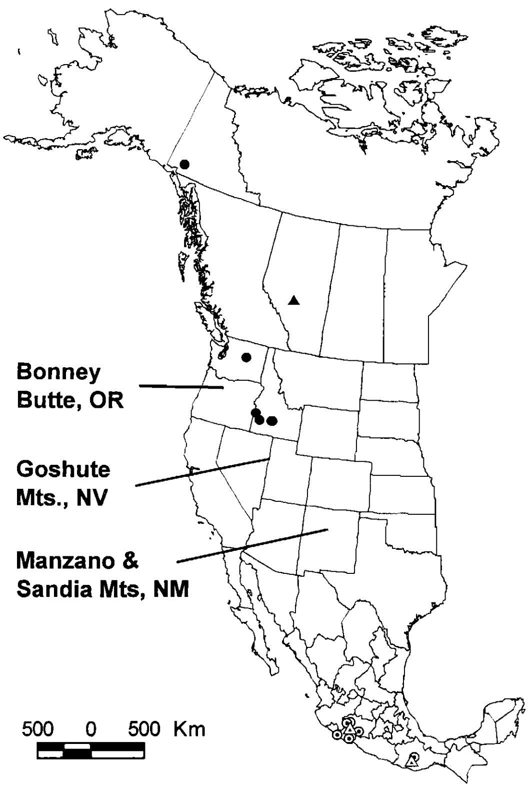

Figure 6. Distribution of foreign encounters and foreign-recapture banding locations for American Kestrels associated with migration-banding sites in New Mexico (triangles) and Nevada (circles) during summer (solid fill) and winter (filled with a dot).

DISCUSSION

Flyway Delineation. Results from the flyway-classification analyses suggest that raptors monitored at the three migration sites travel within three definable, regional flyways: Rocky Mountain, Intermountain, and Pacific Coast (Fig. 1). Only two birds banded in Nevada or New Mexico were recovered west of the Sierra Nevada–Cascade ranges in Oregon or California (Fig. 1). Data from IBO's Boise Ridge site also indicate infrequent crossing of the Sierra Nevada–Cascade boundary (2 of 30 [6%] encounters since 1995; G. Kaltenecker unpubl. data). However, the distribution of encounters with Oregon and Nevada migrants overlapped in Washington and southern British Columbia, and south of the Sierra Nevada range in southern California and northwestern Mexico. Our encounter sample sizes for Oregon migrants were small; therefore, the minimal overlap in the distributions of Oregon and Nevada/New Mexico migrants may be misleading. However, the limited Oregon data are consistent with long-term, band-return data from coastal California, which indicate distribution west of the Cascade and Sierra Nevada ranges from southwestern British Columbia to northern Baja California (Scheuermann 1996, 1997, Acuff 1998, 1999).

The largest geographic overlap (15%) in encounter locations occurred among migrants using the Rocky Mountain and Intermountain flyways. Nevertheless, Intermountain migrants were usually encountered west of the Rocky Mountains and Sierra Madre Occidental, whereas Rocky Mountain migrants were usually found within or east of these ranges. The zones of greatest overlap were on summer ranges in southwestern Alberta and on wintering ranges in the coastal states of southwestern Mexico. Thirty foreign encounters of birds banded at IBO's Boise Ridge site also were all west of the Rocky Mountains (G. Kaltenecker unpubl. data).

The recapture analyses also suggested high fidelity to the Intermountain and Rocky Mountain flyways. The single recapture of a Manzano-banded bird in Nevada, as well as several other outlier encounters, show that Intermountain–Rocky Mountain flyway crossovers do occur, but such events were rare compared to the frequency of within-flyway recaptures and foreign encounters.

Thus, both the Sierra Nevada–Cascade and Rocky Mountain ranges could be considered biogeographic boundaries, albeit permeable, that generally separate individuals inhabiting the three western flyways. This also means that, for most species, migration counts in the three regions represent largely distinct subpopulations. However, significant overlap occurred at the southern and northern extents of the encounter distributions for each flyway. Moreover, limited encounter data from two long-term banding sites in mainland Alaska (mostly Sharp-shinned Hawks) suggest that autumn migrants originating in the state ultimately may travel along any one of the three flyways described herein, with most such birds wintering in the northwestern U.S. (T. Swem and C. McIntyre pers. comm.). Similarly, for those species that migrate into Central and South America (e.g., Peregrine Falcons, *F. peregrinus* or Swainson's Hawks, *B. swainsoni*) all flyways essentially merge in southern Mexico near the Isthmus of Tehuantepec (Bildstein and Zalles 2001). Thus, the delineation of regional flyways in western North America is probably most relevant for distinguishing subpopulations of birds that originate south of mainland Alaska and that winter north of Central America. Furthermore, while migration counts along the three flyways may generally reflect the dynamics of distinct subpopulations responding to unique sets of environmental factors, large landscape-scale events in southern Mexico or the far northwest may influence counts along multiple flyways.

Our description of regional flyways is based primarily on data for Sharp-shinned and Cooper's Hawks, which together comprised 77% of the foreign encounters/recaptures and 91% of the recaptures considered. Nevertheless, the results for our other three study species indicated conformity to the patterns shown for the two accipiters; therefore, we believe the flyway descriptions we propose also apply to other species.

Sharp-shinned Hawk. The range of summer and winter latitudes of Rocky Mountain and Intermountain Sharp-shinned Hawks were most similar to those of migrants encountered at other inland as opposed to coastal migration sites. Rocky Mountain and Intermountain migrants summered as far north as Alaska and wintered primarily along the west coast of Mexico. Migrants from the western Great Lakes region also frequently wintered in southern Mexico (Evans and Rosenfield 1985, Carpenter et al. 1990). Thus, prominent factors operating in southern Mexico (e.g., large-scale habitat changes or heavy shooting pressure) could conceivably affect breeding Sharp-shinned Hawks from across much of interior North America.

Oregon migrants showed similar latitudinal ranges as birds from other coastal states. For example, migrants from the Marin Headlands of California typically traveled relatively short distances from breeding areas in the Pacific Northwest to wintering areas in Oregon and California (Scheuermann 1996, 1997, Acuff 1998, 1999). Similarly, Atlantic Coast (Clark 1985) and eastern Great Lakes (Duncan 1982, Holt 1991) migrants tended to winter in the southeastern U.S.

Cooper's Hawk. Rocky Mountain and Intermountain migrants wintered in concentrations along the Pacific Coast from Sinaloa to Jalisco. Breeding birds from eastern Oregon showed a similar winter range (Henny 1990), whereas migrants banded in coastal California generally remained north of Baja California (Scheuermann 1997) and migrants from the eastern Great Lakes tended to remain in the southern Midwest and southeastern U.S. (Duncan 1981, Holt 1991). Thus, Rocky Mountain and Intermountain Cooper's Hawks likely respond to different environmental factors than Pacific Coast or eastern birds. For example, shooting was a commonly reported cause of winter encounters in our study and that of Henny (1990), whereas Scheuermann (1996, 1997), Acuff (1998, 1999), and Holt (1991) rarely reported shooting as a cause of mortality.

Northern Goshawk. The few foreign encounters we documented corroborate the notion that goshawk movements typically are restricted to dispersal and short-distance migration (Squires and Reynolds 1997). This suggests that migration counts of Northern Goshawks generally reflect relatively localized movements (i.e., 400–500 km or less) and that counts of HY birds may therefore serve as an indicator of regional productivity. This possibility must be tempered, however, with recognition that about every 10 years, goshawks from the northern part of the species' range migrate *en masse* much farther south than usual due to crashes of available prey (Mueller et al. 1977). In fact, our most distant foreign encounter (1200 km from the banding site near Shining Bank, Alberta) involved a Nevada migrant banded as an adult during the 1983 irruption episode.

American Kestrel. Rocky Mountain and Intermountain migrants summered as far north as the Yukon Territory and wintered primarily in far southwestern Mexico. Similar winter ranges were documented for birds banded in the Sierra Nevada range and farther east (Bloom 1985) and for breeding birds from Idaho and eastern Oregon and Washington (Henny and Brady 1994). In contrast, 90% of foreign encounters with birds banded in coastal California were located within 16 km of the original banding location, regardless of season (Bloom 1985). These patterns lend additional support for the hypothesis that the Sierra Nevada and Cascade ranges constitute a biogeographic boundary between the relatively constrained Pacific Coast Flyway and extensive interior flyways.

Similar to Cooper's Hawks, Rocky Mountain and Intermountain kestrels wintered substantially farther south than conspecifics migrating through the eastern Great Lakes (Duncan 1985) and along the Atlantic Coast (Layne 1982). Thus, American Kestrels from the western and eastern halves of the continent likely respond to different sets of environmental pressures.

Red-tailed Hawk. Attempts to partition populations into Rocky Mountain, Intermountain, and Pacific Coast migrants were the most problematic for this species. The summer and winter ranges and migration/dispersal routes of migrants from New Mexico, Nevada, and Oregon often overlapped. For example, Nevada migrants wintered in central New Mexico and along the Texas coast, while New Mexico migrants were later encountered in northern Nevada. Bloom (1985) also documented several cases of extensive juvenile dispersal to the north and east from southern California. Similarly, nestlings banded in southern Idaho dispersed in many directions, including toward southern California, northeastern Idaho, southeastern New Mexico, and southern Guatemala (Steenhof et al. 1984). Nevertheless, satellite tracking has shown that 12 Red-tailed Hawks (one HY, 11 SY or older) outfitted during autumn migration in New Mexico and Nevada all followed southerly routes to wintering grounds in Mexico (HWI unpubl. data). Moreover, three adult birds outfitted in Nevada showed high fidelity to individual migration pathways, winter locations, and summer territories in British Columbia, Montana, and Idaho over a 2.5-yr period. Thus, it appears that Red-tailed Hawks banded in the Rocky Mountains and Intermountain West tend to migrate/disperse south in autumn, but specific bearings and distances may vary, especially with regard to the first-year dispersal of juvenile birds. Similarly, although Bloom (1985) showed that juvenile dispersal from southern California could be extensive, Red-tailed Hawks banded during autumn migration along the central coast of California may subsequently move in almost any direction but tend to remain along the Pacific Coast (Scheuermann 1996, 1997, Acuff 1998, 1999).

Similar to Cooper's Hawks and kestrels, Rocky Mountain and Intermountain Red-tailed Hawks tended to winter farther south and show little longitudinal overlap with migrants from the Great Plains and farther east (Houston 1967, Holt and Frock 1980, Brinker and Erdman 1985).

Sex-biased Encounter Probabilities. For four sexually-dimorphic species, foreign encounters of females occurred more often than expected given sex ratios at banding. The same pattern applied to migrant Sharp-shinned and Cooper's Hawks from the Great Lakes (Duncan 1981, 1982, Evans and Rosenfield 1985, Holt 1991) and to Sharp-shinned Hawks along the Atlantic Coast (Clark 1985). Clark (1985) and Duncan (1982) suggested that this pattern results from competitively dominant females occupying more open habitats than males during winter, a pattern documented for Eurasian Sparrowhawks (*A. nisus*; Newton 1979). These tendencies may cause females to encounter human-related trouble more often and increase the probability that humans will discover dead or injured females. This scenario may apply to kestrels also (Ardia and Bildstein 1997).

Differential Migration Distance. Small sample sizes limited our ability to detect significant differential migration. Nevertheless, winter latitude tended to increase with age for four species, and male Cooper's Hawks and American Kestrels tended to winter farther north than females of the same age. Moreover, the winter distribution pattern for

Cooper's Hawks appeared consistent with the pattern of differential timing documented by DeLong and Hoffman (1999) for Manzano and Goshute migrants (i.e., autumn passage sequence: juvenile females, juvenile males, adult females, and adult males). Thus, our results appear most consistent with predictions of the foraging-efficiency (Rosenfield and Evans 1980) and arrival-time (Myers 1981) hypotheses, but not consistent with predictions of the body-size hypothesis (Ketterson and Nolan 1976). The apparent inconsistency in results for SY versus ASY female Sharp-shinned Hawks may reflect the fact that, compared to Cooper's and Red-tailed Hawks, sharp-shins often begin breeding in their second year (Johnsgard 1990). Thus, this apparent anomaly may favor the arrival-time hypothesis over the foraging-efficiency hypothesis for this species. Relative to the behavioral or social-dominance hypothesis (Gauthreaux 1978, 1985, Newton 1979, Clark 1985), our results appear equivocal. They are consistent with the age-related prediction of the hypothesis (dominant adults winter closer than immature birds of the same sex), but not the sex-related prediction (larger, dominant females should winter closer to the breeding grounds than smaller males of the same age).

Potential Biases. There are several potential biases associated with describing raptor movements based on band encounters. One potential bias may derive from species, sex, or age-related variation in susceptibility of migrants to be captured using live lures (Gorney et al. 1999). Another concerns the higher probability of recovering females; however, if females indeed tend to migrate farther south than males, this factor would not bias delineations of overall flyway dimensions. A third may derive from the positive correlation between the probability of recovery and the density of human habitation (Nichols and Kaiser 1999), which the dearth of summer recoveries, especially north of southern Canada, clearly illustrates (Fig. 1). Thus, we look forward to advances in methodology such as satellite telemetry (Brodeur et al. 1996) and stable-isotope analysis (Meehan et al. 2001), which should further improve our understanding of raptor movements in the western hemisphere and elsewhere.

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