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VAGRANT WESTERN RED-SHOULDERED HAWKS: ORIGINS, NATAL DISPERSAL PATTERNS, AND SURVIVAL

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Abstract. We report the results of a 40-year study of the western Red-shouldered Hawk (*Buteo lineatus elegans*) involving the banding of 2742 nestlings in southern California from 1970 to 2009 (this study) plus 127 nestlings banded in other California studies (1956–2008) and the analyses of 119 records of subsequent recovery from the Bird Banding Laboratory (1957–2009). Of the Red-shouldered Hawks recovered, 109 (91.6%) moved <100 km (short-distance dispersers), while 10 (8.4%) moved >100 km (long-distance dispersers). Three (2.5%), all long-distance dispersers, were vagrants (recovered outside the species' range of residency), and were found 374 to 843 km northeast and south of their banding locations in the Mojave, Great Basin, and Vizcaino deserts. The distribution of directions of short-distance dispersal was bipolar, closely corresponding with the northwest–southeast orientation of the species' range in southern California, while that of long-distance dispersers was mainly to the north. One of 10 long-distance dispersers, a nonvagrant, survived well into the age of breeding (103.0 months), whereas eight of the other nine perished before 14.5 months. The implications of vagrancy for conservation of this resident subspecies are that a relatively small source area can contribute genetic material over a vastly larger receiving area but rarely does so because of high mortality rates. Nonetheless, the movements of vagrants we documented provide evidence for the species' potential to populate new landscapes in response to changing environmental conditions and to maintain genetic heterogeneity within existing populations.

Key words: Buteo lineatus elegans*, California, dispersal, Red-shouldered Hawk, vagrant.*

Individuos Vagabundos de *Buteo lineatus elegans*: Orígenes, Patrones de Dispersión Natal y Supervivencia

Resumen. Presentamos los resultados de un estudio de 40 años de la aguililla *Buteo lineatus elegans*, considerando el anillado de 2742 polluelos en el sur de California, desde 1970 hasta 2009 (este estudio), además de 127 polluelos anillados en otros estudios de California (1956-2008) y del análisis de 119 registros de recuperación subsiguientes del Laboratorio de Anillamiento de Aves (1957 a 2009). De las aguilillas recuperados, 109 (91.6%) se movieron <100 km (dispersores de corta distancia), mientras que 10 (8.4%) se movieron > 100 km (dispersores de larga distancia). Tres individuos (2.5%), todos dispersores de larga distancia, fueron vagabundos (recuperados fuera del rango de residencia de la especie) que se encontraron entre 374 y 843 km al noreste y al sur de sus localidades de anillamiento en los desiertos de Mojave, Gran Cuenca y Vizcaíno. La distribución de las direcciones de dispersión de corta distancia fue bipolar, en estrecha correspondencia con la orientación noroeste-sureste de la distribución de la especie en el sur de California, mientras que la de los dispersores de larga distancia fue principalmente hacia el norte. Uno de los 10 dispersores de larga distancia, un individuo no vagabundo, sobrevivió bien hasta la edad de reproducción (103 meses), mientras que ocho de los otros nueve murieron antes de 14.5 meses. Las consecuencias del vagabundeo para la conservación de esta subespecie residente es que un área fuente relativamente pequeña puede contribuir con material genético para un área sumidero mucho mayor, lo que raramente ocurre debido a las altas tasas de mortalidad. Sin embargo, los movimientos de individuos vagabundos que documentamos en este estudio evidencian el potencial de la especie para poblar nuevos paisajes en respuesta a condiciones cambiantes del medio ambiente y para mantener la heterogeneidad genética dentro de las poblaciones existentes.

INTRODUCTION

Vagrancy, the movement of animals outside of their recognized breeding ranges, winter ranges, or migratory pathways (Newton 2008), is one component of a dispersal continuum that includes philopatry, the tendency for organisms to remain at or return to their birthplace or nearby sites (Shields 1982). Vagrants arise most commonly from migratory populations and are often associated with weather disturbances. Newton (2008) provided a concise summary of factors resulting in vagrancy: (1) normal dispersal, (2) population growth or expansion, (3) drift (due to weather), (4) migration overshoots, (5) deviant directional tendencies, (6)

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mirror-image migration, and (7) reverse-direction migration. In this study we examine a population of a subspecies recognized as resident but known to disperse widely and regularly.

Vagrants may be important to gene flow, colonization, speciation, and conservation. Perhaps in no group of vertebrates has vagrancy been studied in more detail than in birds. Vagrancy is likely one of the routes by which discrete subpopulations become established. As Grinnell (1922) suggested, "These pioneers are of exceeding importance to the species in that they are continually being centrifuged off on scouting expeditions…to seek new country which may prove fit for occupancy." Vagrants are frequently the individuals within a population that have the greatest potential to expand a species' range rapidly (Grinnell 1922, Veit 2000, Trakhtenbrot et al. 2005, McLaren et al. 2006) to instigate speciation (Wright 1943), and perhaps to adapt and/or move with changing environments, including those projected from global climate change (Berthold 1999, Parmesan and Yohe 2003, Crick 2004, Seagar et al. 2007).

Nomadism, at the other extreme of the dispersal continuum, is characterized by organisms that "do not attach to specific sites," wander, and, in some cases, breed at multiple, often vastly different localities throughout their lives (Shields 1982). Among raptors, the Northern Harrier (*Circus cyaneus*) (MacWhirter and Bildstein 1996), Short-eared Owl (*Asio flammeus*) (Clark 1975), and Snowy Owl (*Nyctea scandiaca*) (Parmelee 1992) are often singled out for their propensity to nomadism. Although observations of vagrant birds are common in North America, and research on vagrants concerning abundance, population growth, and range expansion is substantial (DeSante 1983, Johnson 1994, Patten and Marantz 1996, Veit 1997, 2000), empirical evidence for the exact origins of vagrants, or accidentals as they are frequently called, is rare. Although important, the reports are often anecdotal, such as that of a Cattle Egret (*Bubulcus ibis*) banded as a fledgling in California dispersing to Alaska (Gibson and Hogg 1982), and a Common Kestrel (*F. tinnunculus*), evidently of European origin, trapped at Cape May, New Jersey (Clark 1974). For a compilation of transatlantic vagrants, see Newton (2008).

Vagrancy, because of its direct relationship to population spread, population dynamics, and genetic composition, is important to biodiversity conservation but the mechanism of vagrancy is poorly supported by empirical data (Trakhtenbrot et al. 2005). This lack of information on the origins of vagrants has hampered previous studies of this phenomenon. The distances, directions, timing, and destinations of vagrants may have relevance in projecting the possibility of a species adapting to changing environments (e.g., land-use modification and climate change). Examples may include sporadic attempts of warblers to nest outside their usual ranges (Patten and Marantz 1996) or, as with the migratory Swainson's Hawk (*B. swainsoni*), the colonization of a disjunct breeding population (Wenny et al. 2006).

The Red-shouldered Hawk (*Buteo lineatus elegans*) is resident within a relatively narrow range extending north from northwestern Baja California (Grinnell 1928) through California (Garrett and Dunn 1981, Bloom 1985, Small 1994) to recently colonized southwestern Oregon (Wilbur 1973, Henny and Cornely 1985, Burrows and Gilligan 2003) and perhaps southwestern Washington (Wahl et al. 2005, Bell and Kennedy 2006). In southwestern California the Red-shouldered Hawk is a common component of the avian community. It occasionally breeds while in juvenile plumage and may produce up to four young per nesting attempt (Wiley 1975). We selected the subspecies *elegans* for our investigation of vagrancy because of its isolation from the other subspecies, the existence of a substantial database of records of natal dispersal, occasional observations of vagrant Red-shouldered Hawks clearly out of their range, and examples of expanding populations (Wilbur 1973, Henny and Cornely 1985, Patten et al. 2001, Carlisle et al. 2007). The nearest other subspecies (*B. l. texanus*) is found in coastal southern Texas and northeastern Mexico and is separated from *elegans* by approximately 1700 km (Brown and Amadon 1968). In effect, subspecies *elegans* is an insular population surrounded by the Pacific Ocean to the west, desert to the south and east, and unfavorable coniferous woodlands to the north (Fig. 1).

Here we use the records of recovery of 119 Red-shouldered Hawks banded as nestlings in California to ask (1) what percentage of fledged Red-shouldered Hawks are long-distance

FIGURE 1. Long-distance dispersal of the Red-shouldered Hawk: all recoveries at distances >100 km from the site of banding ($n = 10$).

FIGURE 2. Red-shouldered Hawk nest (1999) with adult female and young 4.5 to 5 weeks old, San Juan Creek, Rancho Mission Viejo, Orange County, California. Photo by Richard R. Jackson.

dispersers, (2) what percentage of them are vagrants, (3) what are the destinations of vagrant Red-shouldered Hawks relative to their natal area in southwestern California, and (4) do philopatric individuals have higher life expectancies than long-distance dispersers or vagrants?

METHODS

The 1400-km² study area includes a portion of the cismontane region of southern California from approximately the San Luis Rey River in San Diego County north to the Santa Ana River in Orange County. The Santa Ana Mountains constitute the eastern boundary, the Pacific Ocean the western edge. The study area's habitats have been described in detail by Pequegnat (1951) and Bloom (1989). The topography consists of low, rolling hills with occasional streams meandering through the landscape. The elevation varies from sea level to 300 m. The climate is Mediterranean with precipitation peaking in February (Bloom 1989, Cowling et al. 2005).

In 1991, we fitted 23 fledgling hawks with backpack-mounted (Dunstan 1972) VHF radio transmitters (Communications Specialists, Inc.) that had a transmission range of 10 km and a lifespan of 9 months. We searched for transmitter-equipped hawks over appropriate habitat from a fixed-wing aircraft at an altitude of 2400 m twice per week for 7 months from June through December, covering the area from the Mexican border north to San Luis Obispo, California, and inland from the ocean approximately 100 km. Airspace over military reservations and airports was excluded. We selected the distance of 100 km because it encompassed the Red-shouldered Hawk's known breeding distribution in this region (Wilbur 1973).

Between 1956 and 2009, 2869 nestling western Red-shouldered Hawks (age 2.0 to 6.5 weeks) were banded in their nests with U.S. Fish and Wildlife Service or U.S. Geological Survey bands, 2742 by us, 127 by others (Fig. 2). For this analysis, we examined all of the Bird Banding Laboratory's records of recoveries of nestling Red-shouldered Hawks banded in southern California. No recaptures or color-band sightings from this study were used in this analysis.

We defined Red-shouldered Hawks that moved >100 km as long-distance dispersers, 100 km being the distance at which the frequency distribution for dispersal becomes asymptotic. Dykstra et al. (2004), in a study of the Red-shouldered Hawk in Ohio, also defined long-distance dispersal as exceeding 100 km. Hawks that moved >100 km and were found outside the subspecies' traditional range were, by definition, vagrants (Newton 2008). We excluded from analyses one long-distance disperser recovered at Lake Tahoe because it was temporarily held at a rehabilitation center.

Bird Banding Laboratory records of fledglings that were banded and recovered in the same 10-min block showed a

TABLE 1. Nestling Red-shouldered Hawks recovered >100 km from location of banding.

ID	Date banded	Band number	Date recovered	Age[a] (months) at time of recovery	Recovery location	Distance from location of banding	Direction moved
1	20 Jun 1956	0527-89512	2 Jan 1957	8.3	Bakersfield, CA	120 km	N
2	18 May 1990	0816-99644	7 Mar 1991	10.4	Guadalupe, CA	290 km	NW
3	25 May 1990	0816-99666	24 Jul 1990	3.0	Las Vegas, NV	374 km	NE
4	5 May 1991	0816-90877	fall 1991	7.5	near San Hipólito, Baja California Sur, Mexico	804 km	SE
5	1 May 1997	2206-47701	4 Aug 1997	3.3	Big Bear City, CA	111 km	NE
6	9 May 1998	2206-49289	10 Jul 1999	14.5	Fernwood, CA	119 km	NW
7	8 May 2001	2206-52298	23 Nov 2009	103.0	Topanga, CA	144 km	NW
8	11 May 2001	2206-51624	16 Sep 2001	4.7	Ventura, CA	143 km	NW
9	1 May 2004	2206-70558	30 Jul 2004	3.2	Wendover, NV	843 km	NE
10	13 May 2004	2206-66609	24 Nov 2004	7.0	San Diego, CA	112 km	S

[a]Calculated on the basis of 25 April as the mean date of hatching (Wiley 1975).

distance of 0 km, although the actual distance may have ranged from a minimum of 0 km to a maximum of 19.4 km. Therefore, we assigned these recoveries (n = 19) a dispersal distance of 9.7 km, or roughly the distance to the center of the block, when the exact recovery location was unknown. A small percentage of Red-shouldered Hawks may breed as early as 1 year of age (Wiley 1975). Most are unsuccessful, and the majority of first-time, successful breeders are >22 months of age (P. H. Bloom, unpubl. data). The percentage of successful territories occupied by birds in juvenile plumage (age <17 months) is so small that for this study we consider hawks <22 months of age to be nonbreeders or unsuccessful.

We used NCSS statistical software (NCSS 2007) to analyze dispersal distances and directions and the nonparametric Mann–Whitney U test to compare groups; we report means with ±SD.

RESULTS

Of 2869 nestlings banded in southern California, 119 (4.1%) were recovered. An additional 28 were recaptured during this study but we did not analyze them because of potential bias resulting from birds captured within the study area (Koenig et al. 1996). Of the 119 recovered nestlings, 113 (95.0%) were banded during this study and six (5.0%) were banded by other researchers. The mean dispersal distance of the 119 hawks was 55.2 ± 112.2 km (SE = 10.3, range 0–843 km). Dispersal was skewed to the shorter distances, and the median was 24.1 km. Ten (8.4%) of the 119 recoveries represented long-distance dispersal (>100 km), of which three (2.5% of 119 recoveries) represented vagrancy. Eight of the 10 long-distance dispersers traveled north. Seven of the 10 long-distance dispersers were found in Guadalupe, Bakersfield, Topanga, Ventura, Fernwood, San Diego, and Big Bear City, California, all areas where the western Red-shouldered Hawk breeds. The three vagrant hawks arrived at localities as diverse as Las Vegas, Nevada; near San Hipólito, Baja California Sur, Mexico; and Wendover, Nevada, and moved 374, 804, and 843 km, respectively (Fig. 1, Table 1). The three vagrants traveled significantly farther than the 116 hawks that were recovered within the breeding range (Mann–Whitney U test, P = 0.0016). However, it should be recognized that as these three hawks became vagrants by definition as soon as they left the subspecies' known range; they could have been defined as vagrants at distances much less than 100 km (Fig. 1).

We did not determine the direction of dispersal of 19 of 119 hawks because they were recovered within the 10-min block where they were banded. The mean direction of short-distance dispersers (hawks that traveled <100 km) was 315.9 ± 108.2° (n = 90). The distribution was strongly bipolar, however, with the majority of hawks (86.7%) traveling either northwest (53.3%) or southeast (33.3%). The mean direction of birds that traveled northwest (270–0°) was 314.7° ± 34.2 (n = 48), while that of those traveling southeast (90–180°) was 147.2 ± 32.2° (n = 30). These directions correspond closely with the northwest–southeast orientation of the species' breeding range in southern California, which in turn corresponds with the orientation of the coastline in the same area (Fig. 1). Also, only three hawks moved southwest, which corresponds with the close proximity of the study area to the coast.

Although conclusions are limited by sample size, the mean direction of long-distance dispersal was 338.9 ± 79.6° (n = 10). Eight long-distance dispersers traveled north (270–90°), whereas two traveled south.

Short-distance dispersers survived longer than long-distance dispersers. Sixty (55%) of short-distance dispersers were >22 months of age when encountered, and the oldest lived 19.9 years. In contrast, only one (10%) of 10 long-distance dispersers was >22 months of age (Table 1) when found, and eight were found dead or near death when ≤14.5 months old; the oldest long-distance disperser was found dead at an estimated age of 8.6 years. The lone surviving long-distance disperser with a transmitter was found near Guadalupe, California; it lived to an age of at least 10.4 months when it was last relocated before the transmitter signal was lost.

All 23 radio-tagged hawks were found within their natal territories up to 4 weeks after fledging (including two found dead). Despite extensive efforts at aerial searching, we were able to relocate only six birds after 6 weeks, suggesting a very rapid and direct departure of as many as 15 birds out of the region. After 12 weeks only three hawks were found in southwestern California. Three of the hawks equipped with VHF transmitters (13.0%) were eventually encountered as long-distance dispersers, and two of the three were vagrants, ultimately recovered far outside the aerial search area.

All three vagrants perished when <7.5 months of age (Table 1). The bird recovered at Wendover, Nevada, in the Great Basin desert was sick when found and succumbed to West Nile virus; the bird in Las Vegas, Nevada, in the Mojave Desert was found dead in the city; the bird near San Hipólito, Baja California Sur, Mexico in the Vizcaino Desert was found sick in a palm grove and presumed to have died.

DISCUSSION

DISTRIBUTION

As evidenced by recent range expansions, the distribution of the western Red-shouldered Hawk is not static (Wilbur 1973, Henny and Cornely 1985), and individuals are observed sparingly but predictably outside of the subspecies' breeding range in the Great Basin Desert (Hinde et al. 2002, Carlisle et al. 2007, Giddings 2007), western Washington (Tweit 2005), western Oregon (Henny and Cornely 1985, Scheuering and McAtee 2003, Burrows and Gilligan 2003), Arizona (Glinski 1998), British Columbia, Canada (Cruickshank and Melcer 2010) and Baja California, Mexico (P. H. Bloom, unpubl. data). The western Red-shouldered Hawk has previously demonstrated its ability to adjust to and establish itself in association with human-caused habitat change in the form of urban forests composed predominantly of exotic trees in southern California (Bloom and McCrary 1996, Rottenborn 2000). That adaptability and the fact that vagrant Red-shouldered Hawks are regularly observed outside of their breeding range suggest some level of endogenous control and survival value for long-distance dispersal at the species level.

Adult and juvenile Red-shouldered Hawks have been observed in Washington only since 1979 (Bell and Kennedy 2006), but the species likely nests around Ridgefield National Wildlife Refuge. After a nearly 100-year absence from Oregon, the subspecies began reappearing in 1971 (Henny and Cornely 1985, Burrows and Gilligan 2003). In Arizona the species is considered a "rare wandering" vagrant (Glinski 1998) with one confirmed nesting along the Colorado River (Monson and Phillips 1941, Glinski 1982). In California the Red-shouldered Hawk is nonmigratory, individuals retaining the same mates and territories for years (P. H. Bloom, unpubl. data). With respect to conservation status the subspecies is considered stable (Harlow and Bloom 1989) or expanding (Wilbur 1973, Bloom and McCrary 1996).

In California the Red-shouldered Hawk is strongly associated with riparian and forested habitat (Dixon 1928, Bloom et al. 1993). Along the western fringe of the Mojave Desert it nests regularly in the cottonwood-willow reaches of the Owens (Wilbur 1973) and Morongo valleys (P. H. Bloom, unpubl. data). Despite the marginal quality of the agricultural habitat in the desert, observations of dispersing Red-shouldered Hawks in the Sonoran Desert valleys of Coachella and Imperial have been increasing since the early 1970s (Wilbur 1973, Patten et al. 2001, 2003), and the subspecies is now breeds regularly in mature date palm orchards in the Coachella Valley (P. H. Bloom, unpubl. data). Utilizing patchily distributed date palm orchards in Baja California, the subspecies is prospecting southward at least to San Ignacio, 700 km south of San Diego, California, but is not known to be nesting (P. H. Bloom, unpubl. data) south of its traditional breeding range in northwestern Baja California (Grinnell 1928, Patten et al. 2001).

Of interest, two of the 15 hawks equipped with VHF transmitters that could not be relocated after 6 weeks were grounded and found alive by the public as much as 804 km away, suggesting that others in this group might also have been outside the species' range and hence not found within the area of our aerial searches.

Furthermore, recent records of 25 widely dispersed Red-shouldered Hawks in Arizona (Glinski 1998) likely represent the western subspecies given their proximity to California (approximately 500 km for *elegans* versus over 1000 km for *texanus*) and suggest that wide-ranging dispersal of this subspecies to the east may be more common than band-recovery data suggest (Glinski 1982). W. S. Clark examined two specimens of the Red-shouldered Hawk collected in Arizona and identified one as *B. l. elegans*, the other as *B. l. lineatus*, the eastern subspecies (Glinski 1982). Another record (Museum of Wildlife and Fish Biology 4819, University of California, Davis) of the eastern subspecies from Sacramento County, California (Pyle et al. 2004), provides more evidence of an occasional vagrant from outside the breeding range of *elegans*.

The distribution of band recoveries across the landscape can be biased by the location and abundance of human populations that might find and report banded birds and may have played a role in this study; seven of the 10 long-distance disperers were recovered in the heavily populated coastal region of southern California, which may be overrepresented, while the apparent distribution (Fig. 1) and low number of band recoveries in the deserts may, in part, reflect the low human population in these areas. The evidence from tagged hawks in this study and the large number of sightings in the Sonoran Desert of Arizona (Glinski 1998) suggest that vagrant Red-shouldered Hawks may be more numerous in the southwestern deserts than previously thought. On basis of Grinnell (1922), this study, and Dykstra et al. (2004) these birds are likely young of the year.

A small fraction (2.5%) of fledglings in this study emigrated outside the subspecies' normal distribution and attempted to penetrate and move across substantial ecological barriers of desert. These severe deserts provide few mesic habitats that would support survival of a raptor specializing in riparian or woodland habitat. Available climate predictions point to higher temperatures in the future, suggesting a potential for higher mortality and selection against would-be colonizers of riparian oases in the deserts of the Southwest (Berthold 1998, Seagar et al. 2007).

Occasional individuals (mostly juveniles), apparently dispersing, have been observed during fall in the Great Basin in Oregon, Nevada and Utah. Bloom observed vagrant juvenile Red-shouldered Hawks for several days during each fall in 1975, 1976, 1977, and 1978 at Cedarville, in the Surprise Valley, Modoc County, California, on the western edge of the Great Basin and well outside the breeding range in northwestern California, suggesting occasional dispersal to the east. However, extensive observations on the Santa Barbara Channel Islands and Southeast Farallon Island (Richardson et al. 2003) have failed to detect any westward emigrants. Grinnell (1922) also proposed that hatch-year birds should be the dominant age class of "pioneers." The above observations support Grinnell's suggestion that occurrences of "accidental" species are in fact the result of fairly predictable movements that occur in a tiny component of any population.

The question of whether the Red-shouldered Hawk's range expansion (Wilbur 1973, Henny and Cornely 1985) is new depends upon the landscape in question. The expansion into the Pacific Northwest appears to be recent and perhaps due to logging and other land-use changes that may have benefited the species. Movements of vagrants into the less hospitable Great Basin and other deserts suggest either genetic control or random pulses of individuals (Hinde et al. 2002, Carlisle et al. 2007, Giddings 2007, Glinski 1998). Potential effects of climate change on habitats, both positive and negative, could also be invoked for both regions in terms of effective colonization.

DISPERSAL

Given their focus on islands and speciation, Darwin (1859) and Wallace (1876) were perhaps the first to draw attention to the significance of dispersal. Much later, Grinnell (1922) stated that, "The 'accidentals' are the exceptional individuals that go farthest away from the metropolis of the species; they do not belong to the ordinary mob that surges against the barrier, but are among those individuals that cross through or over the barrier, by reason of extraordinary complement of energy, in part by reason of hardihood with respect to the particular factors comprising the barrier, and in part of course, sometimes through merely fortuitous circumstances of a favoring sort." We consider here that the three vagrant or "accidental" Red-shouldered Hawks we report, which attempted to cross three different deserts during summer, were the type of individual that Grinnell was contemplating. An important difference between these three birds and many other vagrants is that it is unlikely, given the mild Mediterranean climate of the region of their origin, that their movements were prompted by bad weather (Elkins 1995, Newton 2008), as southwestern California experienced no severe storms during June or July 1990 and 1991 (http://www.wrh.noaa.gov/sgx/document/weatherhistory.pdf) when two of the vagrants would have been moving. However, the June–July departure of the two vagrants with transmitters corresponds with the onset of high summer temperatures and the departure on migration of transmitter-equipped young Red-tailed Hawks (*Buteo jamaicensis*; Bloom, unpubl. data). Although it is plausible that a minor storm, depression, or unrecorded upper atmospheric condition might have prompted long-distance movements, it is more likely that these birds moved as a result of genetic influence (Berthold 1998, 1999, Pulido and Berthold 2003), prey availability (Sinclair 1983), or other density-dependent factors (Sutherland et al. 2002). While eight of the 10 long-distance dispersers we recorded did not contribute to their own fitness, future generations pulsed out at irregular intervals may some year find the habitat and opportunities for mating required to pioneer and establish a new population.

The three vagrants from the study area were of the sort that might, but not necessarily (Newton et al. 1994), colonize remote areas well in front of the leading edge of the expanding range of a species (Shigesada and Kawasaki 2002). As demonstrated for the Osprey (*Pandion haliaetus*) and Marsh Harrier (*Circus aeruginosus*), long-distance dispersal may also increase the velocity of expansion substantially, and the more individuals disperse long distances, the faster a species' range will increase (Lensink 1997). This pattern is in contrast to short-distance dispersal (Shigesada and Kawasaki 2002) of the type characteristic of the slow expansion of the breeding range, over at least the past 4 decades, north along the coast from northwestern California into Oregon (Henny and Cornely 1985) and potentially into Washington. In southern California, expansion includes the Coachella Valley (Wilbur 1973; P. H. Bloom, unpubl. data). It is also of the type of slow but consistent range reestablishment of the Red Kite (*Milvus milvus*) in Wales documented in detail from 1946 to 1993 (Newton et al. 1994) where the distances moved were all short. The relevance to conservation of the recolonization of Wales by the Red Kite and the limited role of long-distance dispersal in it is relevant here because, although the kite's recovery rate was nearly 5% per year, the occupied breeding area expanded only slowly and only on one edge of the growing population (Newton et al. 1994). Similarly, with the Red-shouldered Hawk, at least 8 of 10 would-be long-distance colonizers we recorded were found dead or died soon after while still in juvenile plumage at <22 months of age (Table 1), also suggesting that successful breeding of long-distance dispersers and, most importantly, vagrants outside of their traditional habitat, are indeed rare. In sharp contrast, only 49 of 109 (45.0%) short-distance dispersers were found dead or near death at <22 months of age. Our results from California largely complement those of Dykstra et al. (2004) from Ohio.

Those hawks that moved shorter distances from their natal nest and hence were more philopatric survived longer than those traveling longer distances. In contrast, most long-distance dispersers perished before the age of breeding, and the oldest survived only 8.6 years. Of the long-distance dispersers, only the bird recovered in Topanga, California, at 103.0 months of age was a probable successful breeder (Table 1). This also provides evidence of the importance of philopatry in inhibiting the spread and natural reestablishment of bird populations, even for species, such as the Red-shouldered Hawk and Red Kite, with the morphological adaptations and ecological propensities needed to disperse widely.

VAGRANCY

Including individuals banded by other researchers, this study involves a period of 53 years of potential successful nesting. Our efforts were relatively intensive. Given that one individual of each sex is required for a sexually reproducing animal to reproduce, the probability of a populations being founded successfully via vagrancy in any year must be near zero.

In none of the studies that we reviewed of avian dispersal or migration involving large data sets or summarizing movement of banded or transmitter-equipped raptors were examples of vagrancy of birds of known origin reported (Schmutz and Fyfe 1987, Lensink 1997, Walls et al. 1999, Steenhof et al. 1984, 2005, Dykstra et al. 2004, Wiens et al. 2006, Bildstein 2006). The failure of this sample of studies to document vagrancy or long-distance disperal supports our finding that vagrancy is indeed very rare and that uncovering the provenance of vagrants is even less likely.

Like that for migration, the proximate reason for vagrancy is likely genetic. As stated by Berthold (1998), "It has been shown that all the basic processes and features of migration, such as migratory drive, migratory disposition and activity, and orientation behavior, are under direct genetic control." This genetic control also includes cessation of migration (Berthold 1999). Berthold's findings (1998, 1999) suggest that at least a small percentage of individuals in some avian populations are preprogrammed to disperse in particular directions and distances, possibly generating vagrants. Under endogenous control mechanisms, some birds might be considered "obligate vagrants." Whether the three vagrants in this sample had reached their termini or died en route will never be known because they never nested. The proportion of individuals within a population that prove to be vagrants, although rarely successful, are likely an important variable in the species' survival equation; long-distance dispersal of individuals may allow a species to escape harm, explore, and perhaps take the "sweepstakes route," colonizing a new range (Simpson 1952).

The short-distance dispersers we recorded tended to move northwest (55%) or southeast (33%), staying within the species' range. The Pacific Ocean to the west and relatively unfavorable habitats to the east likely inhibit movements in those directions. The three vagrants all moved east (0–180°) from their location of banding.

POTENTIAL CAUSAL FACTORS FOR DISPERSAL MOVEMENTS

Density-dependent factors (Sutherland et al. 2002), avoidance of inbreeding, and behavioral dominance (Gauthreaux 1978) have been postulated as reasons for dispersal of young animals (Greenwood 1980, Gandon and Michalakis 2001), while climate change has been suggested as an explanation for recent changes in birds' migratory behavior (Berthold 1999). Although long-distance dispersers have a high mortality rate, usually never find a mate, and rarely breed successfully, the existence of some long-distance dispersers in a population has survival value for the species by providing the potential for range expansion (Grinnell 1922, Howard 1960, Murray 1967). The disparate locations of recoveries in the Mojave, Great Basin, and Sonoran (Vizcaino) deserts of vagrant hawks with origins in coastal southern California suggest that the exploratory movements of the birds involved were not migration in the truest sense but dispersal, or as Grinnell (1922) referred to such birds, "accidentals," the vanguard of a species' range expansion. Our findings indicate that weather apparently had no effect on three vagrants from a nonmigratory (Garrett and Dunn 1981, Bloom 1985, Small 1994) southern California population, which suggests some level of endogenous control may be involved in the movements of some vagrant Red-shouldered Hawks.

CONSERVATION IMPLICATIONS

This 40-year study of a common resident raptor of California implies that while a relatively small source area has the potential to contribute genetic material to a much larger receiving area, vagrancy rarely results in pairing, much less reproduction, outside of the species' normal breeding range. This also suggests that most birds' philopatry will inhibit the advancement and speed of successful reintroductions of endangered species, particularly in the face of climate change on a large landscape scale. Accordingly, since natural repopulation of a landscape by recovering species is often slow, effective reintroductions and conservation strategies will achieve faster results with the implementation of release programs (Cade 2000).

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LITERATURE CITED

Bell, B. H., and G. Kennedy. 2006. Birds of Washington state. Lone Pine, Auburn, WA.

Berthold, P. 1998. Bird migration: genetic programs with high adaptability. Zoology 101:235–245.

Berthold, P. 1999. A comprehensive theory for the evolution, control and adaptability of avian migration. Ostrich 70:1–11.

Bildstein, K. L. 2006. Migrating raptors of the world: their ecology and conservation. Cornell University Press, Ithaca, NY.

Bloom, P. H. 1985. Raptor movements in California, p. 313–323. *In* M. Harwood [ed.], Proceedings of Hawk Migration Conference IV. Hawk Migration Association of North America, Rochester, NY.

Bloom, P. H. 1989. Red-shouldered Hawk home-range and habitat use in southern California. M.Sc. thesis, California State University, Long Beach, CA.

Bloom, P. H., and M. D. McCrary. 1996. The urban buteo: Red-shouldered Hawks in southern California, p. 31–39. *In* D. M. Bird, D. E. Varland, and J. J. Negro [eds.], Raptors in human landscapes: adaptations to built and cultivated environments. Academic Press, London.

Bloom, P. H., M. D. McCrary, and M. J. Gibson. 1993. Red-shouldered Hawk home-range and habitat use in southern California. Journal of Wildlife Management 57:258–265.

Brown, L. H., and D. Amadon. 1968. Eagles, hawks and falcons of the world. McGraw-Hill, New York.

Burrows, R., and J. Gilligan. 2003. Birds of Oregon. Lone Pine, Auburn, WA.

Cade, T. J. 2000. Progress in translocation of diurnal raptors, p. 343–372. *In* R. D. Chancellor and B. U. Meyburg [eds.], Raptors at risk. Hancock House, Surrey, BC, Canada.

Carlisle, J. D., G. S. Kaltenecker, and R. S. Brady. 2007. Status of the Broad-winged and Red-shouldered Hawks during fall migration in southwestern Idaho, 1995–2006. Western Birds 38:251–260.

Clark, R. J. 1975. A field study of the Short-eared Owl (*Asio flammeus*) Pontoppidan in North America. Wildlife Monographs 47:1–67.

Clark, W. S. 1974. Second record of the Kestrel (*Falco tinnunculus*) for North America. Auk 91:172.

Cowling, R. M., F. Ojeda, B. B. Lamont, P. W. Rundel, and R. Lechmere-Oertel. 2005. Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone Mediterranean-climate ecosystems. Global Ecology and Biogeography 14:509–519.

Crick, H. Q. P. 2004. The impact of climate change on birds. Ibis 146 (Suppl. 1):48–56.

Cruickshank, I., and R. Melcer Jr. 2010. Observation of a Red-shouldered Hawk on Vancouver Island, British Columbia, during fall migration. British Columbia Birds 20:41–44.

Darwin, C. 1859. The origin of species by means of natural selection. John Murray, London.

DeSante, D. F. 1983. Annual variability in the abundance of migrant land birds on southeast Farallon Island, California. Auk 100:826–852.

Dixon, J. B. 1928. Life history of the Red-bellied Hawk. Condor 30:228–236.

Dunstan, T. C. 1972. Radio-tagging falconiform and strigiform birds. Journal of Raptor Research 6:93–102.

Dykstra, C. R., J. Hays, M. M. Simon, J. B. Hol, Jr., G. R. Austing, and F. B. Daniel. 2004. Dispersal and mortality of Red-shouldered Hawks banded in Ohio. Journal of Raptor Research 38:304–311.

Elkins, N. 1995. Weather and bird behavior. T. & A. D. Poyser, London.

Gandon, S., and Y. Michalakis. 2001. Multiple causes of the evolution of dispersal, p. 155–167. *In* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols [eds.], Dispersal. Oxford University Press, Oxford, England.

Garrett, K., and J. Dunn. 1981. Birds of southern California: status and distribution. Los Angeles Audubon Society, Los Angeles.

Gauthreaux, S. A. Jr. 1978. The ecological significance of behavioral dominance, p. 17–54. *In* P. P. G. Bateson and P. H. Klopfer [eds.], Perspectives in ethology, vol. 3. Plenum, New York.

Gibson, D. D., and N. D. Hogg. 1982. Direct recovery in Alaska of California-banded Cattle Egret. American Birds 36:335

Giddings, L. 2007. The birds of San Juan County, Utah. Utah Birds 20:15–44.

Glinski, R. L. 1982. The Red-shouldered Hawk (*Buteo lineatus*) in Arizona. American Birds 36:801–805.

Glinski, R. L. 1998. The raptors of Arizona. University of Arizona Press, Tucson, AZ.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140–1162.

Grinnell, J. 1922. The role of the "accidental." Auk 39:373–380.

Grinnell, J. 1928. A distributional summation of the ornithology of Lower California. University of California Publications in Zoology 32:1–300.

Harlow, D., and P. H. Bloom. 1989. Status of buteos and the Golden Eagle in the western United States, p. 102–110. *In* B. G. Pendleton [ed.], Proceedings on the status of western raptors. National Wildlife Federation, Washington, DC.

Henny, C. J., and J. E. Cornely. 1985. Recent Red-shouldered Hawk range expansion north into Oregon including first specimen record. Murrelet 66:29–31.

Hinde, A., K. Grant, and R. Yosef. 2002. Banding and communal roosts of wintering raptors of the Great Basin Desert: 1987–1998, p. 112–117. *In* R. Yosef, M. L. Miller, and D. Pepler [eds.], Raptors in the new millennium: proceedings of the World Conference on Birds of Prey and Owls. International Birdwatching Centre, Eilat, Israel.

Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. American Midland Naturalist 63:152–161.

Johnson, N. K. 1994. Pioneering and natural expansion of breeding distributions in western North American birds. Studies in Avian Biology 15:27–44.

Koenig, W. D., D. Van Vuren, and P. N. Hooge. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Ecology & Evolution 11:514–517.

Lensink, R. 1997. Range expansion of raptors in Britain and the Netherlands since the 1960s: testing an individual-based diffusion model. Journal of Animal Ecology 66:811–826.

MacWhirter, R. B., and K. L. Bildstein. 1996. Northern Harrier (*Circus cyaneus*), no. 210. *In* A. Poole and F. Gill [eds.], The birds of North America. Academy of Natural Sciences, Philadelphia.

McLaren, I. A., A. C. Lees, C. Field, and K. J. Collins. 2006. Origins and characteristics of nearctic landbirds in Britain and Ireland in autumn: a statistical analysis. Ibis 148:707–726.

Monson, G., and A. R. Phillips. 1941. Bird records from southern and western Arizona. Condor 43:108–112.

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

NCSS. 2007. NCSS statistical system. NCSS, Kaysville, UT.

Newton, I., P. E. Davis, and D. Moss. 1994. Philopatry and population growth of Red Kites, *Milvus milvus*, in Wales. Proceedings of the Royal Society London B 257:317–323.

Newton, I. 2008. The migration ecology of birds. Academic Press, London.

Parmelee, D. 1992. Snowy Owl (*Nyctea scandiaca*), no. 10. *In* A. Poole, P. Stettenheim, and F. Gill [eds.], The birds of North America. Academy of Natural Sciences, Philadelphia.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Patten, M. A., and C. A. Marantz. 1996. Implications of vagrant southeastern vireos and warblers in California. Auk 113:911–923.

Patten, M. A., G. McCaskie, and P. Unitt. 2003. Birds of the Salton Sea. University of California Press, Berkeley, CA.

Patten, M. A., E. Mellink, H. G. de Silva, and T. E. Wurster. 2001. Status and taxonomy of the Colorado Desert avifauna of Baja California. American Birding Association Monographs in Field Ornithology 3:29–63.

Pequegnat, W. E. 1951. The biota of the Santa Ana Mountains. Journal of Entomology and Zoology 42:1–84.

Pulido, F., and P. Berthold. 2003. Quantitative genetic analysis of migratory behavior, p. 53–77. *In* P. Berthold, E. Gwinner, and E. Sonnenschein [eds.], Avian migration. Springer-Verlag, Berlin.

Pyle, P., A. Engilis Jr., and T. G. Moore. 2004. A specimen of the nominate subspecies of the Red-shouldered Hawk from California. Western Birds 35:100–104.

Richardson, T. W., P. Pyle, R. Burnett, and P. Capitolo. 2003. The occurrence and seasonal distribution of migratory birds on southeast Farallon Island, 1968–1999. Western Birds 34:58–96.

Rottenborn, S. C. 2000. Nest site selection and reproductive success of urban Red-shouldered Hawks in central California. Journal of Raptor Research 34:18–25.

Scheuering, R. W., and G. McAtee. 2003. Red-shouldered Hawk Buteo lineatus, p. 153–154. *In* D. B. Marshall, M. G. Hunter, and A. L. Contreras [eds.], The birds of Oregon: a general reference. Oregon State University Press, Corvallis, OR.

Schmutz, J. K., and R. W. Fyfe. 1987. Migration and mortality of Alberta Ferruginous Hawks. Condor 89: 169–174.

Seager, R., M. Ting, I. Held, Y. Kushnir, J. Lu, G. Vecchi, H.-P. Huang, N. Harnik, A. Leetmaa, N.-C. Lau, C. Li, J. Velez, and N. Naik. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316:1181–1184.

Shields, W. M. 1982. Philopatry, inbreeding, and the evolution of sex. State University of New York Press, Albany, NY.

Shigesada, N., and K. Kawasaki. 2002. Invasion and range expansion of species: effects of long-distance dispersal, p. 350–373. *In* J. M. Bullock, R. Kenward, and R. S. Halis [eds.], Dispersal ecology: the 42nd symposium of the British Ecological Society. Blackwell, Oxford, England.

Simpson, G. G. 1952. Probabilities of dispersal in geologic time. Bulletin of the American Museum of Natural History 99:163–176.

Sinclair, A. R. E. 1983. The function of distance movements in vertebrates, p. 240–258. *In* I. R. Swingland and P. J. Greenwood [eds.], The ecology of animal movement. Clarendon Press, Oxford, England.

Small, A. 1994. California birds: their status and distribution. Ibis, Vista, CA.

Steenhof, K., M. N. Kochert, and M. Q. Moritsch. 1984. Dispersal and migration of southwestern Idaho raptors. Journal of Field Ornithology 55:357–358.

Steenhof, K., M. R. Fuller, M. N. Kochert, and K. R. Bates. 2005. Long-range movements and breeding dispersal of Prairie Falcons from southwest Idaho. Condor 107:481–496.

Sutherland, W. J., J. A. Gill, and K. Norris. 2002. Density-dependent dispersal in animals: concepts, evidence, mechanisms and consequences, p. 134–151. *In* J. M. Bullock, R. E. Kenward, and R. S. Hails [eds.], Dispersal ecology: the 42nd symposium of the British Ecological Society. Blackwell, Oxford, England.

Trakhtenbrot, A., R. Nathan, G. Perry, and D. M. Richardson. 2005. The importance of long-distance dispersal in biodiversity conservation. Diversity and Distributions 11:173–181.

Tweit, B. 2005. Red-shouldered Hawk, p. 116. *In* T. R. Wahl, B. Tweit, and S. G. Miodinow [eds.], Birds of Washington: status and distribution. Oregon State University Press, Corvallis, OR.

Veit, R. R. 1997. Long-distance dispersal and population growth of the Yellow-headed Blackbird *Xanthocephalus xanthocephalus*. Ardea 85:135–143.

Veit, R. R. 2000. Vagrants as the expanding fringe of a growing population. Auk 117:242–246.

Wahl, T. R., B. Tweit, and S. G. Mlodinow. 2005. Birds of Washington: status and distribution. Oregon State University Press, Corvallis, OR.

Walls, S. S., S. Mañosa, R. M. Fuller, K. H. Hodder, and R. E. Kenward. 1999. Is early dispersal enterprise or exile? Evidence from radio-tagged buzzards. Journal of Avian Biology 30:407–415.

Wallace, A. R. 1876. The geographical distribution of animals. Harper & Brothers, New York.

Wenny, D., L. Anderson, D. Kirk, J. Bergstrom, D. Enstrom, and K. Paige. 2006. Ecology and genetics of an isolated population of Swainson's Hawks in Illinois. Journal of Raptor Research 40:270–276.

Wiens, J. D., R. T. Reynolds, and B. R. Noon. 2006. Juvenile movement and natal dispersal of Northern Goshawks in Arizona. Condor 108:253–269.

Wilbur, S. 1973. The Red-shouldered Hawk in the western United States. Western Birds 4:15–22.

Wiley, J. W. 1975. The nesting and reproductive success of Red-tailed Hawks and Red-shouldered Hawks in Orange County, California, 1973. Condor 77:133–139.

Wright, S. 1943. Isolation by distance. Genetics 28:114–138.