Dispersal Movements of Juvenile Mexican Spotted Owls (*Strix occidentalis lucida*) in New Mexico

David P. Arsenault[1], Angela Hodgson[1,2] and Peter B. Stacey[1]

Abstract.—Tail-mounted radio transmitters were attached to 12 juvenile and 3 sub-adult (yearling) Mexican Spotted Owls (*Strix occidentalis lucida*) in southwestern New Mexico from 1993 to 1996. Most juveniles dispersed from their natal territories during September. Intervals between dispersal of siblings ranged from 3 to more than 15 days. Juveniles exhibited two types of dispersing behavior; moving rapidly across the landscape (up to 11.3 km/night) and extensive local exploration. Two juveniles moved between separate mountain ranges and crossed at least 25 km of grassland and pinon/juniper (*Pinus*/*Juniperus* spp.) savanna habitat, suggesting that isolated populations in the southwest U.S. could function as a metapopulation. During dispersal juveniles were found to roost in habitat unlike that normally used by adults, including open ponderosa pine (*Pinus ponderosa*) and pinon/juniper habitat. The three sub-adult females paired temporarily with adult males in their first summer, but then left in the fall, suggesting that dispersal can continue through an owl's second year.

Dispersal is the movement an individual makes from its birth site to first breeding site (natal dispersal) or movement between successive breeding sites (breeding dispersal; Greenwood 1980). Dispersal can play an important role in population dynamics, and is known to have a large influence on the genetic structure of populations (Brookes and Butlin 1994, Slatkin 1985, Stacey and Taper 1992, Verhulst *et al.* unpubl. data, Wright 1951, Zink and Dittman 1993). Therefore, characterizing dispersal behavior is critical to understanding the demography and population structure of species, especially the persistence of rare and endangered species.

The Mexican Spotted Owl (*Strix occidentalis lucida*) is found in forested mountain and deep canyon terrain throughout the southwest U.S. and into Mexico (Ganey and Balda 1989). In southwestern New Mexico, spotted owls roost in riparian/canyon bottom or mixed conifer/oak habitats (Hodgson and Stacey 1997). Nests are located in caves or large trees with high canopy closure, most often Douglas-fir (*Pseudotsuga menziesii*; see also Seamans and Gutierrez 1995). Adult spotted owls have high breeding site fidelity with only a few cases of breeding dispersal observed (Gutierrez *et al.* 1996). Therefore, the majority of individuals that disperse are juveniles.

There is evidence that the Mexican Spotted Owl's distribution was once more continuous, occupying lowland riparian forests dominated by cottonwoods (*Populus* spp.) (Bendire 1892, Phillips *et al.* 1964, Woodhouse 1853). Spotted owl habitat is presently fragmented in New Mexico, and owls are restricted to the higher elevations of isolated mountain ranges (fig. 1). Furthermore, annual variation in reproductive success is high, with few or no young produced in some years (Miller 1989, Forsman *et al.* 1984, this study). Demographic models predict that small, isolated populations with high variance in reproductive success should quickly go extinct, unless the populations are connected to other populations by dispersal, thus forming a larger metapopulation (Gilpin

[1] Department of Environmental and Resource Sciences, University of Nevada-Reno, Reno, NV 89557.
[2] Current address: International programs, Wildlife Conservation Society, 185th Street and Southern Blvd., Bronx, NY 10460.

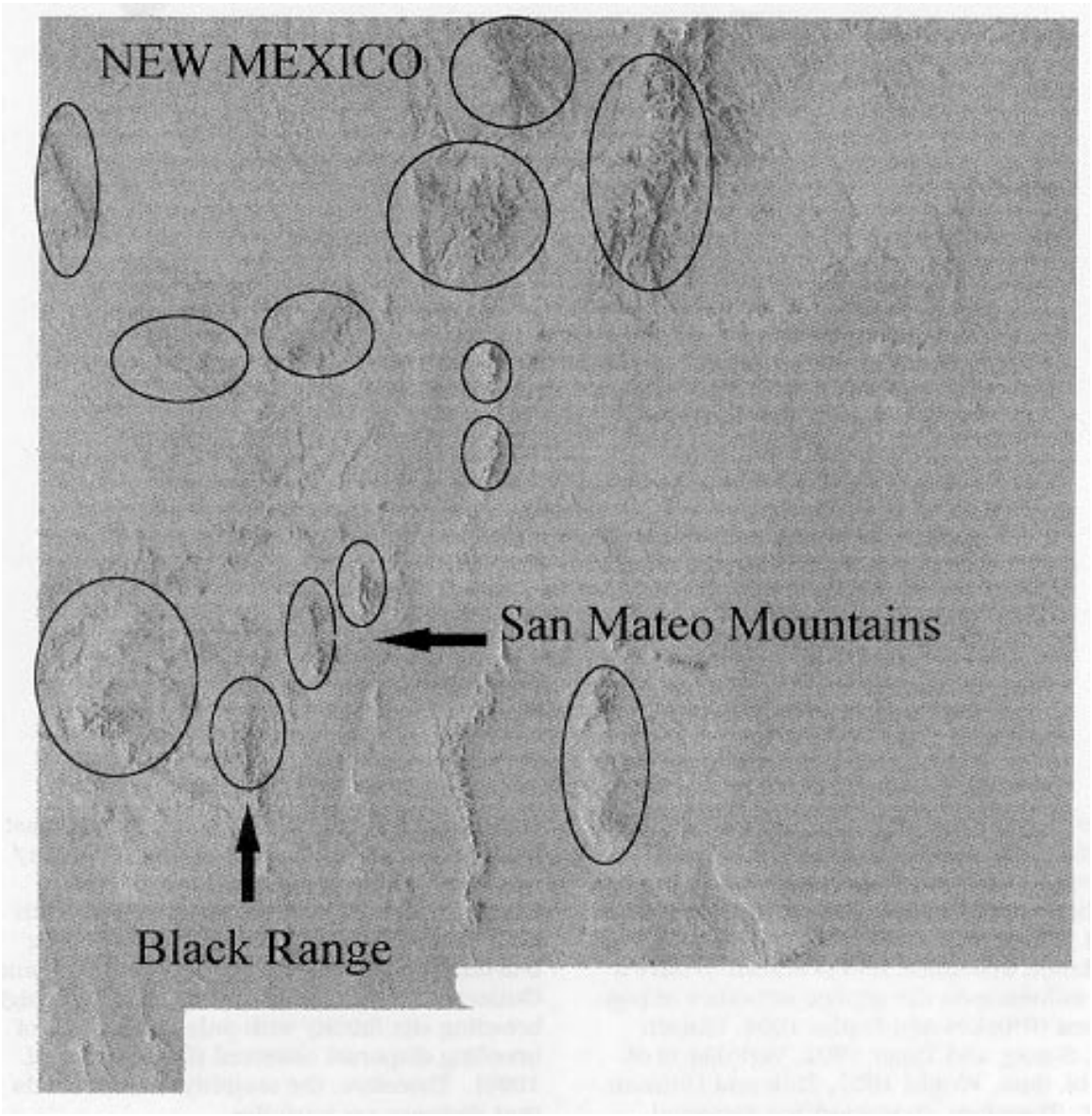

Figure 1.—*The fragmented distribution of the Mexican Spotted Owl in New Mexico, occurring within the circled mountain ranges, and the location of the Black Range and San Mateo Mountains. Map scale is 1:3,520,000.*

and Hanski 1991, Levins 1969, Stacey and Taper 1992, Stacey *et al.* 1997). If Spotted Owl populations in isolated mountain ranges are connected, owls must disperse across large areas of unsuitable habitat, including grassland and pinon/juniper (*Pinus*/*Juniperus* spp.) savanna habitat, to reach other populations. Here we consider initial dispersal movements of juvenile Mexican Spotted Owls away from their natal areas.

STUDY AREA

We studied dispersal of the Mexican Spotted Owl in the Black Range and San Mateo Mountains of southwestern New Mexico (fig. 1). The Black Range runs 90 km north-south and is located in the Gila National Forest, 60 km west of Truth or Consequences, New Mexico. The San Mateo Mountains run 55 km north-south and are located in the Cibola National

Forest, 50 km southwest of Socorro, New Mexico. These mountain ranges contain few roads and include three National Forest Service Wilderness Areas. They are separated from each other by approximately 20-40 km of grassland and pinon/juniper savanna habitat characterized by widely scattered low trees in a grass matrix (Dick-Peddie 1993). The topography within the mountain ranges is dominated by high mesas, mountain peaks and deep forested canyons. Spruce-fir forest is found on the high mountain peaks, usually above 2,800 m. Mixed conifer forests consisting of Douglas-fir, white fir (*Abeis concolor*), ponderosa pine, southwestern white pine (*Pinus strobiformis*), aspen (*Populus tremuloides*) and often a component of gambel oak (*Quercus gambelii*) are usually found on north and east facing slopes at middle elevations of about 2,400-3,100 m. Gambel oak and remnant narrowleaf cottonwood (*Populus angustifolia*) are found in most canyon bottoms. Warm and dry woodlands consisting primarily of ponderosa pine, Colorado pinyon (*Pinus edulis*), alligator juniper (*Juniperus deppeana*), one-seed juniper (*Juniperus monosperma*), and gray oak (*Q. Grisea*) are found at elevations generally below 2,600 m, on south and west-facing mountain slopes, and on ridge-tops and mesas (Dick-Peddie 1993).

METHODS

Nocturnal calling techniques (Forsman 1983) were used to detect Mexican Spotted Owls from 1993 to 1996. Surveys were done from April through August by walking along canyon bottoms, with potentially suitable habitat, and regularly imitating a spotted owl four-note location call. Roost trees and nests were located during the day by searching areas where owls were detected during surveys. Owl pairs were determined to be nesting by repeated observations, particularly listening for female contact whistles and juvenile vocalizations from nests at dawn and dusk. Owls were captured with a Bal-chatri trap baited with mice or a 3.4 m noose pole (Forsman 1983). Each captured owl was fitted with a combination of a USFWS aluminum band on one leg and a plastic color band on the other. Wing chord, retrix length, and weight were taken, plumage characteristics noted and about 200 ul of blood taken from the brachial artery. Owls were sexed by behavior, vocalizations, and weight. Juveniles cannot be sexed with these criteria. Age was determined to be juvenile, sub-adult or adult by plumage characteristics (Forsman 1981). A sub-adult can be identified by white tipped retrices which are maintained until approximately 26 months old.

Tail-mounted radio transmitters (5 g or 7.5 g; Holohil Systems, Ltd., Woodlawn, Ontario, Canada) with a battery life of approximately 12 to 18 months were used. These were attached to the underside of the center retrices of juveniles no sooner than 50 days post-fledging when their retrices reached at least 185 cm in length. A TRX 1000S radio-telemetry receiver and a three element Yagi antennae (Wildlife Materials, Inc, Carbondale, IL) were used to track juveniles from the ground. Prior to dispersal, juveniles were located one to seven times per week at their roost sites as well as periodically at night while foraging, depending on the accessibility of their locations. Home range sizes of juveniles prior to dispersal were determined using the minimum convex polygon method with Calhome, a home range analysis program (U.S. Forest Service, Pacific Southwest Research Station, Fresno, CA). Juveniles were located as frequently as possible once dispersal began, facilitated by two telemetry flights in 1993, one in 1994, and four in 1996 (kindly provided by U.S. Fish and Wildlife Service in 1996). Aerial surveys consisted of flying transects throughout the study area while scanning for frequencies either manually or with a ATS R2100 automatic scanning receiver (Advanced Telemetry Systems, Inc., Isanti, MN) from an aircraft equipped with two wing antennas and an antennae switching box.

RESULTS

Observations of juvenile dispersal behavior reported here were from five juveniles from three nests in 1993 and seven juveniles from four nests in 1996. Reproduction in the study area was high in 1993 (8 of 10 (80 percent) known owl pairs nested), low in 1994 and 1995 (1 of 13 (8 percent) and 4 of 15 (27 percent) known pairs nested, respectively) and moderate in 1996 (10 of 22 (45 percent) known pairs nested).

Behavior Prior to Dispersal

Juveniles typically fledged during the first few weeks of June. They generally roosted within 50 m of one or both parents for about 2 months after fledging (27 of 29 (93 percent) roosts prior to August 15, n = 3 individuals)

and then only seldomly roosted within 50 m of one or both parents during the month prior to dispersal (4 of 24 (17 percent) roosts after August 15, n = 3 individuals). Sibling pairs usually roosted in the same tree as each other, or within close proximity (< 50 m; 33 of 43 (77 percent) roosts, n = 4 pairs), until just prior to dispersal.

The mean observed home range size of juveniles before dispersal was 61.8 ha (n = 7, range = 11.5 - 223.0 ha; table 1), considerably less than the area used by adults. The minimum mean home range size of four adult pairs radio-tagged in the San Mateos was 261.4 ha, calculated from data collected only during the breeding season. Other studies of the Mexican Spotted Owl report home range sizes of 381 to 1551 ha (p. 27, USDI 1995). The area used by juveniles increases sharply in September, just prior to dispersal from the natal area (fig. 2). All radio tagged juveniles are known to have survived to disperse except for J630 which dropped its transmitter in its natal area sometime before December 14, 1996. This juvenile was located on the edge of its parents territory on September 21, prior to which it used a home range of 24.3 ha. J630 was not detected anywhere after September 21, 3 days after its sibling J830 had dispersed, until it was found back on the natal area again on September 28. Apparently this juvenile had made an exploratory move and then returned to its natal territory, although the extent of this move is

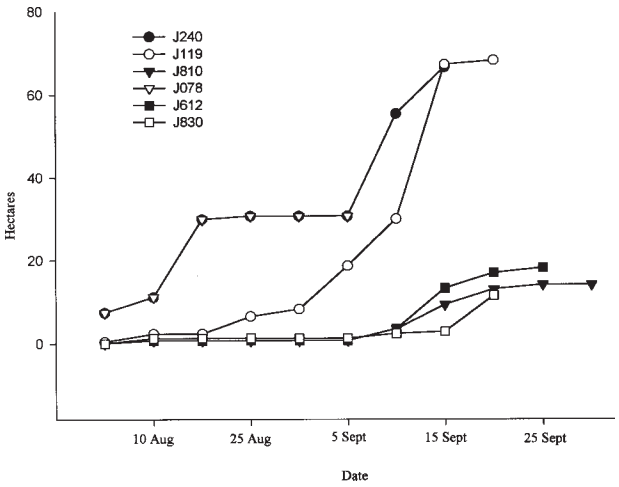

Figure 2.—*Change in the total area used by juvenile Mexican Spotted Owls in New Mexico prior to dispersal.*

Table 1.—*Dispersal dates of juvenile Mexican Spotted Owls in New Mexico.*

Owl	Last date located in natal area	Date known to have dispersed	Home range size (ha) prior to dispersal	Days between dispersal of siblings
1993				
J430[1]	August 24	September 10	NA	8-23
J078[2]	September 10	September 11	30.6	5-7
J240[2]	September 15	September 18	66.7	5-7
J449[1]	September 16	September 23	NA	8-23
J119	September 21	September 25	68.3	No sibling
1996				
J571[3]	August 14	September 10	NA	4-30
J689[3]	September 13	September 15	NA	4-30
J670	September 13	September 15	NA	No sibling
J830[4]	September 17	September 19	11.5	16-?
J612[5]	September 25	September 26	18.1	3
J810[5]	September 28	September 29	14.1	3
J630[4]	October 3	Unknown[6]	223.0	16-?
			61.8 (mean)	

[1] Water Spring siblings.
[2] Apache siblings.
[3] Taylor Cabin siblings.
[4] Limestone siblings.
[5] Escondido siblings.
[6] Transmitter dropped in natal area sometime before December 3, 1996

unknown. J630 remained in the vicinity of its natal area until at least October 3, during which time its home range size increased to 223 ha (fig. 3). After this time its fate is unknown. Our observations suggest that juvenile Mexican Spotted Owl dispersal is preceded by a sudden increase in home range as well as by siblings roosting apart more frequently.

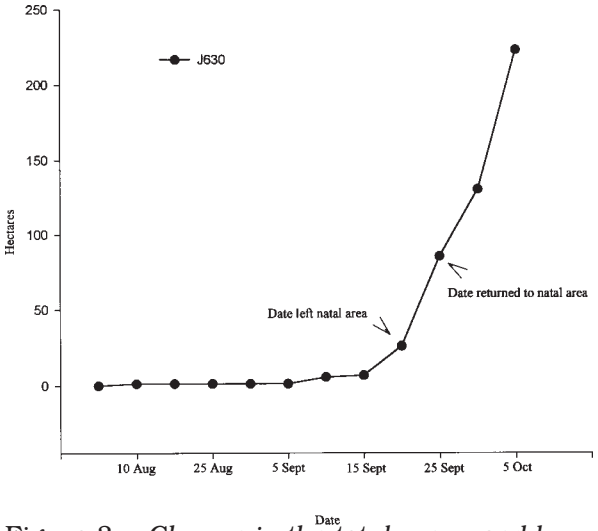

Figure 3.—*Change in the total area used by J630 before and after its exploratory move away from the natal area in New Mexico.*

Juvenile Dispersal

Nine of the 12 juveniles are known to have dispersed from September 10 to September 29 (table 1); two (J430 and J571) dispersed either during late August or early September (table 1). The length of time that elapsed between the dispersal of siblings was 3 to more than 15 days (table 1). Once juveniles dispersed from their natal areas they moved rapidly across the landscape. In their first week of dispersal, juveniles moved from 9.7 to 44.8 km traveling up to 11.3 km in 1 day (table 2). Juveniles were observed traveling through up to three occupied owl territories in 1 night.

After these initial rapid movements juveniles were observed remaining in the area they had traveled to for 3 to 16 days, before making subsequent long-distance movements. One juvenile (J612) moved 14.5 km southeast from its natal area in its first 2 nights of dispersal. Thereafter it remained in the same area for at least 1 week. This juvenile's transmitter was found on the ground in December, 22.5 km south of its last known location (fig. 4). Another juvenile (J689) moved 11.3 km east to Stiver Well in the first 2 nights after leaving its natal area. This juvenile remained in this area for 3 days, made a second movement of 11.1 km to Mineral Creek where it remained for 4 days, and then returned to Stiver Well for another 6 days. J689 then moved 6.4 km southeast, where it stayed for 1 day before disappearing. This juvenile was found December 18, 22 km southeast of its last known location (fig. 4). A third juvenile (J571) moved 12.9 km from its natal area to Diamond Creek, where it remained for 16 days before continuing to disperse four more km southwest to a location where it dropped its transmitter (fig. 4). In summary, juveniles exhibited two types of dispersal behavior, moving rapidly across the landscape and extensive local exploration.

The mean straight line distance that juveniles were observed moving from their nest site to their last known location was 21.8 km, and ranged from 1.3 km (J630 which dropped its transmitter in its natal area) to 57.6 km (table 3). Five juveniles dropped their radio transmitters, six juveniles were "lost" (undetected) 35 to 331 days (mean = 100) after their transmitters were attached and one juvenile's location was known as of the last telemetry

Table 2.—*Distances moved by juvenile Mexican Spotted Owls in the first week of dispersal from their natal areas in New Mexico.*

Owl	Greatest distance observed moving in one night (km)	Total distance moved during first week of dispersal (km)	Average distance moved per night during first week of dispersal (km)
J689	11.3	19.4	2.8
J119	11.2	44.8	11.2 (4 days)
J810	10.5	14.5	7.3 (2 days)
J612	8.9	16.3	2.3
J830	3.8	26.6	3.8

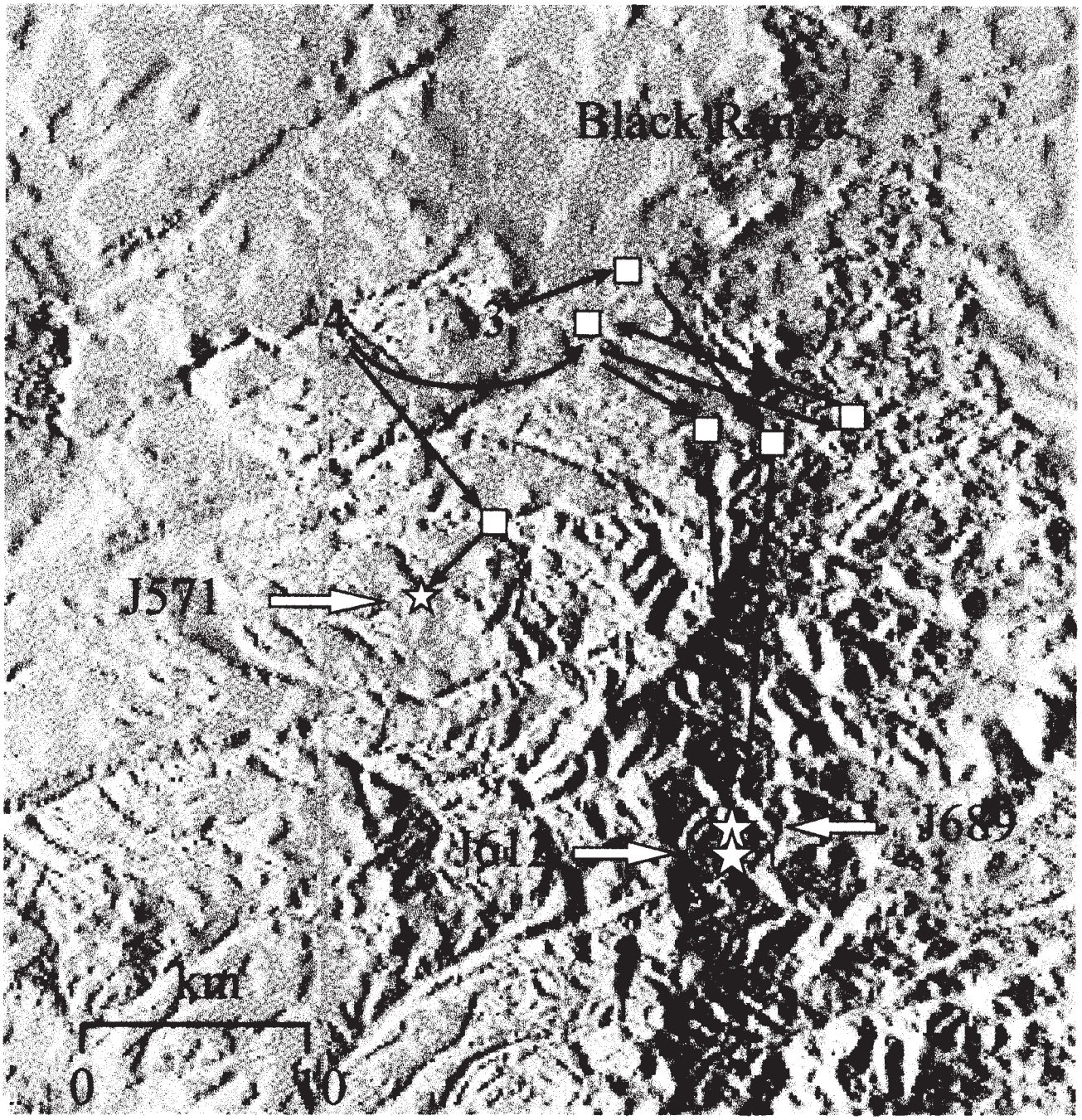

Figure 4.—*Dispersal of three juvenile Mexican Spotted Owls in the Black Range, New Mexico. Natal areas indicated by numbers: 3 = J612, and 4 = J571 and J689. □= locations of dispersing juveniles. ☆ = last known locations of dispersing juveniles.*

flight on December 18, 1996 (table 3). Five juveniles were observed moving only within the San Mateo Mountains and five juveniles were observed moving only within the Black Range. Two juveniles crossed 20-40 km of grassland and pinon/juniper savanna habitat from the San Mateo Mountains to the Black Range. One of these juveniles (J119) flew 44.8 km from the San Mateo Mountains to the Black Range in only 4 days, thus moving a minimum of 11.2 km/night (fig. 5). The other (J430) first moved within the San Mateo Mountains 15 km southwest of its natal area. Subsequently this juvenile moved 31 km southeast to the northern Black Range. A second, and final, location for this juvenile in the Black Range was obtained 22 km south of the previous location (fig. 5).

Table 3.—*Observed dispersal distances by juvenile Mexican Spotted Owls in New Mexico.*

Owl	Date radio-tagged	Last date detected	Straight line distance (km) to last known location	Status
J630	08/02/96	10/03/96 (62 days)[1]	1.3	Dropped transmitter
J240	07/03/93	11/16/93 (135 days)	6.8	Undetected
J670	07/26/96	09/30/96 (65 days)	8.4	Dropped transmitter
J078	07/02/93	11/16/93 (136 days)	11.6	Undetected
J810	07/23/96	09/30/96 (68 days)	15.5	Undetected
J571	08/10/96	09/30/96 (51 days)	18.0	Dropped transmitter
J449	08/05/93	07/01/94 (331 days)	18.4	Dropped transmitter
J830	08/02/96	09/30/96 (59 days)	25.0	Dropped transmitter
J612	08/07/96	10/04/96 (58 days)	32.0	Dropped transmitter
J689	07/24/96	12/18/96 (146 days)	32.2	Detected last effort
J119	08/21/93	09/25/93 (35 days)	44.8	Undetected
J430	08/05/93	09/26/93 (52 days)	57.6	Undetected
Mean		(99.8 days)	22.6	

[1] Number of days between date transmitted and last date detected.

Juveniles were found roosting in habitat unlike that normally used by adults. Five of the seven juveniles radio tagged in 1996 were observed roosting in open ponderosa pine forest on several occasions prior to and during dispersal. Another juvenile (J449) was found November 17 roosting on the ground under a pinon tree near the top of a dry, west facing slope of pinon/juniper woodland. This juvenile was found again in July 1994. It had moved within the same drainage from a lower elevation site (2,256 m), with little canopy closure, to a higher elevation site (2,658 m) with greater canopy closure.

Transects were flown over the Black Range and San Mateo Mountains during two telemetry flights in September and November 1993, one in March 1994, one in March 1996 and three in September and December 1996. No juveniles have been tracked from birth site to first breeding site so natal dispersal has not been documented. In our entire study of spotted owl demography in New Mexico, no banded juveniles (n = 36) have been observed breeding. No radio-tagged juveniles have been found dead.

Sub-adult Dispersal

Observations of sub-adults were from three owls in 1994 and one in 1995. Early in the breeding season, three radio-tagged sub-adults were paired with adult males and were found regularly roosting with their males from May through July, however pairs were not observed attempting to breed. In August, pairs began roosting apart, with the adult males remaining within the established territory and sub-adult females roosting up to 9 km from the roosting area of their mate. Two sub-adults roosted 9 km and 5 km from their mates, and then returned to roost with them for approximately 2 weeks before leaving the territory again. At the end of September these two sub-adults could no longer be located during ground searches of the surrounding vicinity. The third sub-adult female also made forays of up to 4 km from the roosting area of the adult male during August and September. The following April, after an extensive ground search, this sub-adult also was not located and its previous mate had paired with a new adult female.

A female radio-tagged as a juvenile (J449) in 1993 was also observed as a sub-adult in 1994. She had moved 18.4 km from her natal area to a location near a spring at 2,800 m elevation within spruce-fir habitat. This location was higher in elevation than any other owl we have located and could be considered sub-optimal. She stayed in this area for the summer and was not located there in 1995.

DISCUSSION

The number of Mexican Spotted Owl pairs attempting to breed in our study area varied greatly from year to year (from 8 to 80 percent). High reproductive variance has also been

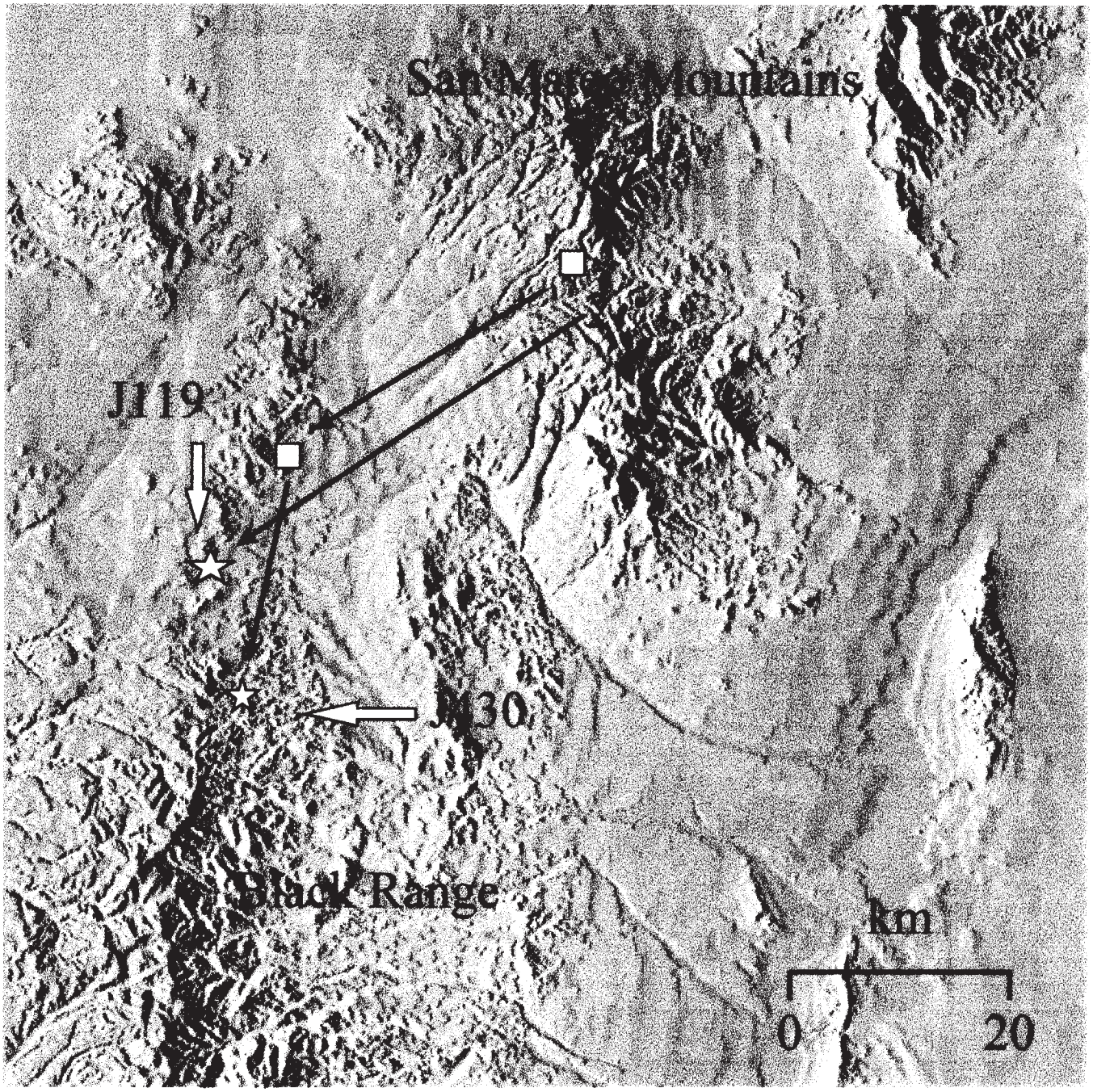

Figure 5.—*Dispersal of two juvenile Mexican Spotted Owls from the San Mateo Mountains to the Black Range, New Mexico. Natal areas indicated by numbers: 1= J430, and 2= J119.□= locations of dispersing juveniles. ☆= last known locations of dispersing juveniles.*

observed in the Northern Spotted Owl (*S.O. caurina*) (from 14 to 89 percent of pairs attempting to breed; Forsman *et al*. 1984, Miller 1989) and the California Spotted Owl (S.O. *occidentalis*) (Gutierrez *et al*. 1985). Demographic models predict that small populations with high variance in reproductive success, such as the spotted owl, should quickly go extinct unless individuals disperse between isolated populations, thus forming a metapopulation (e.g., Stacey and Taper 1992, Stacey *et al.* 1997). This may be true of spotted owl populations in the southwest U.S. which are often small and restricted to isolated mountain ranges. We observed two individuals which dispersed from the San Mateo

Mountains across 20-40 km of unsuitable habitat to the Black Range. These types of dispersal events may be fairly common in the southwest U.S., connecting otherwise isolated mountain ranges which together may function as a metapopulation.

The Recovery Plan for the Mexican Spotted Owl (USDI Fish and Wildlife Service 1995) determined that nearly all isolated habitat patches defined as mixed conifer or ponderosa pine (although not preferred Mexican Spotted Owl habitat) in New Mexico, and throughout the Southwest, could be reached if an owl could disperse at least 60 km between isolated habitat patches. The movement distances of juvenile Spotted Owls given in the literature and the findings of this study indicate that Mexican Spotted Owls are capable of dispersing between nearly all isolated habitat patches in New Mexico and the Southwest. Whether they do or not is unknown except for our observations of juveniles moving between the Black Range and San Mateo Mountains in southwestern New Mexico.

Juvenile Mexican Spotted Owls most likely disperse far greater distances than we were able to detect during this study. Of 36 juveniles banded we have not resighted or recaptured any of them in other mountain ranges. This suggests that either juveniles are not detected as adults (unlikely if breeding), they die, or they move beyond our study area. The distances we observed dispersing radio-marked juveniles moving was 1.3 km to 57.6 km, similar to what other studies have reported (22 to 145 km for the Mexican Spotted Owl: p. 33 USDI Fish and Wildlife Service 1995, Gutierrez *et al.* 1996; 22 to 99 km for the California Spotted Owl: Gutierrez *et al*. 1985; and 3.2 to 78 km for the Northern Spotted Owl: Miller 1989). However, these numbers are only distances to the last known location of juveniles and not actual natal dispersal distances. In a technical assessment of the California Spotted Owl (Verner *et al*. 1992), the results of all radio-tracking studies of dispersing juvenile Northern and California Spotted Owls were compiled and only one juvenile out of 56 was ever found as a member of a mated pair, but it never nested. Sixty-eight percent of the juveniles died, 27 percent of their transmitters failed and 5 percent disappeared. Furthermore, our observations of sub-adult movements indicate that dispersal may continue into some spotted owls' second year making radio-tracking to breeding sites even more challenging. These difficulties make the observation of natal dispersal to a first breeding site difficult and rare.

The most recent demographic models being used to predict the viability of the spotted owl are spatially defined, considering dispersal both within and between clusters of suitable habitat to simulate fragmentation and predict optimal reserve designs (Doak 1989; Lamberson *et al.* 1992, 1994). Many of these models incorporate the ideas presented by Murray (1967) that competition for resources determines dispersal distance and individuals are most likely to settle on the first available breeding site they encounter. In these models a juvenile first searches her (only females are considered) natal cluster for an available site and if she is not successful is forced to disperse between clusters. Our results indicate that juvenile owls seem not only to be very efficient at searching the landscape (moving through up to three owl territories and up to 11.3 km in one night), but they also appear to keep moving past suitable and currently unoccupied spotted owl territories. Additionally, J119 was observed crossing over at least 25 km of unsuitable habitat between the Black Range and San Mateo Mountains moving a distance of 44.8 km in less than 4 days after dispersing from its natal area. This owl apparently did not search for available habitat in the San Mateo Mountains, but rather moved immediately to a new mountain range. Furthermore, if juveniles chose to occupy the available habitat around their natal areas we would expect that more banded juveniles would be found nesting within large study areas, yet in New Mexico these instances are rare. These observations suggest that juvenile spotted owls may not settle on the first available and suitable location they find, because of a tendency to continue dispersal, and that their ability to search the landscape may be very efficient. This type of juvenile search pattern should be included in any future model of population viability for the Mexican Spotted Owl in the Southwest.

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LITERATURE CITED

Bendire, C.E. 1892. Life histories of North American birds. U.S. National Museum. Special Bulletin 1.

Brookes, M.I.; Butlin, R.K. 1994. Population structure in the small ermine moth *Yponomeuta padellus*: an estimate of male dispersal. Ecological Entomology. 19: 97-107.

Dick-Peddie, William A. 1993. New Mexico vegetation, past, present and future. Albuquerque, NM: University of New Mexico Press.

Doak, D. 1989. Spotted Owls and old growth logging in the Pacific Northwest. Conservation Biology. 3: 389-396.

Forsman. E.D. 1981. Molt of the Spotted Owl. Auk. 98: 735-742.

Forsman, E.D. 1983. Methods and materials for locating and studying Spotted Owls. Gen. Tech. Rep. PNW-162. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Forsman, E.D.; Meslow, E.C.; Wight, H.M. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildlife Monograph. 87: 1-64.

Ganey, J.L.; Balda, R.P. 1989. Distribution and habitat use of Mexican Spotted Owls in Arizona. Condor. 91: 355-361.

Gilpin, M.; Hanski, I. 1991. Metapopulation dynamics: empirical and theoretical investigations. San Diego, CA: Academic Press.

Greenwood, Paul J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior. 28: 1140-1162.

Gutierrez, R.J.; Seamans, M.E.; Peery, M.Z. 1996. Intermountain movement by Mexican Spotted Owls (*Strix occidentalis lucida*). Great Basin Naturalist. 56: 87-89.

Gutierrez, R.J.; Franklin, A.B.; LaHaye, W.; Meretsky, V.J.; Ward, J.P. 1985. Juvenile Spotted Owl dispersal in northwestern California: preliminary results. In: Gutierrez, R.J.; Carey, A.B., tech. eds. Ecology and management of the Spotted Owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 60-65.

Hodgson, A.; Stacey, P.B. 1997. Habitat use of Mexican Spotted Owls in New Mexico. Submitted.

Lamberson, R.H.; McKelvey, K.; Noon, B.R.; Voss, C. 1992. The effects of varying dispersal capabilities on the population dynamics of the Northern Spotted Owl. Conservation Biology. 6: 505-512.

Lamberson, R.H.; Noon, B.R.; Voss, C.; McKelvey, K.S. 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. Conservation Biology. 8: 185-195.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America. 15: 237-240.

Miller, G.S. 1989. Dispersal of juvenile Northern Spotted Owls in western Oregon. Corvallis, OR: Oregon State University. 139 p. M.S. thesis.

Murray, B.G. 1967. Dispersal in vertebrates. Ecology. 48: 975-978.

Phillips, A.R.: Marshall, J.T., Jr.; Monson, G. 1964. The birds of Arizona. Tucson, AZ: University of Arizona Press.

Seamans, M.E.; Gutierrez, R.J. 1995. Breeding habitat of the Mexican Spotted Owl in the Tularosa Mountains, New Mexico. Condor. 97: 944-952.

Slatkin, S. 1985. Gene flow in natural populations. Annual Review of Ecology Systematics. 16: 393-430.

Stacey, P.B.; Taper, M. 1992. Environmental variation and the persistence of small populations. Ecological Applications. 2: 18-29.

Stacey, P.B.; Johnson, V.A.; Taper, M.L. 1997. Migration within metapopulations: the impact upon local population dynamics. In: Hanski, I.; Gilpin, M., eds. Metapopulation biology: ecology, genetics and evolution. New York, NY: Academic Press: 267-291.

U.S. Department of Interior, Fish and Wildlife Service. 1995. Recovery plan for the Mexican Spotted Owl: Vol. I. Albuquerque, NM. 172 p.

Verner, J.; Gutierrez, R.J.; Gould, G.I., Jr. 1992. Chapter 4. The California Spotted Owl: general biology and ecological relations. In: Verner, J.; McKelvey, K.S.; Noon, B.R.; Gutierrez, R.J.; Gould, G.I., Jr.; Beck, T.W., tech. coords. The California Spotted Owl: a technical assessment of its current status. Gen. Tech. Rep. PSW-133. Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. 285 p.

Woodhouse, S.W. 1853. Report on the natural history of the country passed over by the exploring expedition under the command of Brev. Capt. L. Sitgreaves, U.S. Topographical Engineers, during the year 1851. [and] Zoology. Birds. In: Sitgreaves, Capt. L., ed. Report of an expedition down the Zuni and Colorado Rivers. Washington, DC: Robert Armstrong, Public Printer: 33-40, 58-105.

Wright, S. 1951. The genetical structure of populations. Ann. Eugenics. 15: 323-354.

Zink, R.M.; Dittman, D.L. 1993. Gene flow, refugia, and evolution of geographic variation in the Song Sparrow (*Melospiza melodia*). Evolution. 47: 717-729.