Western Specialty: LeConte’s Thrasher

Photo by © Steve N. G. Howell of Bolinas, California: Le Conte’s Thrasher (Toxostoma lecontei arenicola) Guerrero Negro, Baja California Sur, Mexico, 11 October 2012 The subspecies of LeConte’s Thrasher inhabiting the Vizcaíno Desert of the west-central Baja California peninsula, Toxostoma lecontei arenicola, differs from that of the desert regions of the southwestern U.S. and northwestern Mexico, T. l. lecontei, in its slightly darker back, distinctly darker breast, and less graduated tail, as well as by 3.5% in mitochondrial DNA. The vocalizations of T. l. arenicola remain unstudied. English names applied to this subspecies in the 1900s include “Desert Thrasher,” “Rosalía Thrasher,” and “Santa Rosalia Thrasher” (the type locality is Santa Rosalia Bay); today’s birders often call it the “Vizcaíno Thrasher.”
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Front cover photo by © Gary Lindquist of Visalia, California: Common Cuckoo (*Cuculus canorus*), Watsonville, Santa Cruz Co., California, 1 October 2012, representing a first record for California. Elsewhere in western North America, this species is known only as a casual migrant in western Alaska. The unbarred rump, evident in other photos, best distinguishes the Common Cuckoo and Oriental Cuckoo (*C. optatus*), also a vagrant to Alaska.


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MORPHOLOGICAL AND MOLECULAR EVIDENCE CONFIRM THE FIRST DEFINITIVE EASTERN WHITE-BREASTED NUTHATCH (SITTA C. CAROLINENSIS) FOR NEW MEXICO

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ABSTRACT: We report the first confirmed eastern White-breasted Nuthatch (Sitta carolinensis carolinensis) from New Mexico. The bird was collected on 15 October 2011, at Boone’s Draw, Roosevelt County. Morphological and plumage characters matched those of the eastern White-breasted Nuthatch, the bill being markedly shorter and the back paler than those of the subspecies resident in New Mexico, S. c. nelsoni, and other western subspecies. The DNA sequence of the mitochondrial gene for NADH dehydrogenase subunit 2 (ND2) was an exact match to published sequences from Michigan and Pennsylvania and was phylogenetically nested within a monophyletic and deeply divergent eastern clade.

The White-breasted Nuthatch (Sitta carolinensis) is a common and geographically variable resident of mature deciduous, mixed deciduous, and coniferous forests through most of North America. Grubb and Pravosudov (2008) recognized seven subspecies that constitute eastern (S. c. carolinensis), interior western (S. c. tenuissima, S. c. nelsoni, S. c. mexicana, and S. c. lagunae), and Pacific (S. c. aculeata and S. c. alexandrae) groups of populations. The seven subspecies are based on differences in bill size and shape and plumage coloration, but at least some of the variation in these characters is clinal. The eastern subspecies averages the shortest in bill length and palest in back color, while interior western and Pacific populations have longer bills and darker mantles (Phillips 1986, Pyle 1997, Sibley 2000, Wood 1992). There are three distinct vocal groups, based on typical call notes, that are concordant with boundaries between subspecies: (1) eastern United States and Canada (nasal yenk); (2) Great Basin, Rocky Mountains and Mexico (a rapid vijijijiji or viji-viji-viji), and (3) Pacific slope (high-pitched, drawn-out aaarn) (Gaines 1988, Sibley 2000, Dunn and Alderfer 2011). Recent multi-locus phylogenetic analyses of the White-breasted
Nuthatch uncovered four geographically distinct clades, with boundaries that are also consistent with vocal groups and subspecies: (1) eastern, (2) eastern Sierra Nevada and northern Rockies, (3) Rocky Mountain, Great Basin, and Mexico, and (4) Pacific (Spellman and Klicka 2007, Walstrom et al. 2012). Clades two and three are sister groups that together constitute vocal group 2. The deep phylogenetic structure and overall concordance between patterns of geographic variation in measurements, vocalizations, plumage, mitochondrial DNA, and nuclear DNA suggest that there may be more than one species of White-breasted Nuthatch.

In New Mexico, the White-breasted Nuthatch is a common resident in practically all wooded areas of the state. It descends to lower elevations and withdraws from high peaks during the winter (Ligon 1961), but little else is known about its seasonal movements. The resident subspecies in New Mexico is the interior west S. c. nelsoni (AOU 1957, Phillips 1986), which has been placed in the Rocky Mountain, Great Basin, and Mexico phylogenetic clade (Spellman and Klicka 2007). Only one previous specimen of the White-breasted Nuthatch from New Mexico (University of Arizona [UAZ] 5057) has been identified as any subspecies other than S. c. nelsoni. That specimen, collected in Socorro County by Gale Monson on 23 December 1941, was identified by Alden H. Miller as S. c. tenuissima (J. P. Hubbard pers. comm.), a subspecies constituting the eastern Sierra Nevada clade (Spellman and Klicka 2007) and for which the type locality is in the Panamint Mountains, Inyo County, California. Birders have reported White-breasted Nuthatches of the eastern subspecies in Curry and Sandoval counties on the basis of calls, but they were unable to obtain recordings or conclusive photos (W. H. Howe and C. R. Rustay pers. comm.). This phenotypically distinctive and genetically divergent eastern subspecies of the White-breasted Nuthatch has therefore not yet been fully documented in New Mexico (S. O. Williams pers. comm.).

Here we describe a female eastern White-breasted Nuthatch collected on 15 October 2011 from the eastern plains of New Mexico, representing the first definitive state record of S. c. carolinensis. Morphological and molecular data independently support assignment of the specimen to the eastern clade.

METHODS

At 08:10 on 15 October 2011, Baumann, Nicholas D. Pederson, and Cole J. Wolf mist-netted a White-breasted Nuthatch at Boone’s Draw, Roosevelt County (34° 06' 41" N, 103° 31' 44" W), a first record of this species at this locality over three previous seasons of netting. We collected the bird (New Mexico Department of Game and Fish permit 3217; U.S. Fish and Wildlife Service permit MB094297-1) because measurements taken in the field and compared to Pyle (1997) suggested tentatively that it was of the eastern subspecies. We took the specimen to the Museum of Southwestern Biology (MSB) at the University of New Mexico, where Andrew B. Johnson prepared it as a study skin MSB 37575 and frozen tissue sample (NK174933). We compared the plumage patterns and bill measurements of MSB 37575 to those of specimens at the MSB, UAZ, and University of Kansas Museum of Natural History.
Molecular Methods

Following the manufacturer’s protocol, we extracted DNA from frozen muscle tissue of MSB 37575 with a Qiagen DNEasy kit. We amplified the gene for mitochondrial NADH dehydrogenase subunit 2 (ND2) by using the primers H6313 and L5219 (Sorensen et al. 1999) in a 15-μL reaction with 1 μL of DNA and the following reagents: 0.5 mM of each primer, 2 mM of each dNTP, 0.75 units AmpliTaq Gold (Life Technologies), 1.5 μL of MgCl, and 1.5 μL of Taq Gold buffer. Amplification reactions were done according to the following protocol: 95 °C for 8 min, (95 °C for 45 sec, 50 °C for 30 sec, 72 °C for 45 sec) × 35 cycles, 72 °C for 10 min. We visualized products of the polymerase chain reaction on a 1% agarose gel, then cleaned with Exo-Sap-It (USB Corporation). Using BigDye 3.1 chemistry (Life Technologies), we sequenced the products with external primers and read them with an ABI 3130 automated sequencer. We assembled the sequences and inspected them manually with Sequencher 4.7 (GeneCodes). We used the software packages Muscle (Edgar 2004) and Phyml (Guindon and Gascuel 2003), respectively, to align the sequence with previously published ND2 sequences and analyze it phylogenetically. We used the program Mega (Kumar et al. 2008) to calculate average uncorrected pairwise distances between MSB 37575 and the four major clades identified by Spellman and Klicka (2007).
RESULTS

Plumage

The forecrown of MSB 37575 is dark blue, while the hindcrown and nape are black, contrasting with the white face and sides of the neck. The black of the nape expands out toward the anterior edge of the mantle. The mantle is pale bluish gray, notably lighter than the dark bluish gray of S. c. nelsoni (Figure 1). The tertials of MSB 37575 are also pale bluish gray with black inner webs, while the tertials of S. c. nelsoni are darker blue and less contrasting than those of MSB 37575 (Figure 1). The greater coverts are pale blue with large black centers and white edging on the distal ends of the feathers. The primaries are brownish with paler tips. The rectrices, except the pale blue central pair, are black with large white corners. The throat, upper breast, and...
lower belly are white with the belly and lower breast tinged buffy. The flanks of MSB 37575 are white with a pale salmon wash, while the flanks of S. c. nelsoni are bluish gray (Figure 2). The undertail coverts are white with limited rufous edging on some feathers.

Measurements

The exposed culmen of MSB 37575 measures 17.1 mm, which fits with our measurements for 13 female eastern White-breasted Nuthatches (mean 17.3 mm, SD 1.0; Table 1). It is below the range of our measurements of 15 female specimens of S. c. nelsoni from New Mexico and Arizona (range 17.5–19.8 mm; Table 1).

Molecular Results

We successfully amplified and sequenced a 968-base-pair fragment of the ND2 gene. Chromatograms of the sequence were clear and unambiguous, without double peaks or internal stop codons that would indicate the erroneous amplification of a nuclear pseudogene. The complete sequence is available at Genbank (accession no. JQ965152). Comparison with published sequences of the White-breasted Nuthatch confirmed that MSB 37575 is part of the eastern clade with 100% bootstrap support. Over the area sequenced, the ND2 gene from MSB 37575 is a 100% match with published haplotypes of S. c. carolinensis from Michigan and Pennsylvania (haplotypes E11, E19, and E23 in Spellman and Klicka 2007). The average pairwise difference between the New Mexico specimen and sequences from other eastern specimens was 0.3% (Table 2). Average divergences between the New Mexico specimen and the other clades were substantially higher: 3.8% with the Pacific clade, 6.3% with the Rocky Mountain, Great Basin, and Mexico clade, and 6.9% with the eastern Sierra Nevada clade (Table 2).

DISCUSSION

MSB 37575 can safely be identified as an eastern White-breasted Nuthatch on the basis of measurements, plumage color, and mitochondrial DNA sequence. The bill measurements are within the expected range of the eastern subspecies but below the range of S. c. nelsoni, resident in New Mexico, on the basis of measurements from a series of specimens. The most noticeable plumage features distinguishing eastern and western populations are the mantle color, flank color, and the degree of contrast on the tertials, and these differences are consistent between the sexes. In S. c. carolinensis and MSB 37575, the mantle and tertials are pale bluish gray, making the black inner webs of the tertials contrast sharply, while the mantle of western populations is dark bluish gray and the tertials are less contrasting (Figure 1). S. c. carolinensis and MSB 37575 show whitish flanks with a pale salmon wash, while S. c. nelsoni has bluish gray flanks (Figure 2). These plumage distinctions can be used in the field, with care, by birders or banders for subspecific identification and are described in several widely used identification guides (Pyle 1997, Sibley 2000, Dunn and Alderfer 2011).

Molecular data corroborate the morphological analysis. The mitochondrial
DNA sequence matches published sequences that are phylogenetically nested within the deeply divergent eastern clade, with 100% bootstrap support. Because the geographic sampling of published sequences is thorough, the only reasonable explanation for these data is that MSB 37575 originated within the range of *S. c. carolinensis*. The approximate western limit of *S. c. carolinensis* extends from central Texas north through central Oklahoma, central Kansas, northeastern Colorado, western Nebraska, and the Dakotas to southern Manitoba (AOU 1957, 1998, Grubb and Pravosudov 2008, Sullivan et al. 2009, Such and Such 2012; ). As northern populations of *S. c. carolinensis* move irruptively (Heintzelman and MacClay 1971), primarily in fall (Phillips et al. 1964, Phillips 1986), the occurrence of this subspecies in New Mexico should be expected, especially given the closeness of breeding populations and the subspecies’ apparent regularity in eastern Colorado during migration (Leukering et al. 2012). It is likely that many observed seasonal movements represent young of the year dispersing farther in higher numbers in late summer and fall (Grubb and Pravosudov 2008). MSB 37575 was in its first year on the basis of 30% skull ossification and the presence of a bursa of Fabricius.

Previous reports suggest that other eastern White-breasted Nuthatches have occurred in New Mexico. C. R. Rustay (pers. comm.) heard a White-

**Table 1** Measurements of Exposed Culmen (mm) of MSB 37575, *Sitta c. carolinensis*, and *S. c. nelsoni*, by Sex

<table>
<thead>
<tr>
<th>Subspecies or specimen</th>
<th>Sex</th>
<th>n</th>
<th>Exposed culmen (mean, mm)</th>
<th>SD</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>MSB 37575</td>
<td>F</td>
<td>—</td>
<td>17.1</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>S. c. carolinensis</em>a</td>
<td>F</td>
<td>13</td>
<td>17.3</td>
<td>1.0</td>
<td>15.0–18.5</td>
</tr>
<tr>
<td><em>S. c. nelsonib</em></td>
<td>F</td>
<td>15</td>
<td>18.3</td>
<td>0.6</td>
<td>17.5–19.8</td>
</tr>
<tr>
<td><em>S. c. carolinensis</em>a</td>
<td>M</td>
<td>16</td>
<td>17.6</td>
<td>0.9</td>
<td>15.9–18.7</td>
</tr>
<tr>
<td><em>S. c. nelsonib</em></td>
<td>M</td>
<td>15</td>
<td>19.5</td>
<td>0.7</td>
<td>18.1–20.5</td>
</tr>
</tbody>
</table>

*a Specimens from Kansas in the University of Kansas Museum of Natural History

*b Specimens from New Mexico and Arizona in the Museum of Southwestern Biology.

**Table 2** Mean Levels of Percent Divergence (p) in the Mitochondrial Gene ND2 between the MSB 37575 and the Four Major Clades of *Sitta carolinensis*

<table>
<thead>
<tr>
<th></th>
<th>(1)</th>
<th>(2)</th>
<th>(3)</th>
<th>(4)</th>
</tr>
</thead>
<tbody>
<tr>
<td>MSB 37575</td>
<td>0.003</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eastern clade</td>
<td>0.038</td>
<td>0.038</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pacific clade</td>
<td>0.063</td>
<td>0.061</td>
<td>0.073</td>
<td></td>
</tr>
<tr>
<td>Rocky Mountain, Great Basin, and Mexico clade</td>
<td>0.069</td>
<td>0.068</td>
<td>0.080</td>
<td>0.017</td>
</tr>
</tbody>
</table>

*a As defined by Spellman and Klicka 2007.*
breasted Nuthatch giving “yenk” calls like those of S. c. carolinensis at Hillcrest Park on 18 December 2010 in Clovis. Similarly, White-breasted Nuthatches have been heard giving vocalizations reminiscent of the eastern subspecies in the Corrales bosque (~35° 14’ N, 106° 35’ W), Sandoval County, on several occasions between December and March (Williams and Howe 2011). As of December 31 2006, the Melrose migrant trap (~34° 26’ N, 103° 48’ W), Roosevelt County, had four records of the White-breasted Nuthatch on dates ranging from 1 August to 21 September (Parmeter 2007), but none of these individuals was identified to subspecies. Additionally, Wyoming has a single report of a vocal eastern White-breasted Nuthatch from Rawhide Wildlife Habitat Management Unit, Goshen County, in April (Faulkner 2010).

Four subspecies of White-breasted Nuthatch have been described from the eastern United States: S. c. carolinensis, S. c. cookei, S. c. atkinsi, and S. c. litorea (Oberholser 1917, AOU 1957, Phillips 1986, Dickinson 2003). An analysis of the eastern White-breasted Nuthatches by Wood (1992), however, found much of the variation to be clinal, with no appreciable difference in back coloration. For this reason, he proposed that all eastern White-breasted Nuthatches should be considered one subspecies, S. c. carolinensis. Spellman and Klicka (2007) subsequently found that all of the eastern populations are monophyletic by mtDNA, with little or no geographic structure. The eastern clade of the White-breasted Nuthatch may warrant species status on the basis of its deep level of molecular divergence, reciprocal monophyly, and morphological and vocal distinctness (Spellman and Klicka 2007, Walstrom et al. 2011).

In conclusion, MSB 37575 represents the first confirmed eastern White-breasted Nuthatch for the state of New Mexico. Its occurrence there has been reported on several occasions, and it likely occurs with some regularity on the eastern edge of the state. White-breasted Nuthatches found in New Mexico should be scrutinized for potential vagrants of the eastern or other subspecies, particularly during fall migration and when found away from areas of known breeding. Identification should be based on a combination of characters, potentially including vocalizations, back and flank color, tertial pattern, bill length, and mitochondrial DNA.

ACKNOWLEDGMENTS

We thank Andrew B. Johnson for curation of MSB 37575. We thank Nicholas D. Pederson and Cole J. Wolf for their assistance in the field. We thank Natalie A. Wright and Mark B. Robbins for help obtaining measurements from the University of Kansas Museum of Natural History. The University of Arizona (George Bradley and Alex Badyaev) provided a loan of specimens. We thank John P. Hubbard for his assistance on previous records of the White-breasted Nuthatch in New Mexico. William H. Howe and Christopher R. Rustay provided valuable information about previous experience with probable eastern White-breasted Nuthatches in New Mexico. We thank Gregg Moore for allowing access to his property for our field work. We thank Doug Faulkner, Kimball Garrett, and Philip Unitt for perceptive comments on the manuscript.
EASTERN WHITE-BREASTED NUTHATCH IN NEW MEXICO

LITERATURE CITED


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CHRONIC LOW REPRODUCTIVE SUCCESS OF THE COLONIAL TRICOLORED BLACKBIRD FROM 2006 TO 2011

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ABSTRACT: I studied the Tricolored Blackbird (Agelaius tricolor) in California's Central Valley over six breeding seasons from 2006 through 2011 and documented fates of nesting attempts, reproductive success of colonies, and relative abundance of insect prey in foraging areas. I found widespread and chronic reproductive failures except in cases of relatively high insect abundance. My observations suggest that the productivity of Tricolored Blackbird colonies is food-limited and that the relatively high reproductive success at few colonies is primarily a function of unusually high abundance of insects in nearby foraging areas.

The Tricolored Blackbird (Agelaius tricolor) forms the largest breeding colonies of any North American songbird (Beedy and Hamilton 1999). Over 99% of the world’s population occurs in California, with small numbers also in Washington, Oregon, Nevada, and Baja California (Beedy and Hamilton 1999). In California, for decades the largest colonies and the vast majority of the population have occurred in the Central Valley (Neff 1937, Beedy and Hamilton 1999, Cook and Toft 2005).

Over the 20th century, the number of Tricolored Blackbirds plummeted from habitat loss through conversion to agriculture and urbanization, market hunting, poisoning, and the birds being shot as an agricultural pest (Neff 1937, Beedy and Hamilton 1999). This decline resulted in a petition by the Center for Biological Diversity to list this blackbird under the state and federal endangered species acts (CBD 2004). Although these petitions were declined, the Tricolored Blackbird is considered a federal species of conservation concern (USFWS 2008) and a California Bird Species of Special Concern (Shuford and Gardali 2008).

Recent statewide surveys and intensive monitoring of colonies in the Central Valley have shown that its abundance has continued to decline, falling 35%, from about 400,000 to 250,000 individuals, from 2008 to 2011 (Kyle and Kelsey 2011, Meese 2011).

Large numbers formerly nested in coastal marshes in southern California (Baird 1870, Neff 1937, Unit 2004), but workers in this region have recently documented severe population declines in this population segment (Unit 2004, Feenstra 2009).

I report here on field work in the Central Valley over six breeding seasons, from 2006 through 2011, during which I sought to detect, monitor, and estimate the productivity of each of the Tricolored Blackbird’s largest breeding colonies. Key goals were to examine the relationship between the blackbird’s reproductive success and insect abundance and to use these results to inform conservation decisions intended to increase the species’ numbers.
LOW REPRODUCTIVE SUCCESS OF THE COLONIAL TRICOLORED BLACKBIRD

METHODS

My field work from 2006 to 2011 covered the Tricolored Blackbird's breeding season from late March through July, addressing the following topics.

Surveys of Previously Occupied Locations

I began surveys in early spring in the San Joaquin Valley, where Tricolored Blackbirds breed for the first time each season (Hamilton 1998), then moved north to the Sacramento Valley as the season progressed (Figure 1). I surveyed by car on public roads the locations of all previously occupied colonies known by or reported to me. I was especially interested in documenting those colonies where the nesting substrate is ephemeral, primarily grain fields near dairies, as these colonies were at risk from loss of nests by the harvest of triticale, a wheat (Triticum) × rye (Secale) hybrid grown for dairy cows (Beedy and Hamilton 1999, Cook and Toft 2005, pers. obs.; Figure 2).

Surveys for New Locations

I supplemented the surveys of existing colony locations with intensive searches for new ones in grain and weedy fields adjacent to dairies and in freshwater wetlands in state wildlife areas, national wildlife refuges, and accessible private duck clubs. In both the San Joaquin Valley and southern California, from the 1980s to the present, many of the largest colonies have been located adjacent to dairies (Beedy and Hamilton 1999). Therefore, to enhance colony detection, I used available GIS layers to map the locations of all dairies in the San Joaquin Valley, then transferred these locations to paper maps that I took into the field to guide survey efforts.

After birds completed their breeding efforts in the San Joaquin Valley, I used similar methods to survey for colonies in the Sacramento Valley. I surveyed locations of previously documented colonies and sites that had been reported to me by numerous collaborators (state and federal agency personnel, observers posting messages to the central_valley_birds listserv, birders) or entered into the Tricolored Blackbird Portal (http://tricolor.ice.ucdavis.edu).

Colony Monitoring

I monitored colonies from within days of the arrival of adults and the initiation of breeding until breeding ceased and the adults had departed. In most cases, I monitored colonies twice a week to assess current conditions and the colony's chronology to estimate the optimal times for making estimates of reproductive success and the size of the breeding population. Monitoring entailed making observations from the closest public road for colonies located on private property that I lacked permission to access, or from immediately adjacent roads for colonies located on public property or on private property I had permission to access.

Estimating Area Occupied

I estimated the dimensions of the available nesting substrate and the area occupied by breeding birds in one of two ways. On public or private property
with access, I measured these dimensions directly with a hand-held GPS. On private property where I lacked access, I visually estimated these dimensions from a distance and sketched them in a field notebook. The area occupied by breeding Tricolored Blackbirds is reliably estimated from careful observation of the birds’ behavior, as birds leave and return to nests at intervals defined by the stage of the breeding cycle. The interval is longest when females are incubating eggs, shortest when females are building nests or when both adults are feeding young. I confirmed the perimeter of the occupied area as initially outlined by the birds’ behavior through subsequent monitoring. To

Figure 1. Locations of Central Valley Tricolored Blackbird colonies studied from 2006 to 2011. Numbers correspond to records in Table 1. Some locations were occupied in more than 1 year (see Table 1).
measure the size of the occupied area, I plotted both the dimensions from visual estimates and the coordinates measured by GPS into Google Earth. After birds had finished breeding, I also searched accessible but apparently unoccupied areas to confirm the absence of nests.

Estimating the Number of Breeding Birds

I estimated the number of breeding birds in a colony either visually at the time of nesting and/or by sampling nests after the breeding season. I made visual estimates of the number of breeding birds each time I monitored a colony by carefully observing it for 5–30 minutes per visit. When possible, I observed colonies from multiple vantage points to enhance detection and to increase the precision of the estimate.

At sites to which I was granted access, I re-entered colonies after the young had fledged and both young and adults had left the area and estimated nest densities by one of two methods depending on the nesting substrate. In relatively impenetrable substrates, such as some colonies established in milk thistle (\textit{Silybum marianum}) or in Himalayan blackberry (\textit{Rubus armeniacus}), I counted nests within samples of randomly placed 1- × 2-m sampling frames of 2-cm PVC pipe. In all other nest substrates, I counted nests within line transects 2 m wide and varying in length from 20 to 100 m. I marked the start and end points of transects by a handheld GPS unit and computed the transects’ lengths by GPS or by the length-measurement tool in Google Earth.

Using the densities of nests in the sampled areas, I calculated the number of nests in the colony by multiplying the average number of nests per hectare by the number of hectares occupied by breeding birds. I assumed that on average each male breeds with two females (Beedy and Hamilton 1999) so multiplied the number of nests by 1.5 to estimate the number of breeding birds at a colony. This provided an independent estimate of the number of breeding birds for comparison with my visual estimate during monitoring.

Estimating Relative Abundance of Insects

Each time I monitored a colony I spent 15–60 minutes observing the flight lines of actively foraging birds, which typically move back and forth from the colony to foraging destinations along nearly single-file flight paths. These
flight lines are conspicuous and persistent (Hoffmann 1927, Beedy and Hamilton 1999) and typically consist of several hundred to several thousand birds (pers. obs.). The distances from the colonies to foraging destinations varied from tens of meters to 9 km (Table 1).

After determining the foraging destinations, I walked or drove to the areas where the largest numbers of birds were actively foraging and, where permissible, I visually estimated the relative abundance of insects in terrestrial habitats by walking (at a pace of 1 step every 3–5 seconds) over the substrate where birds had been foraging moments before and counting the number of insects seen. I waded in rice paddies adjacent to large colonies in Yuba and Colusa counties and supplemented my visual observations by reaching into and sweeping the muddy substrate with my fingers extended in an attempt to detect aquatic insect larvae.

I subsequently categorized the number of insects observed per minute as low (1–10), moderate (11–100), or high (>100; Table 1). I estimated the relative abundance of insects 3–6 times per site within a 4-week interval while the site was occupied by breeding birds.

Estimating Reproductive Success

I estimated reproductive success, defined as the average number of young fledged per nest, either by visual estimates or by sampling. Visual estimates were derived from the number of breeding birds estimated visually during monitoring and the number of fledglings observed at the end of the breeding season. As one male breeds, on average, with two females (Beedy and Hamilton 1999), each two nests have three birds associated with them, so the product of the number of breeding birds multiplied by 2/3 provides an estimate of the number of nests constructed. The visual estimate of the number of young fledged divided by the estimate of the number of nests constructed yields an estimate of the number of young fledged per nest.

For accessible colonies, prior to the fledging of young, I estimated reproductive success by counting the contents of a random sample of nests when the average age of nestlings was 7 to 9 days and calculated reproductive success by dividing the number of young by the number of nests in the sample.

Estimating the Number of Young Produced

I estimated the number of young produced at a colony by repeated observations of young in groups (“crèches”) following fledging and/or by multiplying the number nests constructed times the average reproductive success of sampled nests (see above).

At most colonies, the number of fledged birds may be counted. After fledging, the young spend a minimum of several days in groups, perching and begging conspicuously from the tops of vegetation at the colony’s margins (Beedy and Hamilton 1999, pers. obs.). Typically, young begin to leave the nesting substrate to perch high in nearby shrubs or trees approximately 4 days after fledging. However, crèches remain within the colony’s boundaries for up to 2 weeks or more if there are no nearby taller shrubs or trees, as is often the case in the “silage belt” of the southern San Joaquin Valley (pers. obs.).
LOW REPRODUCTIVE SUCCESS OF THE COLONIAL TRICOLORED BLACKBIRD

Statistical Analyses

I used Spearman’s rank correlation to test for a relationship between insect abundance and reproductive success and Pearson’s product-moment correlation to test for a relationship between colony size and reproductive success. I used a Kruskal–Wallis test to evaluate potential relationships between reproductive success and breeding season, type of nesting substrate, and the location of colonies by county. I excluded Butte County from the analysis for counties as I estimated reproductive success at only one site there. Finally, I used a Mann–Whitney test to look for a difference in reproductive success between the San Joaquin and Sacramento valleys and between colonies near and distant from dairies.

RESULTS

During the 6 years of this study the Tricolored Blackbird’s reproductive success across all sites and years averaged 0.62 young fledged/nest (540,000 young fledged from 870,000 nests; Table 1). Only 11% of the colonies studied (5/47) fledged an average of 1 or more young per nest.

The relative abundance of insects on foraging substrates varied greatly by site and year, from a low of zero insects per 10 minutes of searching in the case of larvae of the water scavenger beetle (Coleoptera: Hydrophilidae) or other insects in rice paddies in Colusa County in 2007 to a high of over 1000 individuals per 10 minutes of searching in the case of grasshoppers in open pasture near a colony in Merced County in 2010 (Table 1). Within a site and year, however, estimates of relative abundance of insects varied little: at any single colony, they did not differ spatially or temporally.

Insect abundance was positively correlated with reproductive success (Spearman’s rank correlation coefficient \( \rho = 0.737, P << 0.05 \)), and the colony with the highest reproductive success (1.44), situated in milk thistle in Merced County in 2010, was surrounded by open rangeland in which grasshoppers were extraordinarily abundant (Table 1).

Colony size was positively correlated with reproductive success (\( r = 0.53, r^2 = 0.28 \)). Reproductive success did not differ by type of nesting substrate (Kruskal–Wallis \( H = 6.049, P = 0.109 \)), year (Kruskal–Wallis \( H = 8.8, P = 0.117 \)), or county (Kruskal–Wallis \( H = 7.841, P = 0.165 \)). The presence of a dairy did not affect reproductive success (Mann–Whitney \( U = 208, P = 0.298 \)), and the reproductive success of colonies in the San Joaquin and Sacramento valleys was similar (Mann–Whitney \( U = 189.5, P = 0.41 \)).

DISCUSSION

The Tricolored Blackbird’s reproductive success was chronically low throughout the Central Valley, in all six breeding seasons studied from 2006 to 2011, and in all types of nesting substrate. Higher reproductive success was associated with greater abundance of favored insect groups in foraging habitats surrounding colonies and was not associated with dairies.

Both terrestrial and aquatic insects varied widely in abundance. Caterpillars and grasshoppers dominated the terrestrial prey and dragonflies and larval
### Table 1 Distribution, Characteristics, and Reproductive Success of Tricolored Blackbird Colonies Studied in California’s Central Valley, 2006–2011

<table>
<thead>
<tr>
<th>Year and site&lt;sup&gt;a&lt;/sup&gt;</th>
<th>County</th>
<th>Nesting substrate</th>
<th>No. breeding birds</th>
<th>Foraging substrates</th>
<th>Distance to primary foraging destinations</th>
<th>Insect groups taken</th>
<th>No. insect samples/relative insect abundance</th>
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<tbody>
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<td>2006</td>
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<th>Year and site</th>
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<th>Distance to primary foraging destinations</th>
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<td>Year and site&lt;sup&gt;a&lt;/sup&gt;</td>
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</table>

<sup>a</sup>See Figure 1 for locations.
water scavenger beetles dominated the aquatic insects foraging Tricolored Blackbirds chose. My attempts to estimate the relative abundance of aquatic insects were unsuccessful, as I observed no larval aquatic insects while sampling. The only aquatic insects observed in abundance were recently hatched dragonflies (giant green darners, *Anax junius*) at one site in Yuba County in 2007 and hatching caddisflies (Trichoptera) at one site in Kern County in 2009. The dragonflies hatched in mid-July, when only a single blackbird colony was known to be active, and although they were extremely abundant and easily captured, they were fed primarily to fledglings and emerged too late to result in high productivity at this colony. The caddisfly hatch was similarly dramatic but brief, lasting less than an hour, and did not appear to enhance the blackbirds’ productivity. It is possible that greater overlap between the Tricolored Blackbird’s breeding season and the peak of dragonfly hatching would have enhanced the blackbirds’ reproductive success, but aquatic insects, as a group, did not appear to contribute to high reproductive success at any colony I studied.

Previous researchers have documented poor reproductive success of Tricolored Blackbird colonies, but mine is the first study to confirm low reproductive success at colonies throughout the Central Valley over a 6-year interval and the first to assess insect abundance at sites where breeding birds forage. The reproductive success of entire colonies can be reduced severely by both mammalian and avian predators (reviewed by Beedy and Hamilton 1999), but rates of predation are highly variable in space and time and, until recently, predators have not been known to cause sustained reproductive failures of multiple colonies across a wide geographic area. Since 2006, predation by Cattle Egrets (*Bubulcus ibis*) has caused nearly complete reproductive failures of even very large colonies in Tulare County (Meese 2012), but predation by Cattle Egrets on Tricolored Blackbird eggs and nestlings is unknown outside of Tulare County. The lack of influence of substrate type on reproductive success also suggests that predation is not responsible for the widespread and sustained reproductive failures I documented, as some substrates with thorns or stinging hairs, such as Himalayan blackberries and stinging nettles (*Urtica dioica*), appear to confer some defense against predators, while others lacking such armaments, such as cattails (*Typha latifolia*), are believed to expose nesting blackbirds to higher rates of predation (Beedy and Hamilton 1999, Cook and Toft 2005).

Beedy and Hayworth (1992) documented the reproductive failure of a colony in Merced County and found that lethal levels of selenium were likely responsible for mortality of nestlings and the failure of this colony. To my knowledge, theirs is the only study that has attributed a colony’s failure to environmental contaminants, but because the potential role of environmental contaminants in reducing the blackbird’s productivity has not been assessed, it deserves further study.

Food limitation is known to reduce reproductive success in many groups of birds (reviewed by Martin 1987), but my study provides evidence of food-limited reproduction that is spatially widespread and temporally persistent. The Tricolored Blackbird’s reproductive success was low despite the diverse array of foods the species consumes, as documented in this and previous studies (Skorupa et al. 1980), and despite the suggestion that a diverse diet
might allow the blackbird to exploit alternate food sources when a preferred food is limited by weather or other conditions (Crase and DeHaven 1977). During my study, a generalized diet did not appear to provide insurance against food-limited reproductive failures, and relatively high reproductive success was associated with exceptional abundance of a narrow range of favored insect groups (Table 1).

Reproductive success did not differ by major geographical region (San Joaquin vs. Sacramento Valley) or by county of the Central Valley. These results may affect management intended to increase the numbers of tricolors as they suggest there is no temporal or geographical basis for making conservation investments. Thus, all else being equal, efforts intended to benefit a year’s first attempts at breeding in the San Joaquin Valley should be as effective as efforts intended to benefit subsequent attempts in the Sacramento Valley.

I found no effect of nesting substrate on reproductive success. This result differs from that of Cook and Toft (2005), who found that the proportion of colonies suffering complete reproductive failure was greater in native wetlands than in upland substrates. Those authors attributed the differences to rates of predation being higher in wetlands than in uplands. However, Cook and Toft (2005) did not measure insect abundance in nearby foraging areas and did not directly observe predators in blackbird colonies, so comparing my results to theirs is difficult. If rates of predation are substrate-dependent, as suggested by Cook and Toft (2005), the absence of substrate-related differences suggests that predators are not responsible for the chronically low reproductive success I documented.

The Tricolored Blackbird’s low reproductive success from 2006 to 2011 may help to explain the decline in its abundance observed from 2008 to 2011, when methodologically similar statewide surveys of the species found a drop from 400,000 to 258,000 birds (Kelsey 2008, Kyle and Kelsey 2011). Although additional field work is needed to determine whether this recent decline is part of a longer-term trend, the chronically low reproductive success through the breeding season of 2011, which did not figure into the results of the 2011 statewide survey, suggests that the decline in abundance will continue.

Since the 1980s, numerous large dairies have been located in the southern San Joaquin Valley, and dairies appear to be attractive to Tricolored Blackbirds, as for decades some of the largest colonies have been established in grain fields adjacent to dairies (Beedy and Hamilton 1997; Figure 2). The grains stored to feed the dairy cattle appear to provide an ad libitum food source, and the large fields of triticale provide nesting substrate, as the stems of triticale plants are taller and stronger than are the stems of other grains and capable of supporting blackbird nests. Although the stored grains may provide a superabundant food supply, however, they appear to be insufficient to sustain breeding because the reproductive success of colonies adjacent to dairies is as low as that of colonies distant from dairies. To form eggs, breeding females require relatively high levels of essential amino acids and essential fatty acids, and these essential compounds are found in higher proportion in insects than they are in grains (Carey 1996, Ramsay and Houston 1998). In addition, nestling blackbirds require animal foods and do not eat plant materials for the first 9 days of life (Crase and DeHaven 1977, Skorupa et
LOW REPRODUCTIVE SUCCESS OF THE COLONIAL TRICOLORED BLACKBIRD

al. 1980), until they are almost ready to fledge. The dietary requirements of breeding female and nestling blackbirds may help to explain why the reproductive success of colonies adjacent to dairies is low despite the virtually unlimited availability of grains. Additional research is needed to assess the effects of a granivorous diet on clutch size, egg hatchability, rates of brood reduction (Beedy and Hamilton 1999), and nestling starvation.

The apparent attraction to and use of stored and provided grains extends beyond the breeding season and dairies in the San Joaquin Valley. Aggregations of thousands of birds are also observed around dairies and feedlots in winter, especially at dairies at Point Reyes National Seashore in Marin County, around feedlots near Birds Landing in southern Solano County, and at several sites in Merced County (pers. obs.). Given the large number of birds at sources of grain available ad libitum, both the breeding and winter distributions may be influenced if not determined by the sources of these grains. Across much of its range, the Tricolored Blackbird may be largely dependent on grains provided for livestock as a replacement for natural foods that have been lost to agriculture and urbanization, although my results suggest that a granivorous diet is insufficient to support the species’ breeding.

The colonies I studied represent most of the largest colonies documented during this 6-year interval and represent the entire geographic range of the largest colonies of the Tricolored Blackbird (Kelsey 2008, Kyle and Kelsey 2011). Although these colonies had the greatest proportional potential to contribute to the productivity of the species, the chronic poor reproductive success of the largest colonies suggests that they may not serve as an effective core of a conservation strategy. Colonies adjacent to dairies, for decades many of the largest colonies, appear to serve as ecological traps (Dwernychuk and Boag 1972), fledging relatively few young in most years. Entire colonies are also lost when the triticale in which the birds nest is harvested during normal agricultural operations (Beedy and Hamilton 1997, Cook and Toft 2005, pers. obs.), although I included none of these harvested colonies in this analysis.

During the 6 years of my study, the Tricolored Blackbird has experienced chronic, widespread low reproductive success apparently because insects are insufficient. These results support the view expressed by DeHaven et al. (1975) that reductions in the Tricolored Blackbird’s abundance from the 1930s to the 1970s were due at least partially to limitation of its food supply through loss of foraging habitat. This loss of foraging habitat may result in a decline in productivity over a period of years that is difficult to detect, but that decline may ultimately lead to the situation where, despite the availability of suitable nesting substrate, tricolors abandon colonies or decline to extinction in an area where they formerly were abundant. This mechanism is believed to be responsible for the decimation of the species in southern California (Unit 2004, Feenstra 2009) and Baja California (Erickson et al. 2007, Erickson and de la Cueva 2008).

The relationships I describe here suggest that the Tricolored Blackbird’s habit of colonial breeding and the requirements of egg-forming females and nestlings to consume insects place a great burden upon landscapes within the 9-km radius of a colony within which the birds forage (Hamilton and Meese 2006) and that food limitation, not predation, is responsible for widespread,
chronic low reproductive success. These results suggest that future investments in conservation should stress nesting substrates that are free from possible destruction during harvest and are surrounded by secure, productive foraging habitats. The variety of foraging substrates Tricolored Blackbirds use suggests a degree of flexibility in choices of conservation strategies, as both agricultural (alfalfa and sunflowers) as well as native (non-irrigated pasture) foraging habitats supported colonies with relatively high reproductive output (this study and unpubl. data). Where the blackbird’s productivity is a priority in agricultural settings, crops that serve as foraging substrates should not be sprayed with insecticides so as to maximize insect abundance. In regions of extensive pasturelands or grasslands where secure nesting substrates may be absent, management should stress the provision and maintenance of secure nesting substrates. As with foraging substrates, there are several options for nesting substrates, as nesting tricolors use a wide variety of native and non-native vegetation (Table 1).

The conservation of the Tricolored Blackbird will require strategic choices that take into account the species’ unique needs. California’s Central Valley, where for decades the majority of blackbirds have occurred (Neff 1937, Beedy and Hamilton 1997), has been transformed from its origin as a vast region of wetlands and vernal pools (Frayer et al. 1989), capable of supporting millions of birds (extrapolated from Neff 1937), to an agricultural heartland that provides much of the nation’s fresh fruits, nuts, and dairy products (American Farmland Trust 1989) but which is unsuitable for foraging blackbirds. The future of the Tricolored Blackbird depends upon resources in California’s Central Valley that appear in most years to be in short supply, and this future is made uncertain by competition between the needs of a colonial species and land uses that limit the range of strategic conservation choices.

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DIET AND HOME-RANGE SIZE OF CALIFORNIA SPOTTED OWLS IN A BURNED FOREST

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ABSTRACT: Fire is pervasive in forests used by California Spotted Owls (Strix occidentalis occidentalis) and their prey species. We assessed the diets and sizes of the breeding-season home ranges of seven Spotted Owls occupying burned forests in the southern Sierra Nevada 4 years after a fire and compared the results with data from previous studies in unburned forests within the range of the subspecies. Prey captured by owls in the burned area comprised 40.3% (by biomass) pocket gophers (Thomomys spp.) and 25.9% northern flying squirrels (Glaucomys sabrinus). In contrast, in unburned areas of the Sierra Nevada Spotted Owls fed primarily on flying squirrels, or on both flying squirrels and woodrats (Neotoma spp); in unburned southern California forests they fed overwhelmingly on woodrats. The owls’ mean home range in the burned forest covered 402 ha, an area similar to that recorded in unburned forests of the Sierra Nevada. Our results are consistent with hypotheses that the burned habitat in our study area was rich in gophers and that Spotted Owls foraging on gophers in burned forests do not require home ranges substantially larger than do owls in unburned forests. With currently available data we could not conclusively attribute variation in diet or home-range size to the influence of fire, so further testing is warranted. Use of rodenticides and herbicides in managing burned Spotted Owl habitat may reduce the owl’s key prey.

The California Spotted Owl (Strix occidentalis occidentalis) occurs in mixed-conifer and montane hardwood forests throughout the Sierra Nevada and the mountain ranges of southern California (Verner et al. 1992, Gutiérrez et al. 1995). Its vital rates are positively associated with large areas of older conifer-dominated forest and related conditions (Blakesley et al. 2005, Seamans 2005), and within its range the subspecies is viewed as an indicator for management of these forest types.

Forest fire is one of the most important issues affecting the Spotted Owl’s habitat (Weatherspoon et al. 1992). California Spotted Owls typically occupy older forests with greater canopy cover (Bias and Gutiérrez 1992, Call et al. 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004), and this has led to the presumption that fires of moderate and high severity reduce the owl’s survival and pose a significant risk to its habitat (Weatherspoon et al. 1992, U.S. Forest Service 2001, 2004, 2005). However, Spotted Owls can occupy territories and continue to reproduce in burned habitats, including those with large severely burned patches (Gaines et al. 1997, Bond et al. 2002, Jenness et al. 2004, Bond et al. 2009). Franklin et al. (2000) hypothesized that fire could enhance the abundance of and access to prey for the Northern Spotted Owl (S. o. caurina) in California by creating patchy openings in the forest canopy and increasing habitat edges. Indeed, four years after a large, patchy fire in the southern Sierra Nevada, California Spotted Owls selectively foraged in burned forest rather than unburned forest, with the strongest selection for severely burned patches (Bond et al. 2009).
Prey composition is an important determinant of raptors’ use of space (Peery 2000). Zabel et al. (1995) found that prey species predicted the size of the Northern Spotted Owl’s home range in California better than the proportion of older forest in the home range, and Carey et al. (1992) reported that the prey base strongly influenced the size of the Northern Spotted Owl’s home range in Oregon. In both studies, owls with a greater percent biomass of larger prey in their diet had home ranges smaller than those of owls that consumed more of the smaller prey species. Ward et al. (1998) documented that in California Northern Spotted Owls selected foraging sites according to the distribution of larger prey (e.g., woodrats), which provided an energetic benefit to the owls. The California Spotted Owl’s major prey items by biomass are the dusky-footed and big-eared woodrats (Neotoma fuscipes and N. macrotis), northern flying squirrel (Glaucomys sabrinus), and pocket gophers (Thomomys spp.; Thraikill and Bias 1989, Williams et al. 1992, Smith et al. 1999, Munton et al. 2002).

Despite the importance of fire in shaping ecosystems in portions of the Spotted Owl’s range, little is known about the diets and home-range sizes of owls occupying recently burned forests. Understanding the California Spotted Owl’s prey base and space use in burned forests is important because fire is frequent in this subspecies’ habitat, and it is not unusual for owls to continue to occupy and breed in burned forests (Bond et al. 2002, 2009, Roberts et al. 2011). Furthermore, forest management after a fire can include removal of fire-killed trees and applications of rodenticide and herbicide in efforts to enhance the growth of tree seedlings (McGinnis et al. 2010, Swanson et al. 2011), possibly to the detriment of foraging Spotted Owls and their prey. Our objective was to assess the breeding-season diet and estimate the sizes of the home ranges of California Spotted Owls occupying territories in recently burned mixed-conifer forests and compare the results with those of previous studies of owls in unburned forests. We note that the breeding-season home range may differ greatly from the year-round home range, as we have reported previously on the expanded winter movements of the same owls addressed in this study (Bond et al. 2010).

Our sample of owls in burned forests was relatively small (seven owls from four territories), our study included only a single breeding season, and the data from unburned forests we used for comparison were recorded in different years and in different areas. Therefore, rather than testing how fire affected diets and home-range sizes, we report for the first time basic information about the diet and home-range sizes of the California Spotted Owl in a burned forest and address differences from those in unburned forests qualitatively—a basis for developing hypotheses about fire effects to be tested in future studies.

METHODS

Study Areas

We estimated the diets and home ranges of California Spotted Owls during the breeding season of 2006 in forests burned by the 2002 McNally Fire in the Greenhorn Mountains and Kern Plateau in the Sequoia National Forest,
southern Sierra Nevada. Elevation ranged from 1500 m to 2500 m. In July and August 2002, the McNally Fire burned approximately 60,985 ha in the Sequoia and Inyo national forests, including 33,704 ha of conifer-dominated forests (Odion and Hanson 2006). Like most forest fires, the McNally Fire burned with variable severity, leaving a mosaic of severely burned, moderately burned, and unburned patches in the study area (Bond et al. 2009, 2010). Fires of high severity kill most existing vegetation and result in a forest structure dominated no longer by live trees but by herbs, shrubs, and dead trees, those of moderate severity cause patchwork mortality, and those of low severity rarely kill overstory trees and do not substantially alter the forest’s structure (Smith 2000).

For comparison with our burned study area we obtained data from previous studies of the diets and home-range sizes of California Spotted Owls in unburned forests elsewhere within the subspecies’ range (Thrailkill and Bias 1989, Call et al. 1992, Zabel et al. 1992, Smith et al. 1999, Zimmermann et al. 2001, Munton et al. 2002). Of these studies the nearest area matching ours in elevation was in the southern Sierra Nevada in the Sierra National Forest at 1220–2925 m elevation, 150 km north of the McNally Fire area. There Munton et al. (2002) studied the owl’s diet and Zabel et al. (1992) estimated the sizes of home ranges of radio-marked owls during the breeding season of 1988. Farther north in the central Sierra Nevada, in the Eldorado (elevation 266–2257 m) and Tahoe national forests (670–1585 m), respectively, Thrailkill and Bias (1989) studied Spotted Owl diets during the 1986 and 1987 breeding seasons and Call et al. (1992) estimated the sizes of home ranges of radio-marked Spotted Owls during the 1987 breeding season. South of the McNally Fire area in the San Bernardino Mountains, Smith et al. (1999) assessed the owl’s diet (elevation 1000–2500 m) and Zimmermann et al. (2001) estimated home-range sizes by radio telemetry (elevation 2000–2500 m).

In all the study areas summers are dry and hot, winters are wet and cold. At the Sierra Nevada study areas the vegetation is classified as Sierran Mixed Conifer (Allen 1988), dominated by ponderosa pine (Pinus ponderosa), Jeffrey pine (P. jeffreyi), and white fir (Abies concolor). Other common trees include sugar pine (P. lambertiana), incense-cedar (Calocedrus decurrens), canyon live oak (Quercus chrysolepis), and California black oak (Q. kelloggii). Above 2100 m, a transition zone is dominated by red fir (A. magnifica). Study areas in the central Sierra Nevada also included Douglas-fir (Pseudotsuga menziesii). In the San Bernardino Mountains study area the forest is dominated by bigcone Douglas-fir (Pseudotsuga macrocarpa), canyon live oak, coast live oak (Quercus agrifolia), and black oak below 1500 m, by Jeffrey pine, ponderosa pine, white fir, black oak, canyon live oak, sugar pine, incense-cedar, and western juniper (Juniperus occidentalis) above 1500 m (Stephenson and Calcarone 1999). Historically, fire regimes varied but most fires were of mixed severity (Skinner and Chang 1992, Weatherspoon et al. 1992, Minnich et al. 1995).
Field Methods

Prior to our study, U.S. Forest Service (USFS) personnel surveyed for and located California Spotted Owls within and near the McNally Fire’s perimeter during three consecutive breeding seasons, 2003–2005 (W. Rannals and R. Galloway, unpubl. data). During the 2006 breeding season we surveyed for California Spotted Owls by standard methods described by Franklin et al. (1996). We selected four territories confirmed to be occupied by pairs of Spotted Owls. We selected these territories because they were inside or within 1 km of the fire perimeter, Spotted Owls had occupied them continuously since the fire, and there was sufficient road access for effective radio-tracking. We captured the adult owls with mist nets or noose poles and fitted them with color bands and backpack-style radio transmitters (batteries with a life expectancy of 1 year) that were designed to minimize contact with the owl’s back (AVM Instrument Company, Colfax, CA). Radio transmitters were affixed with Kevlar ribbon (0.63 cm wide; Bally Ribbon Mills, Bally, PA). With the harness, the transmitter units weighed <20 g, or <4% of each owl’s body mass. We considered each individual owl as a separate sample because Call et al. (1992) and Zimmerman et al. (2001) found that male and female California Spotted Owls forage independently. All four pairs attempted to nest in 2006, and we located each nest tree. Three attempts failed (Mill Creek, Speas Ridge, Burnt Ridge), and one pair successfully fledged one young (Poison Creek).

From 22 May to 15 August 2006 we radio-tracked the seven owls (4 males and 3 females) by locating each owl nightly or every other night between 21:30 and 04:00. We used a systematic design with a random start to record a representative sample of foraging locations. We randomly assigned each owl to a 1-hour time block on the first night we tracked it, then systematically shifted each owl’s time block by 1 hour (or back to the first time block when the sequence was completed) on each subsequent night of sampling. To estimate the owls’ locations, we triangulated on signals from the radio transmitters from established stations and used at least three compass bearings of the strongest signals, taking all bearings within approximately 30 minutes (Guetterman et al. 1991). For comparison of the sizes of home ranges in our burned study area with those of owls occupying unburned areas, D. Call, T. Munton, and G. Zimmerman provided us with locations of foraging radio-marked Spotted Owls in the Tahoe (n = 7), Sierra (n = 8), and San Bernardino (n = 5) national forests, respectively, during the same seasonal window of mid-May to mid-August. These studies used field methods similar to ours to estimate locations of foraging (Call et al. 1992, Zabel et al. 1992, Zimmerman et al. 2001).

In addition to estimating locations of nighttime foraging, every 7–10 days we recorded the location of each radio-marked owl’s daytime roost. To assess the owls’ diets, we collected regurgitated pellets at roost sites. We included multiple pellets found together in the same location as a single sample because remains of a single animal can be egested in more than one pellet (Forsman et al. 1984).
Data Analyses

We used digital maps and the GIS extension Fragstats (McGarigal et al. 2002) to calculate the area of suitable vegetation burned at high severity within a 2-km radius around the nest of each pair of owls. We chose this radius because >90% of each owl’s foraging locations fell within it. We defined suitable vegetation as conifer and hardwood forest, which are those the California Spotted Owl typically uses (Verner et al. 1992). We report area burned at moderate and high severity because at these severities a fire alters a forest’s structure substantially (Smith 2000) and because most managers consider these levels a threat to the California Spotted Owl (USFS 2004). Cover types and fire severity were derived from Landsat Thematic Mapper imagery developed by the USFS Pacific Southwest Region Remote Sensing Lab and available from the GIS Clearinghouse (http://www.fs.fed.us/r5/rsl/clearinghouse/).

We dissected all California Spotted Owl pellets collected from the McNally Fire study area and isolated all identifiable prey remains, including skulls, mandibles, other bones, bills, feathers, fur, and insect exoskeletons. We used the collection of the California Academy of Sciences, San Francisco, as a reference to identify remains of birds and mammals. We quantified the number of individuals of each species of prey in each sample as the highest count of diagnostic skeletal parts of each species. For example, if there were three right and two left maxillae of Neotoma macrotis in a pellet we considered the number of individuals of this species as three. We estimated the number of insects from the largest number of heads or paired mandibles. We identified two prey taxa (Glaucomys sabrinus and N. macrotis) to species and four others (Thomomys, Peromyscus, Microtus, and Scapanus) to genus only. The remaining prey items were identified to one of four broader taxonomic categories (diurnal squirrel, bird, bat, and insect). We calculated the percent frequency of each category in all pellet samples and estimated the percent biomass for each category from average weights (g) provided by Smith et al. (1999). For each of the four territories we tallied prey items by percent biomass but were unable to separate samples by sex because both members of a pair often roosted together in the same tree. The previously published studies of contents of California Spotted Owl pellets did not present the data by territory (Thrailkill and Bias 1989, Smith et al. 1999, Munton et al. 2002). Therefore, in addition to estimating the diet for each territory, we also pooled samples from all four territories for qualitative comparisons with those of other studies.

To estimate the sizes of the owls’ home ranges, we used a kernel-density estimator, a widely used statistical method (Seaman and Powell 1996). Numerous methods for estimating home ranges with kernel estimators are available, but each method can generate a different estimate. In our analysis we used a fixed-bandwidth kernel estimator, which has been shown to have little bias in comparison to adaptive-bandwidth kernels (Seaman and Powell 1996). The choice of a smoothing parameter or bandwidth, \( h \), to be used in an analysis affects the results critically, and there are several options for calculating the “optimal” bandwidth. The two most widely used methods for choosing \( h \) are the reference bandwidth, \( h_{ref} \) (Worton 1995) and least-
squares cross validation (LSCV; Silverman 1986, Wand and Jones 1995). The LSCV method produces more accurate estimates of simulated home ranges than does \( h_{ref} \) (Seaman and Powell 1996), but LSCV does not always converge, preventing its use in some cases.

We estimated the sizes of the owls' home ranges by kernel density in a two-step process. First, we analyzed sample sizes to test whether the number of points where each owl was relocated was sufficient for unbiased estimation of its home range. We used a bootstrapping algorithm in which, for each owl, we drew at random an increasing number of relocation points (\( n \)) from which we built a kernel-density utilization distribution resulting in an area estimate. We began by sampling 5 points and continued until all the available points for each owl had been drawn. At each \( n \), we repeated the process 200 times, to calculate an incremental mean and standard deviation of kernel-density area. We used the simple \( h_{ref} \) method because small samples of points did not allow convergence with LSCV. We evaluated the simulation results for asymptotic convergence on home-range size as sample size increased, and if values for an individual did not converge, we excluded it from further analysis.

We used owl locations from the unburned study areas that had been recorded during the same seasonal window of mid-May to mid-August, and ran the same power analyses by using bootstrapping simulations.

Second, after the sample-size analysis, we calculated the final home-range size as the 95\(^{th} \) percentile of the fixed-kernel density estimated with LSCV. For all these calculations we used the package AdesnhabitatHR (Calenge 2006) in R, version 2.14.

RESULTS

The average area of suitable (conifer and hardwood) forest burned at moderate severity within 2 km of the four Spotted Owl nests we studied in or near the McNally Fire area was 237.9 ha (SD = 119.1, range 110.9–397.5); that which burned at high severity was 93.3 ha (SD = 35.5 ha, range 42.1–118.8 ha). Thus an average of 23\% (range 10–39\%) of suitable vegetation within the 2-km radius burned at moderate severity and 9\% (range 4–12\%) burned at high severity (Table 1).

We identified 199 individual prey items from 101 pellet samples from Spotted Owls in the McNally Fire area (range 7–35.5 pellet samples per owl territory). Samples from all four territories contained a substantial proportion of gophers and flying squirrels; big-eared woodrats were present in pellets at only two of the territories (Table 1). In the pooled sample of pellets from all four territories, the prey biomass comprised 40\% gophers, 26\% flying squirrels, and 11\% woodrats.

The dominant species of prey that Spotted Owls captured in the closest unburned study area (Sierra National Forest, 1988) was the northern flying squirrel, 46\% by biomass; gophers represented 18\% and woodrats 12\% (Munton et al. 2002; Table 2). In the Eldorado National Forest Spotted Owls primarily captured woodrats (38\% of prey by biomass) and flying squirrels (31\%; Table 2). In the unburned San Bernardino National Forest study area, woodrats were the overwhelmingly dominant prey, constituting 74\% of the owls' diets by biomass (Smith et al. 1999; Table 2).
Table 1  Percent Each Category of Prey Contributed to Total Dietary Biomass, Estimated Home Range, and Severity of Fire within 2 km of Four California Spotted Owl Nests Four Years after the 2002 McNally Fire, Sequoia National Forest, California

<table>
<thead>
<tr>
<th>Prey item</th>
<th>Poison Creek</th>
<th>Mill Creek</th>
<th>Speas Ridge</th>
<th>Burnt Ridge</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thomomys spp.</td>
<td>18.9</td>
<td>48.6</td>
<td>40.4</td>
<td>53.3</td>
</tr>
<tr>
<td>Neotoma macrotis</td>
<td>35.4</td>
<td>0.0</td>
<td>0.0</td>
<td>8.3</td>
</tr>
<tr>
<td>Glaucomys sabrinus</td>
<td>20.7</td>
<td>35.9</td>
<td>35.3</td>
<td>11.6</td>
</tr>
<tr>
<td>Peromyscus spp.</td>
<td>5.2</td>
<td>8.6</td>
<td>2.4</td>
<td>1.6</td>
</tr>
<tr>
<td>sciurid</td>
<td>8.1</td>
<td>6.7</td>
<td>9.8</td>
<td>10.5</td>
</tr>
<tr>
<td>Microtus spp.</td>
<td>4.1</td>
<td>0.0</td>
<td>6.5</td>
<td>0.0</td>
</tr>
<tr>
<td>No. prey items</td>
<td>83</td>
<td>13</td>
<td>44</td>
<td>59</td>
</tr>
<tr>
<td>Male home-range size (ha) (n)</td>
<td>718.0 (40)</td>
<td>252.8 (51)</td>
<td>307.3 (48)</td>
<td>606.3 (53)</td>
</tr>
<tr>
<td>Female home-range size (ha) (n)</td>
<td>129.8 (33)</td>
<td>—</td>
<td>606.0 (45)</td>
<td>197.3 (34)</td>
</tr>
<tr>
<td>Percent burned at moderate severity</td>
<td>38.9</td>
<td>9.8</td>
<td>19.3</td>
<td>23.5</td>
</tr>
<tr>
<td>Percent burned at high severity</td>
<td>11.6</td>
<td>3.7</td>
<td>9.0</td>
<td>11.5</td>
</tr>
<tr>
<td>Average elevation (m)</td>
<td>2167</td>
<td>1679</td>
<td>2052</td>
<td>1833</td>
</tr>
</tbody>
</table>

*a* = Number of night-time relocation points per owl.

*b* Female at Mill Creek was not radio-marked.

The mean number of independent relocations we obtained for each foraging Spotted Owl in the McNally Fire area was 43 (range 33–53; Table 1). Simulation results for all owls in the McNally Fire converged and so we included them in the analysis (Figure 1). We excluded data from three Spotted Owls in the sample from unburned forests because of lack of asymptotic convergence (TH5, TH6, and SB1; Figure 1). The size of the home range of a Spotted Owl in the McNally Fire area averaged 402.5 ha (SE = 88.7, range 129.8–718.0 ha; Tables 1 and 3). The individual with the largest home range was the sole male that reproduced successfully that year (Poison Creek), while his mate’s home range was the smallest (Table 1). Home-range sizes in unburned forests averaged 487.0 ha (SE = 63.9 ha) in the Tahoe National Forest, 529.0 ha (SE = 72.9 ha) in the Sierra National Forest, and 370.4 ha (SE = 58.7 ha) in the San Bernardino National Forest (Table 3).

**DISCUSSION**

Here we report the first data on the diet and the size of home ranges of the California Spotted Owl in a burned landscape. The size of an owl’s home range varies with many factors, including but not limited to forest structure, fire severity, key prey species and temporal fluctuations in their numbers, the owl’s foraging behavior, and whether it is nesting or feeding young (Carey et al. 1992, Zabel et al. 1995, Ward et al. 1998). We could not quantify home-range size rigorously as a function of diet, habitat, or other factors because our sample of owls and the length of our study were not sufficient.
Previous studies of the California Spotted Owl’s breeding-season diet (Thrailkill and Bias 1989, Smith et al. 1999, Munton et al. 2002) and home-range size (Call et al. 1992, Zabel et al. 1992, Zimmerman et al. 2001) were conducted in unburned areas. The dominant prey item we identified in pellets from the McNally Fire area was the pocket gopher; the northern flying squirrel and big-eared woodrat were also important. In comparison, the dominant prey California Spotted Owls took during the breeding season in an unburned area in the Sierra National Forest in the southern Sierra Nevada was the northern flying squirrel, proportions of pocket gophers and woodrats being smaller (Munton et al. 2002; Table 2). In the Eldorado National Forest in the central Sierra Nevada Spotted Owls consumed mainly woodrats and flying squirrels, while to the south in an unburned area in the San Bernardino National Forest, woodrats were the overwhelming prey (Smith et al. 1999).

In the McNally Fire area, owl pellets contained woodrat remains in amounts comparable to those in the nearest unburned study area at similar elevation (Sierra National Forest). But the average percent biomass of gophers in pellets from the McNally fire area was more than twice that in pellets from the unburned study area in the Sierra National Forest and more than 5 times higher than in pellets from the unburned Eldorado National Forest study area. Gophers are found in a variety of habitat types in the Sierra Nevada but are uncommon in mature and older forests with little or no herbaceous ground cover (Williams et al. 1992). They feed largely on

<table>
<thead>
<tr>
<th></th>
<th>Eldorado NF</th>
<th>Sierra NF</th>
<th>McNally Fire</th>
<th>San Bernardino NF</th>
</tr>
</thead>
<tbody>
<tr>
<td>Thomomys spp.</td>
<td>7.8</td>
<td>18.4</td>
<td><strong>40.3</strong></td>
<td>10.4</td>
</tr>
<tr>
<td>Glaucomys sabrinus</td>
<td>30.7</td>
<td><strong>45.6</strong></td>
<td>25.9</td>
<td>3.0</td>
</tr>
<tr>
<td>Neotoma spp.</td>
<td><strong>38.1</strong></td>
<td>11.8</td>
<td>10.9</td>
<td><strong>74.0</strong></td>
</tr>
<tr>
<td>Diurnal squirrel</td>
<td>6.6</td>
<td>0.9</td>
<td>8.8</td>
<td>1.3</td>
</tr>
<tr>
<td>Bird</td>
<td>12.4</td>
<td>12.9</td>
<td>4.0</td>
<td>3.5</td>
</tr>
<tr>
<td>Peromyscus spp.</td>
<td>1.3</td>
<td>5.5</td>
<td>4.5</td>
<td>4.0</td>
</tr>
<tr>
<td>Microtus spp.</td>
<td>0.7</td>
<td>1.2</td>
<td>2.6</td>
<td>1.3</td>
</tr>
<tr>
<td>Scap anus spp.</td>
<td>2.1</td>
<td>1.5</td>
<td>1.5</td>
<td>0.3</td>
</tr>
<tr>
<td>Bat</td>
<td>0.0</td>
<td>0.1</td>
<td>0.8</td>
<td>0.1</td>
</tr>
<tr>
<td>Insect</td>
<td>0.3</td>
<td>0.6</td>
<td>0.6</td>
<td>1.2</td>
</tr>
<tr>
<td>Sylvilagus spp.</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1.0</td>
</tr>
</tbody>
</table>

*Sample size is number of individual prey items. Bold numbers indicate greatest percent biomass by study area.

aData from Thrailkill and Bias (1989).

bData from Munton et al. (2002).

cData from Smith et al. (1999).
herbaceous grasses and forbs and during the winter frequently consume mountain whitethorn (*Ceanothus cordulatus*) leaves and willow (*Salix* spp.) stems (Williams et al. 1992). Four years after the McNally Fire, stands of severely burned forest had significantly greater cover of shrubs and herbs and more dead trees than unburned stands or stands burned at moderate or low severity (Bond et al. 2009). Elsewhere we reported that California Spotted Owls selectively foraged in burned forest over unburned, with the strongest selection for severely burned patches (Bond et al. 2009). Forest fire may have enhanced the habitat for gophers (sensu Williams et al. 1992), and the standing fire-killed trees offered perches for foraging Spotted Owls, resulting in greater biomass of gophers in owl pellets from the McNally Fire area than in unburned areas of the Sierra Nevada.

In the McNally Fire area, Spotted Owl pellets contained less biomass of northern flying squirrels than did those from unburned areas of the Sierra Nevada.

Figure 1. Mean (black line) and standard deviation (gray shading) of sizes of fixed-kernel home ranges for increasing random draws of \( n \) relocation points for representative radio-tracked California Spotted Owls from studies in multiple national forests in California. Plots were assessed for evidence of convergence in home range as \( n \) increased. Three home ranges did not converge, two in the Tahoe National Forest (A, B), and one in the San Bernardino National Forest (C). All other home ranges converged asymptotically (e.g., for a bird on San Bernardino National Forest, D).
Nevada. Waters and Zabel (1995) found that the mean density of the flying squirrel in old-growth forest in northeastern California was greater than in young stands regenerating naturally after forest fire. On the basis of its habitat requirements (Waters and Zabel 1995, Meyer et al. 2007), the northern flying squirrel may take longer than the Spotted Owl’s other prey to recover after severe forest fire. Future research should test the assumptions about the effects of fire on the California Spotted Owl’s major prey species, with our results providing a basis for developing hypotheses.

The mean size of a home range in the McNally Fire area was 402 ha, similar to that in the unburned study areas, as evidenced by overlapping standard errors. The mean home range in our burned study area, however, was 24% smaller than in the nearest unburned area of similar elevation (Sierra National Forest), and pellets contained a greater biomass of gophers. In comparison, owls in the Sierra National Forest study area had the largest mean home ranges and were foraging primarily on flying squirrels.

Our results provide the basis for testable hypotheses on the effects of fire on the California Spotted Owl’s use of space. As the biomass of an individual gopher and northern flying squirrel is similar (Smith et al. 1999), future studies could test the hypothesis that owls foraging primarily on gophers and flying squirrels may not need to forage as widely in burned forests as in comparable unburned forests. Studies could examine whether fire enhanced habitat for gophers and degraded it for flying squirrels, while controlling for any spatial and temporal differences in densities of these two prey species.

Our study of Spotted Owls occupying burned forests documented diets containing a majority of pocket gophers by biomass, with woodrats also a major prey item in one territory (Table 1). Shrubs and herbaceous vegetation provide important habitat for both of these key species of prey (Williams 1992), and these habitats can be abundant in a burned landscape (Bond et al. 2009). Therefore, post-fire management involving use of rodenticides to prevent damage to young trees or herbicides to suppress shrub growth within California Spotted Owl habitat may impair the owls’ foraging.

### Table 3  Characteristics of Home Ranges Estimated by the Fixed-Kernel Method of California Spotted Owls Four Years after the 2002 McNally Fire, Sequoia National Forest, and in Three Unburned Areas

<table>
<thead>
<tr>
<th>Study area</th>
<th>Tahoe NF a</th>
<th>Sierra NF b</th>
<th>Sequoia NF</th>
<th>San Bernardino NF c</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Latitude (° N)</td>
<td>40</td>
<td>37</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>Elevation (m)</td>
<td>670–1585</td>
<td>1220–2925</td>
<td>1500–2500</td>
</tr>
<tr>
<td></td>
<td>Mean home range (ha)</td>
<td>487.0</td>
<td>529.0</td>
<td>402.5</td>
</tr>
<tr>
<td></td>
<td>SE of home range</td>
<td>63.9</td>
<td>72.9</td>
<td>88.7</td>
</tr>
<tr>
<td></td>
<td>Range of home range</td>
<td>284.8–682.3</td>
<td>253.3–718.5</td>
<td>129.8–718.0</td>
</tr>
</tbody>
</table>

a From D. Call, unpublished data.
b From T. Munton, unpublished data.
c From G. Zimmerman, unpublished data.
d Estimated from locations of night-time foraging recorded 22 May–15 August 2006.
ACKNOWLEDGMENTS

We thank K. Bruno and L. Kehas for field assistance and W. Rannals and R. Gal-loway of the Sequoia National Forest for providing Spotted Owl locations prior to our field work and valuable support during our study. We are indebted to D. Call, T. Munton, and G. Zimmerman for providing us with their telemetry data and to J. P. Ward for advice on field methods and data analysis. The California Academy of Sciences graciously allowed us access to its collection for our pellet analysis. We thank R. Gill, D. Herter, and D. Wiens for helpful comments on the manuscript. This study was funded by grants from Environment Now and the Resources Legacy Fund Foundation to The Institute for Bird Populations and was conducted by the Institute’s Sierra Ne-vada Bird Observatory. This is contribution 377 of The Institute for Bird Populations.

LITERATURE CITED


Stephenson, J. R., and Calcarone, G. M. 1999. Southern California mountains and
CALIFORNIA SPOTTED OWLS IN A BURNED FOREST


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HUMAN FOOD SUBSIDIES AND COMMON RAVEN OCCURRENCE IN YOSEMITE NATIONAL PARK, CALIFORNIA

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ABSTRACT: We examined the influence of the availability of human food on the distribution and foraging habits of the Common Raven (Corvus corax), in Yosemite National Park, California. The raven arrived and established itself as a year-round resident in Yosemite in the 1960s, and its population has been increasing ever since. Surveys of nine sites with varying levels of human influence in Yosemite suggest that the Common Raven is most densely distributed in human-influenced regions, especially Yosemite Valley. It is largely absent from Yosemite’s Badger Pass Ski Area in the off season but uses the site as anthropogenic food becomes more available during the ski season. At Badger Pass and four recreational destinations ravens track the availability of human food temporally, preferentially foraging before or after human mealtimes.

The Common Raven (Corvus corax) ranges across North America, Eurasia, and northern Africa, occupying natural landscapes as varied as deserts, forests, and grasslands, as well as human-dominated cityscapes (Boarman and Heinrich 1999). Noted for their opportunistic nature and adaptability to diverse habitats, ravens thrive in developed areas and respond favorably to human transformation of natural landscapes (Boarman and Heinrich 1999). Between 1966 and 2003, according to the Breeding Bird Survey, the raven population increased on the order of 1.5% per year and expanded its range into urbanized regions across the United States and Canada (Figure 1a; www.mbr-pwrc.usgs.gov/bbs/bbs.html). In the American West, over the past half-century, the raven’s expansion has been documented widely in conjunction with increasing human modification of the environment (Marzluff and Angell 2005). On the Olympic Peninsula, ravens cluster more densely and reproduce at higher rates near human settlements (Marzluff and Neatherlin 2006). In the Mojave Desert, the rate of juvenile ravens’ survival increases with their nest’s proximity to anthropogenic resources (Webb et al. 2004) such as landfills, trash bins, and runoff from irrigation (Boarman 1993), and Knight et al. (1993) reported corresponding population increases over the past 30 years—at rates greater than 1500% in some areas.

Joseph Grinnell’s pioneering studies found that ravens were absent from Yosemite National Park in the early 20th century (Grinnell and Storer 1924). Though Grinnell noted that the raven was “common locally” in the Sierra Nevada, he acknowledged that, “conditions in the Yosemite region do not seem to be attractive to the Western Raven, as we saw only a single individual [in 6 years of field study] and that bird was doubtless a wanderer from farther south” (Grinnell and Storer 1924). Furthermore, Wallis (1950) highlighted a ranger’s observations of a “rare” Common Raven “which previously had been unrecorded from Yosemite National Park.” Christmas Bird
Count records (http://netapp.audubon.org/CBCObservation/Historical/ResultsBySpecies.aspx?1) indicate that the raven established itself as a year-round resident in Yosemite in the late 1960s and has been increasing in population since the early 1980s (Figure 1b). Coincidence of the timing of the raven’s population explosion and heightened human visitation to Yosemite National Park (Figure 1b) suggest that in Yosemite ravens may be following a pattern of expansion subsidized by
human resources consistent with that elsewhere in the American West (Marzluff and Neatherlin 2006, Knight et al. 1993). We investigated the raven’s spatial and temporal reliance on human food in Yosemite. Specifically, we tested the hypotheses that ravens (1) are more abundant in human-influenced regions of Yosemite, especially Yosemite Valley, and (2) track human food subsidies temporally at a given site.

METHODS

To examine the spatial extent of human influence on the raven, we surveyed nine sites of varying human influence in Yosemite National Park from 27 June to 18 August 2009 (Figure 2a). At each site, we walked surrounding trails and noted ravens by sight or call between dawn (~05:30) and 09:30. Because of the large area investigated and difficulty of access to some sites, we intended these initial surveys as preliminary data for our subsequent more detailed study. We surveyed for a total of 1812 minutes across all sites.

We also investigated the spatial and temporal interactions between availability of human food and presence of foraging ravens from 28 November 2009 to 4 April 2010 at Badger Pass Ski Area in southern Yosemite National Park. Badger Pass is popular with skiers in winter but is largely abandoned during summer and fall. We surveyed for ravens at Badger Pass once in November, during the off season, as well as on days immediately preceding and following the ski area’s opening date of 18 December 2009. Because of difficulties of access to our field site, we visited Badger Pass only intermittently through the ski season and after the area’s closing in April. Each day of a survey, we arrived before dawn, commenced observations at first light (~06:30), and ended them after dark (~19:00). From the top deck of Badger Pass Day Lodge, we recorded the number of ravens foraging on the ground or deck of the lodge continuously through the day, so as to avoid over-representing the same raven in discrete counts. We also counted the number of people occupying the lodge’s picnic tables every 30 minutes. This count served as a proxy for availability of human food at Badger Pass, though we counted all people seated at the picnic tables regardless of whether or not they were eating.

To further explore the relationship between the timing availability of human food and the raven’s foraging habits, from 21 July to 22 August 2009 we visited four sites ravens frequented in Yosemite Valley: Upper Pines Campground, Swinging Bridge Picnic Area, Nevada Falls Overlook, and Valley View Turnout. We surveyed each site six times, with each survey taking place on a randomly selected different day. We surveyed each site three times between dawn (~05:30) and 14:00 and three times between of 14:00 and dark (~20:30), so that all daylight hours were represented equally. For these surveys, we divided each recreation area into plots of 10 × 10 m and used a random-number generator to determine the plot in which to establish our observation point. One observer sat in a chair at the observation point, counted the ravens, and recorded their activity patterns, as well as counting people eating within a 100-m radius. We distinguished ravens at rest in the trees from those that were “foraging,” that is, on the ground or on a picnic table, fire pit, or cooler. As at Badger Pass, we noted ravens’ presence in the
site continuously through the day to avoid over-representing the same raven in discrete counts. We returned to the same observation point on subsequent visits. Any ravens flying over the study site were not included in our counts.

For our spatial data, we used a 2-way analysis of variance (ANOVA) to test the independence of raven sightings on observational minutes (treated in the model as a continuous variable) and location (treated as a discrete variable). We divided the spatial data into two groups, sightings in the valley and sightings outside of the valley, to make a coarse delineation of variation in human influence on the scale of Yosemite as a whole, as the valley is more extensively developed than other regions of the park. We used linear regres-
sion analysis to examine the relationship between sales of lift tickets at the Badger Pass Ski Area (a proxy for human visitation and availability of human food) and presence of foraging ravens the following day. We compared raven foraging with human visitation to Badger Pass the preceding day because the ravens scavenged primarily in the early morning on remnants left from the day before (ravens are not active after dark). For our time-series data, for both Badger Pass and Yosemite Valley, we used cross-correlation tests to quantify the lag time between availability of human food and the ravens’ foraging response. To create a time-series loop of 24 hours, we assumed people with food and foraging ravens were absent after nightfall at 20:30. Though people may have left food after dark, the raven is an exclusively diurnal animal. For cross-correlation tests we used MATLAB. We set statistical significance for all tests at $P < 0.05$. The computer code with which we ran the ANOVA and cross-correlation analysis is available from the authors.

RESULTS

In summer, in 1812 observer-minutes of surveys across Yosemite National Park, we recorded 125 sightings of the raven. The number of sightings per observer-minute was significantly higher in Yosemite Valley than at all other visited sites (2-way ANOVA; $F = 28.22, df = 1, P = 1.5 \times 10^{-5}$).

During our winter surveys at Badger Pass, we observed few ravens during the November off season and the days preceding the ski area’s opening on 18 December 2009. Then raven foraging at the site increased after the opening and remained high through the ski season (108 days total). After Badger Pass closed at the end of the ski season on April 4, however, raven sightings decreased substantially (Figure 3). Thus, in a regression analysis, foraging ravens were correlated positively with the proxy for availability of human food, sales of lift tickets the preceding day ($r = 0.780, F = 13.98, df = 1, P = 0.004$).

At the Badger Pass and Yosemite Valley sites surveyed daily, human food consumption adhered to predictable mealtime patterns. At Badger Pass, Swinging Bridge, and Nevada Falls, mean human food consumption peaked once a day, between 12:30 and 14:30. At Upper Pines Campground, mean human food consumption peaked twice in a given day, at 10:30 and 19:30. The pattern was more complex at Valley View Turnout, where visitors stopped for shorter periods at less defined mealtimes, though the availability of human food increased in the late afternoon and peaked at 17:30. Raven foraging was greatest at times of day that were slightly offset from peak human food consumption (Figure 2b): cross-correlation analysis revealed a lag time between the ravens’ foraging behavior and the peak of human food consumption. At those sites where human food consumption predictably peaked only once, at midday—Badger Pass, Swinging Bridge, and Nevada Falls—our cross-correlation function indicated lag times of 5, 6, and 5 hours, respectively. At Upper Pines Campground, where human food consumption peaked twice a day, the lag time was 3 hours. At our most complex site, Valley View, where human food was sporadic, the lag time was 2 hours.
DISCUSSION

As predicted, we found an association between raven and human presence in Yosemite National Park. Ravens occurred disproportionately in Yosemite Valley, the most developed region of the park, and ravens concentrated at Badger Pass Ski Area during the winter when people—and human food resources—were available. We interpret the patterns of raven foraging we observed as direct responses to human food left over from previous periods of peak consumption. At Badger Pass, ravens arrived abruptly on 19 December, one day after the ski area opened and the first morning that leftover human food became available.

As at Badger Pass, in our time-series studies in summer 2009, ravens frequently foraged in the early morning before people were eating; we infer that ravens were scavenging scraps remaining from the previous day and/or night. At those sites with the longest lag time between the peaks of human food consumption and raven foraging—Badger Pass, Swinging Bridge, and Nevada Falls—we speculate that ravens traveled to these sites to forage after human mealtimes, then departed for other locations. At Upper Pines Campground, with a 3-hour lag time, the ravens may have been forced to forage more quickly, depart, and then return following the second human mealtime. And at Valley View, a 2-hour lag time suggests a more immediate and opportunistic foraging behavior. At Upper Pines Campground and Valley View Turnout, ravens resident to these sites may be able to forage more frequently and at shorter lag times.

Our study is observational, not experimental, so we cannot prove a differing pattern of availability of human food to be the cause of the observed lag times in raven foraging. However, while a variety of factors independent of human food availability might motivate peaks in the raven’s foraging effort, one would expect such peaks to take place at similar times in similar
RAVENS SUBSIDIZED IN YOSEMITE

habitats, all else being equal. The raven is a generalist that demonstrates considerable ingenuity in exploiting diverse habitats worldwide (Boarman and Heinrich 1999), so we assume the minor differences in habitat between our five observational sites—all located within or on the outskirts of Yosemite Valley—to be negligible from the perspective of the raven’s habitat preference. Therefore, we attribute differences in the pattern of raven foraging to differences in patterns of availability of human food. Further study of the diurnal movements and foraging patterns of individual ravens in Yosemite National Park—through radio-telemetry tracking—is needed to disentangle the human factors driving the raven’s activity patterns.

The raven first arrived in Yosemite National Park in the 1960s, which, intriguingly, coincided with an increase in the park’s management of visitors’ effect on the surrounding ecosystem. The open-air landfills in Yosemite were closed in 1969 and 1970, and in 1975, all trash bins were bear-proofed (Figure 1b; Greene 1987). While the park’s policy reduced human conflicts with bears (Harms 1980), raven populations continued to climb through the 1980s. Notably, the number of ravens recorded on the Christmas bird count in 1980 increased by over 200% during the same year in which overnight human visitation to Yosemite campgrounds increased 39% (Wendt 1981). Conversely, in 1998, those numbers declined 69% from the previous year (Wendt 1981), following the elimination of some 353 campsites by the severe flood of 1997.

While the association between the raven’s expansion and history of wildlife management in Yosemite National Park will likely never be anything more than correlative, the link between contemporary ravens and people in Yosemite is undeniable. Our study does not address the effects of an expanding raven population on the rest of the Yosemite ecosystem, but as ravens are known nest predators (Marzluff and Restani 1999), raptor mobbers (Dawson 1981), and predators (Kristan and Boarman 2003), we suspect that their effect on the dynamics of the surrounding ecosystem is significant. Previous studies have demonstrated increased rates of nest predation by corvids in more human-modified landscapes (Andrén 1992), but patterns of predation by the raven specifically remain unclear (Marzluff et al. 2007). Further studies of the raven’s effects on declining songbird populations in Yosemite Valley (S. Stock pers. comm.), including experiments investigating predation on model nests and observations via motion-detecting cameras, are needed to elucidate the responsible factors.

Although America’s national parks are commonly assumed to be pristine, we found that even in regions of minimal habitat alteration, large numbers of people may be affecting the dynamics of surrounding ecosystems in dramatic ways. While more obvious disturbances, such as the introduction of exotic species and land conversion, have received substantial attention in the ecological literature, the far-reaching effects of more subtle forms of human land use remain unknown. While the observable effects of availability of human food on large vertebrates like bears are widely recognized, our studies suggest that even micro-scale waste can have tangible effects on a natural habitat. As the first ecological investigation of the raven’s expansion into Yosemite to date, our study sheds light on the extent of a subtler human influence on a seemingly wild ecosystem.
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LITERATURE CITED


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GENETIC EVIDENCE FOR MIXED MATERNITY AT A LARK SPARROW NEST

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ABSTRACT: Among passerines not nesting in cavities, mixed maternity within a clutch is rare and has been recorded at <1% of the nests of four North American species. Using genetic methods, we report the first case of mixed maternity in the Lark Sparrow (Chondestes grammacus). Within an unusually large clutch in Texas, we found that the attending female shared the same mitochondrial haplotype with an unhatched egg and one nestling, but not with another nestling. Analysis with microsatellite DNA confirmed mixed maternity at the nest; the female and a nestling did not share alleles at five of nine loci analyzed. Various behaviors may lead to mixed maternity, including intraspecific reuse of nests, conspecific usurpation, and conspecific parasitism. Our study stresses the important roles that intensive nest monitoring and genetic tests can play in detecting cryptic reproductive strategies.

Mixed maternity at nests is rarely reported among passerines (Yom-Tov 2001, Lyon and Eadie 2008). However, mixed maternity may be common but underdetected in certain species or populations; such a context could alter our interpretation of evolutionary adaptations such as egg recognition, nest defense, and parenting behavior (Yom-Tov 2001). For instance, Latif et al. (2006) only recently recorded the first evidence of conspecific nest parasitism and egg ejection in the Song Sparrow (Melospiza melodia) despite widespread study of that species’ nesting over the past century (see Smith et al. 2006). In addition to nest parasitism, multiple maternity at a nest can also arise via several mechanisms (see review in Lyon and Eadie 2008): nest reuse (i.e., when a female lays among eggs left in an abandoned nest), errors in nest ownership—possibly paired with the need to lay (Harms et al. 1991), mate change during laying (Griffith et al. 2004), or usurpation (i.e., the forcible takeover of an active nest by a female other than the owner) (Sullivan et al. 1989; reviewed by Ellison 2008).

The Lark Sparrow (Chondestes grammacus) appears unusual in its propensity to reuse inactive nests constructed by other individuals (McNair 1984, 1985). Lark Sparrows also attempt to use active nests of other birds, sometimes resulting in successful usurpation of nests of the same or other species (McNair 1984, Ellison unpubl. data). Detecting such mixed maternity at a nest requires intensive monitoring, often encompassing the use of egg marking, video surveillance, or genetic testing (Latif et al. 2006). Clutches that exceed twice the species’ mean clutch size can alert researchers to the possibility of conspecific nest parasitism (Yom-Tov 1980). The mean number of eggs Martin and Parrish (2000) reported for the Lark Sparrow is 3.84 ± 0.70 (n = 209 nests). Among 200 nests of the Lark Sparrow (Ellison et al.
2006), we encountered one with seven eggs and therefore suspected that multiple females had used it. To determine if there was evidence for mixed maternity in this nest, we examined mitochondrial DNA sequences and nuclear genotypic data of the adult female, eggs, and nestlings. We hypothesized usurpation, reuse, or intraspecific parasitism as possible explanations for any mixed maternity, and we considered the likelihood of each in light of the physical and genetic evidence.

METHODS

The Lark Sparrow nest was found on 28 April 2002 in Kinney Co., Texas. It was on the ground, under an overhanging pad of prickly pear (Opuntia spp), and contained four eggs when discovered. Two days later, the nest held five Lark Sparrow eggs and we found another two eggs 25 and 38 cm outside the nest. We collected one egg outside the nest; the other was damaged and discarded in the field. On 11 May, we observed five hatchlings were in the nest, and on 13 May we captured an adult female at the nest, banded her, and took a blood sample. This banded female was then observed carrying food to the nest and fledglings through 22 May. On 14 May we banded and sampled the blood of two nestlings (A and B); the third remaining nestling (C) was too small to be banded or bled. On 18 May A and B (the only young we detected) had fledged; we recaptured B and sampled its blood again. We therefore had samples from a nesting female, one egg, and two young from this nest.

Blood samples were stored in Queen’s lysis buffer (Seutin et al. 1991) at 4°C. The egg was stored in a sealed bag at –20 °C. To prepare the egg for DNA extraction, we removed the shell while the egg was still frozen and sealed it in a 1.5-mL microcentrifuge tube. We thawed each egg’s contents separately and checked for any evidence of a developing embryo. DNA from blood and eggshell samples was extracted by a proteinase-K digestion followed by a standard phenol–chloroform extraction protocol (Sambrook et al. 1989, Strausberger and Ashley 2001). To check against possible contamination we concurrently extracted DNA from an unrelated Lark Sparrow from Nebraska, which we used as a positive control, and performed a blank extraction as a negative control.

Using primer set L16743 (Tarr 1995) and H920 (5′-GTC CGG CAA CCA TTA CAC TA-3′; Ross 2011), we amplified 910 base pairs of the mitochondrial control region (d-loop) from each sample. We purified the products of the polymerase chain reaction by ethanol precipitation and sequenced them with ABI BigDye Terminator version 3.1 (Applied Biosystems, Foster City, CA). For sequencing we used the H920 and two additional nested primers, H598 (5′-TTC AAC CGA CCA CTT GTA TCT G-3′; Ross 2011) and L437 (Tarr 1995). We sequenced the gene on an ABI377 Genetic Analyzer (Applied Biosystems) and checked the accuracy of the scoring visually, then exported the sequences to BioEdit (version 7.09, Hall 1999) to check those from the same sample for mismatched base pairs.

We genotyped nine nuclear microsatellites from each sample: Dpμ16 (Dawson et al. 1997), Maμ23 (Alderson et al. 1999), ESCμ1 (Hanotte et al., 1994), Asμ09 and Asμ15 (Delany et al. 2000), Cuμ02 (Gibbs et al.
1999), Pdoμ3 (Griffith et al. 1999), Gf01b (Rasner et al. 2004), and Gf05 (Petren 1998). We had tested these microsatellites previously, finding them to be polymorphic in the Lark Sparrow. The polymerase chain reactions for amplification of the microsatellites followed conditions described by Ross (2011). We genotyped the microsatellites with an ABI377 Genetic Analyzer and scored them with GeneScan software (Applied Biosystems).

RESULTS

Sequences of the mitochondrial d-loop of the adult female banded at the nest, the eggshell, and nestling B were identical (Table 1). That of nestling A was different, with 9 base-pair substitutions in the DNA fragment of 910 base pairs. As expected, the mitochondrial d-loop of the control sample yielded a completely different haplotype (Table 1).

The female shared at least one allele at each microsatellite locus with nestling B, which is consistent with a mother–offspring relationship (Table 1). Also, the female and nestling A did not share any alleles at five microsatellite loci (Table 1). Although we were not able to genotype all the loci for the eggshell, genotypes at four loci (Maμ23, Dpμ16, Asμ09, and Gf05) were identical to those of the attending female. Since the embryo in the egg was undeveloped and we extracted the DNA from tissue remaining in the eggshell, we can assume that the genotypes of the eggshell correspond to those of the mother. Neither the blank extraction nor the negative controls of the polymerase chain reaction yielded any product. Thus we are confident that the products of DNA amplification from the eggshell were not from contamination.

Table 1 Mitochondrial DNA Haplotypes and Microsatellite Genotypes of the Attending Female Lark Sparrow, Two Young Sampled in the Nest, and the Shell of an Egg

<table>
<thead>
<tr>
<th>mtDNA haplotypea</th>
<th>Female</th>
<th>Nestling A</th>
<th>Nestling B</th>
<th>Eggshell</th>
<th>Nebraska sample</th>
</tr>
</thead>
<tbody>
<tr>
<td>Microsatellite genotypesb</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dpμ16</td>
<td>H1 156/158</td>
<td>158/160</td>
<td>156/158</td>
<td>156/158</td>
<td>158/160</td>
</tr>
<tr>
<td>Maμ23</td>
<td>143/145</td>
<td>141/143</td>
<td>143/145</td>
<td>143/145</td>
<td>143/143</td>
</tr>
<tr>
<td>ESCμ1</td>
<td>169/179</td>
<td>129/155</td>
<td>151/179</td>
<td>—</td>
<td>127/127</td>
</tr>
<tr>
<td>Asμ09</td>
<td>133/133</td>
<td>133/133</td>
<td>129/133</td>
<td>133/133</td>
<td>129/133</td>
</tr>
<tr>
<td>Asμ15</td>
<td>121/143</td>
<td>131/145</td>
<td>143/143</td>
<td>—</td>
<td>119/133</td>
</tr>
<tr>
<td>Cuμ02</td>
<td>112/112</td>
<td>112/112</td>
<td>112/112</td>
<td>—</td>
<td>110/112</td>
</tr>
<tr>
<td>Pdoμ3</td>
<td>91/91</td>
<td>83/147</td>
<td>91/91</td>
<td>—</td>
<td>119/119</td>
</tr>
<tr>
<td>Gf01b</td>
<td>216/224</td>
<td>220/222</td>
<td>216/216</td>
<td>—</td>
<td>216/220</td>
</tr>
<tr>
<td>Gf05</td>
<td>185/185</td>
<td>187/187</td>
<td>185/185</td>
<td>185/185</td>
<td>185/189</td>
</tr>
</tbody>
</table>

aHaplotypes H1, H2, and H3 correspond to Genbank sequences FJ348339, FJ348340, and FJ348341.

bAlleles of microsatellite genotypes are reported in number of base pairs; those matching the attending female are in bold.
DISCUSSION

As far as is known, mixed maternity in nests of North American passerines is rare. For cup-nesting species, conspecific parasitism or usurpation has been previously noted in 10, the Cave Swallow (*Petrochelidon fulva*), Cliff Swallow (*P. pyrrhonota*), Hooded Warbler (*Setophaga citrina*), Song Sparrow, Field Sparrow (*Spizella pusilla*), Yellow-eyed Junco (*Junco phaeonotus*), Red-winged Blackbird (*Agelaius phoeniceus*), Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*), Brewer’s Blackbird (*Euphagus cyanocephalus*), and Bullock’s Oriole (*Icterus bullockii*), though at relatively few nests (Sullivan et al. 1989, Petter et al. 1990, Harms et al. 1991, Arnold and Owens 2002, Latif et al. 2006). Our genetic analyses revealed that an attending female Lark Sparrow was not related to at least one nestling (nestling A) at a nest where she was the biological mother of nestling B and an egg found outside the nest (Table 1).

The mixed maternity of the clutch may reflect intraspecific reuse of the nest, as the nest could have been abandoned with one or more eggs in it when a second female took over the nest. Indeed, birds are more apt to abandon nests during laying when the parental investment in the nest is low and the benefit of choosing a more desirable nest site may outweigh the costs of abandonment (Hosoi and Rothstein 2000). However, this conclusion implies that the female that reused the nest had ejected at least one of her own eggs, since the genetic analyses revealed that the egg found outside the nest was laid by the nesting female.

Mixed maternity of the clutch may also have arisen through usurpation; that is, the banded female may have usurped the nest, with one or more unrelated eggs within it (Lindell 1996). Attempted usurpation followed by the banded female regaining her nest and raising unrelated young alongside her own is equally likely. Under this scenario, a would-be usurper ejected part of the host’s clutch, laying at least one egg of her own (nestling A). We cannot say how many of the three new eggs in the nest were laid by either female. Nevertheless, the banded female raised at least one related and one unrelated young.

Mixed maternity at the nest could have also occurred as a result of conspecific parasitism. We are unable to distinguish conspecific usurpation and nest parasitism as each can result in the same outcome. We do note that, in several instances, Lark Sparrows have raised unrelated young, including those of other species. This occurred despite some nests containing eggs of the previous owner (McNair 1984, Ellison unpubl. data). Further study is needed to determine if Lark Sparrows can eject eggs. Peer et al. (2000) reported that they rejected 2 of 3 undersized non-mimetic eggs but appear unable to discriminate undersized mimetic model eggs, as they accepted 2.

Ross (2011) closely monitored approximately 75 color-banded Lark Sparrows in Ohio. In each of three years, both females and males defended territories from conspecific invaders of both sexes. None of 14 nests known to be built by marked females was permanently usurped. On three occasions (in 51 territories studied in 2006 and 2007), however, when a fledgling barely capable of flight was flushed and produced an alarm call, it was defended by three adults, two being the juvenile’s social parents and the third an unbanded adult of unknown sex. These observations might signal
GENETIC EVIDENCE FOR MIXED MATERNITY AT A LARK SPARROW NEST

a parasitic/usurping female offering parental support to what could be her offspring. As Lark Sparrows apparently saturated the suitable habitat at this site, females may have adopted strategies that allowed them to breed where no territories were available.

In summary, we report here the first case of mixed maternity in a wild population of the Lark Sparrow. We cannot determine how the eggs of two females came to be in the same nest. Regardless, our observation reflects a behavior of interest and should serve as an added impetus for the consideration of alternative reproductive tactics that may be revealed by intensive monitoring of nests.

ACKNOWLEDGMENTS

We thank the land owners of Fort Clark Springs for the permission to study the Lark Sparrow on their property and the Ohio Department of Natural Resources for financial support. We also thank Mike D. Boyd for his assistance in the field.

LITERATURE CITED

GENETIC EVIDENCE FOR MIXED MATERNITY AT A LARK SPARROW NEST


Accepted 9 March 2013
NOTES

REFUTATION OF WYOMING NESTING RECORD OF THE PACIFIC WREN

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The nesting status of the Pacific Wren (*Troglodytes pacificus*) in Wyoming is not clear. According to several sources (Hellmayr 1934, AOU 1957, Peters 1960, AOU 1998, Dickinson 2003, Clements 2007), Wyoming is not part of the distribution, but this is contradicted by several other sources. On the basis of two immature specimens (USNM 228577 and 228578), collected by Alexander Wetmore in the Tetons on 27 August and 15 September 1910, Phillips (1986) suggested there might be an undescribed subspecies that nests in northwest Wyoming. Saucier examined these specimens and confirmed they are Pacific Wrens, already in adult plumage, although they appear lighter and grayer than specimens from elsewhere. Cary (1917) is the only additional paper we have found mentioning these specimens. We cannot exclude the possibility that they were migrants from elsewhere in the distribution (Toews and Irwin 2012), as information on the schedule of the Pacific Wren’s migration in the Rocky Mountains is still lacking. Wyoming has two winter records of the Pacific Wren but none for fall (D. W. Faulkner pers. comm.).

According to Faulkner (2010), there is one record of nesting and five other summer reports of the Pacific Wren for Wyoming. These include two documented reports of singing birds in the Tetons during late June of 1981 and 1985; while nesting seems possible, there was no further evidence. The other three reports are undocumented (Faulkner 2010). The only physical confirmation of nesting in the state is reportedly a single specimen taken from a nest with two fledglings in the Freezeout Hills of central Wyoming in 1897 (Knight 1902, Ridgway 1904, McCreary 1939, Faulkner 2010). Unfortunately, at some point between 1897 and 1910, this specimen was removed from the University of Wyoming Museum of Vertebrates (UWYMV) and could not be located for examination (Faulkner 2010).

Specimens housed at UWYMV were not properly curated for decades; many of them were removed and placed in a poorly organized teaching collection. While recently inventorying, organizing, and returning specimens from the teaching collection that belong in the vertebrate collection, Maley found the missing specimen (UWYMV 740). Charles W. Gilmore collected it on 15 July 1897 along Tepee Creek, Freezeout Hills, Carbon County. Gilmore was an undergraduate in the Department of Zoology hired to assist Wilbur C. Knight in collecting and preparing specimens (Faulkner 2010). Knight (1902) reported that Robert Ridgway identified the specimen. Notes written on other specimen tags indicate that Ridgway identified several specimens collected during the 1890s and now housed at UWYMV.

Examining the specimen closely, we identified it as a juvenile House Wren (*T. aedon*). It is a small, short-tailed wren that is slightly more brightly colored than an adult House Wren. The bird has gray scalloping on the breast, a whitish throat and breast, and buffy flanks and undertail coverts. It lacks the rich cinnamon coloration characteristic of adult (UWYMV 751, 752) and immature (USNM 228577, 228578) Pacific Wrens that we examined. The exposed culmen measures 7.8 mm, the wing chord 43.4 mm, the tail 17.5 mm, and the tarsus 15.6 mm. The bill and wing length are below the range of adults of either species (Pyle 1997). The tail is growing in and also shorter than the range of either species (Pyle 1997). It may not have been made
clear to Ridgway that this was a juvenile taken from the nest, not one of the parents. We compared the plumage and measurements to a specimen of a juvenile House Wren (UWYMV 2191) that either was about to fledge or had recently fledged and found them to be very similar. Therefore we conclude that despite suspected nesting of Pacific Wren in Wyoming, this has yet to be confirmed.

We thank M. Ralph Browning, Daniel D. Gibson, Douglas W. Faulkner, and Philip Unitt for their constructive reviews.

LITERATURE CITED


Accepted 5 March 2013
Lack of Recovery of the Yellow-billed Magpie from the West Nile Virus in California’s Central Valley

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The 2005 outbreak of West Nile virus (WNV) in California’s Central Valley was followed by declines in several species of birds, including the Loggerhead Shrike (Lanius ludovicianus), Western Scrub-Jay (Aphelocoma californica), Yellow-billed Magpie (Pica nuttalli), American Crow (Corvus brachyrhynchos), and Oak Titmouse (Baeolophus inornatus) (Airola et al. 2007, Koenig et al. 2007, Pandolfino 2007, Crosbie et al. 2008, Pandolfino 2008a, Wheeler et al. 2009, Smallwood and Nakamoto 2009). Prior to the 2005 outbreak, the Loggerhead Shrike was acknowledged to be in decline across most of its range (Yosef 1996, U.S. Fish and Wildlife Service 2002), and the Yellow-billed Magpie had declined locally in some areas in the Coast Range and southern California (Roberson 1985, Lehman 1995, Koenig and Reynolds 2009).

From 2008 to 2010 I monitored results from Central Valley Christmas Bird Counts (CBC) for signs of recovery among these species, finding that abundances of the Western Scrub-Jay, American Crow, and Oak Titmouse appear to have recovered to levels comparable to their pre-WNV level, while the Loggerhead Shrike and Yellow-billed Magpie showed no evidence of recovery (Pandolfino 2008b, 2009, 2010).

For this analysis I used data from CBC circles (http://netapp.audubon.org/cbcobservation/) and Breeding Bird Survey (BBS) routes (Sauer et al. 2011) in the Central Valley (Figure 1) from 1979 to 2012. To ensure that I was using data from within the normal range of the Yellow-billed Magpie, I included only CBC circles that had averaged at least one Yellow-billed Magpie per party hour prior to 2005 and BBS routes that had averaged at least 10 Yellow-billed Magpies per run prior to 2005. The numbers of Yellow-billed Magpies recorded on both CBCs (winter) and BBS routes (summer) every year since the 2005 WNV outbreak were lower than any recorded between 1979 and 2005 (Figure 2). The apparent effect of WNV can be seen on every CBC circle and BBS route (Table 1). Post-WNV numbers were lower on all 16 CBC circles and on all 10 BBS routes. The overall declines of 62% from CBC data and 56% from BBS data are comparable to prior published results for both the breeding season (declines of 22–83%; Koenig et al. 2007, Crosbie et al. 2009, Wheeler et al. 2009, Smallwood and Nakamoto 2009) and winter (42–64%; Airola et al. 2007, Pandolfino 2008b, Crosbie et al. 2009) and support the conclusion that recovery is not evident.

Since 2006, anecdotal reports of local recovery of Yellow-billed Magpie numbers have appeared in various California list-serve discussions and web sites (e.g., http://ebird.org/content/ca/news/yellow-billed-magpie-survey-report). At the suburban Cardinal Oaks Park east of Sacramento I noted that magpies, which were present in double-digit numbers prior to 2005, were completely absent during 2006 and 2007. Magpies began to reappear in this park in 2008 and were back to pre-2005 numbers by 2009. These anecdotal observations suggest that magpies may be reoccupying some prime locations where the local population was severely reduced or eliminated. However, data from CBCs and BBS routes showed no recovery on a broader scale.

As noted above, even prior to WNV, the Yellow-billed Magpie had been extirpated from some localized areas in the Coast Range and southern California (Roberson 1985, Lehman 1995, Koenig and Reynolds 2009). Nevertheless, prior to 2005 the population was stable in the Central Valley and at the scale of the species’ entire range (Butcher and Niven 2007).

The lack of recovery of the Yellow-billed Magpie in the Central Valley may be due to the continued presence of WNV. While there has been no outbreak on the scale...
Figure 1. Approximate locations of the 16 CBC circles (filled circles) and 10 BBS routes (crosses) used for analyses of trends in numbers of the Yellow-billed Magpie. CBC circles: 1, Redding; 2, Red Bluff; 3, Chico; 4, Oroville; 5, Peace Valley; 6, Marysville; 7, Lincoln; 8, Folsom; 9, Sacramento; 10, Putah Creek; 11, Rio Cosumnes; 12, Wallace–Bellota; 13, Stockton; 14, Caswell–Westley; 15, La Grange–Waterford; 16, Los Banos. BBS routes: A, Red Bluff; B, Cohasset; C, Orland; D, Glenn; E, Oroville; F, Pennington; G, Zamora; H, Staten Island; I, Hughson; J, Westley.
seen in 2005 since that year, WNV continues to be present in the region (Wheeler et al. 2009, Centers for Disease Control 2012). Infected magpies’ extremely high rate of mortality (Crosbie et al. 2008, Wheeler et al. 2009) and the apparent absence of seropositive birds (with antibodies to WNV) among magpies that survived the 2005 outbreak (Crosbie et al. 2008) suggest that there may be very few WNV-resistant individuals in the Central Valley. Another major WNV outbreak could cause a further loss of Yellow-billed Magpies in the region.

Data on the numbers of infected birds and human beings suggest that 2012 saw the highest levels of WNV in the southern Central Valley since 2005 (Centers for Disease Control 2012). Therefore, monitoring of CBC and BBS data after 2012 may show further local declines in magpies there. Wheeler et al. (2009) noted that, with WNV now endemic to the Central Valley, localized species are less likely to recover from population losses. The entire range of the Yellow-billed Magpie lies within areas of persistent WNV. Therefore, recovery of the population to pre-WNV levels may be unlikely. In addition, the continuing conversion of oak savanna to urbanization and intensive agriculture such as vineyards (Zach et al. 2002) further reduces the habitat available for magpies. On a more positive note, the Yellow-billed Magpie population in the Central Valley has adapted well to human-altered landscapes such as rural residential and suburban areas. This provides some hope that, if a WNV-resistant
subpopulation develops, it may find ample habitat in which to expand. In contrast to magpies in the Central Valley, those in the Coast Range and southern California do not readily use urbanized landscapes (Koenig and Reynolds 2009), and that population may be at higher risk of further declines and/or range contractions.

I thank Dan Airola, Walter Koenig, Paul Lehman, and Philip Unitt for their helpful reviews and suggestions, which improved the focus and clarity of the paper. I am also indebted to the many volunteers who participate in Christmas Bird Counts and run Breeding Bird Surveys. These data sources are invaluable tools to help us understand avian population trends.

LITERATURE CITED


Table 1  Average Abundance of the Yellow-billed Magpie pre- and post-West Nile Virus

<table>
<thead>
<tr>
<th>CBC circle</th>
<th>Pre-WNV a</th>
<th>Post-WNV b</th>
<th>Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chico</td>
<td>5.7 ± 1.0</td>
<td>2.8 ± 0.5</td>
<td>−52%</td>
</tr>
<tr>
<td>Caswell–Westley</td>
<td>22.9 ± 3.6</td>
<td>3.6 ± 0.7</td>
<td>−84%</td>
</tr>
<tr>
<td>Folsom</td>
<td>1.7 ± 0.7</td>
<td>0.4 ± 0.04</td>
<td>−78%</td>
</tr>
<tr>
<td>Lincoln</td>
<td>5.1 ± 0.6</td>
<td>1.1 ± 0.2</td>
<td>−78%</td>
</tr>
<tr>
<td>Los Banos</td>
<td>6.4 ± 0.6</td>
<td>3.0 ± 1.4</td>
<td>−53%</td>
</tr>
<tr>
<td>La Grange–Waterford</td>
<td>3.9 ± 0.5</td>
<td>2.2 ± 0.4</td>
<td>−43%</td>
</tr>
<tr>
<td>Marysville</td>
<td>37.9 ± 20</td>
<td>1.6 ± 0.2</td>
<td>−96%</td>
</tr>
<tr>
<td>Orovil</td>
<td>1.0 ± 0.1</td>
<td>0.2 ± 0.1</td>
<td>−75%</td>
</tr>
<tr>
<td>Putah Creek</td>
<td>3.8 ± 0.2</td>
<td>2.4 ± 0.2</td>
<td>−38%</td>
</tr>
<tr>
<td>Peace Valley</td>
<td>2.5 ± 0.2</td>
<td>0.5 ± 0.2</td>
<td>−79%</td>
</tr>
<tr>
<td>Red Bluff</td>
<td>3.3 ± 0.3</td>
<td>1.6 ± 0.1</td>
<td>−52%</td>
</tr>
<tr>
<td>Rio Cosumnes</td>
<td>3.7 ± 0.3</td>
<td>0.9 ± 0.1</td>
<td>−76%</td>
</tr>
<tr>
<td>Redding</td>
<td>1.3 ± 0.1</td>
<td>0.6 ± 0.1</td>
<td>−49%</td>
</tr>
<tr>
<td>Sacramento</td>
<td>6.1 ± 0.4</td>
<td>3.1 ± 0.3</td>
<td>−48%</td>
</tr>
<tr>
<td>Stockton</td>
<td>1.4 ± 0.1</td>
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</tr>
<tr>
<td>Wallace–Bellota</td>
<td>2.8 ± 0.2</td>
<td>1.7 ± 0.2</td>
<td>−39%</td>
</tr>
<tr>
<td>All circles combined</td>
<td>4.2 ± 0.2</td>
<td>1.6 ± 0.1</td>
<td>−62%</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>BBS route</th>
<th>Pre-WNV a</th>
<th>Post-WNV b</th>
<th>Change</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cohasset</td>
<td>19 ± 2</td>
<td>13 ± 1</td>
<td>−30%</td>
</tr>
<tr>
<td>Glenn</td>
<td>26 ± 3</td>
<td>3 ± 1</td>
<td>−87%</td>
</tr>
<tr>
<td>Hughson</td>
<td>49 ± 5</td>
<td>33 ± 8</td>
<td>−34%</td>
</tr>
<tr>
<td>Orland</td>
<td>35 ± 4</td>
<td>9 ± 2</td>
<td>−74%</td>
</tr>
<tr>
<td>Orovil</td>
<td>40 ± 3</td>
<td>24 ± 3</td>
<td>−40%</td>
</tr>
<tr>
<td>Pennington</td>
<td>29 ± 3</td>
<td>9 ± 2</td>
<td>−70%</td>
</tr>
<tr>
<td>Red Bluff</td>
<td>11 ± 1</td>
<td>2 ± 1</td>
<td>−86%</td>
</tr>
<tr>
<td>Staten Island</td>
<td>12 ± 3</td>
<td>7 ± 1</td>
<td>−44%</td>
</tr>
<tr>
<td>Westley</td>
<td>60 ± 5</td>
<td>17 ± 7</td>
<td>−72%</td>
</tr>
<tr>
<td>Zamora</td>
<td>54 ± 7</td>
<td>28 ± 6</td>
<td>−48%</td>
</tr>
<tr>
<td>All routes combined</td>
<td>35 ± 2</td>
<td>15 ± 2</td>
<td>−56%</td>
</tr>
</tbody>
</table>

NOTES

Table 1  Average Abundance of the Yellow-billed Magpie pre- and post-West Nile Virus


NOTES


Accepted 15 March 2013
FIRST RECORD OF THE RED-BELLIED WOODPECKER IN NEVADA

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On the afternoon of 12 June 2012 Anderson found an unfamiliar woodpecker in cottonwoods (*Populus* sp.) near the Bressman Historic Cabin at Ruby Lake National Wildlife Refuge, Elko County, Nevada (40.2° N, 115.4° W). She observed the bird for approximately 20 minutes as it foraged, during which time she obtained several excellent photographs from which she was able to identify it as a female Red-bellied Woodpecker (*Melanerpes carolinus*).

Because Anderson did not realize the significance of her find, she did not report it. Two days later she shared a photo with Burton, who suspected it represented a first state record and notified the Nevada Bird Records Committee. The committee’s secretary, Martin Meyers, posted the sighting on the state birding e-list, but by then several days had elapsed and the bird was not refound. On the basis of Anderson’s
definitive photographs, however, the committee subsequently voted unanimously in the first round to accept the record (2012-030), and it stands as the first for Nevada (M. Meyers pers. comm.).

The photos clearly show the combination of red nape and nasal tufts; white-barred back and central rectrices; gray face, crown, and underparts; and nearly concealed red belly patch diagnostic of a female Red-bellied Woodpecker (Figures 1 and 2). The similar female Golden-fronted Woodpecker (M. aurifrons) has yellow head patches,

Figure 2. Female Red-bellied Woodpecker (Melanerpes carolinus) at Ruby Lake National Wildlife Refuge, Nevada, 6 June 2012; dorsal view.

Photo by Leslie Scopes Anderson
NOTES

black central rectrices, and no belly patch. Some of the photos appear to show worn, brown primaries contrasting with fresher, blacker secondaries and secondary coverts, suggesting a bird in its first plumage cycle; during the preformative molt, a small proportion of individuals retain a variable number of outer primaries, while subsequent molts include all primaries (Pyle 1997).

The Red-bellied Woodpecker’s normal range extends from the eastern United States up river valleys onto the Great Plains as far west as extreme northeast Colorado (South Platte River; Winternitz 1998), approximately 1100 km due east of Ruby Lake. Since the mid-1900s, the species has expanded its range north and west, likely as a result of climate change and supplemental feeding (Shackelford et al. 2000); Breeding Bird Survey data show strong population increases from 1966 to 2010 across most of its range (Sauer et al. 2011). Like most other woodpeckers, it is essentially nonmigratory (Shackelford et al. 2000), although northern populations are prone to some southward movement during cold winters (Winkler et al. 1995), and it is at that season that vagrants may be expected. In fact, there is a limited pattern of winter records west of the breeding range (e.g., at least two for Alberta and one for Idaho; http://birdscalgary.wordpress.com, http://geobirds.com, http://idahobirds.net), and it may be expected that continued population growth will result in an increase in extralimital records. A Red-bellied Woodpecker in Coeur d’Alene, Idaho, in the winter of 2002–2003 (Rogers 2003) is the only one recorded west of Ruby Lake, and there are no records in any of the other states bordering Nevada. The June date of the Ruby Lake bird makes the sighting all the more remarkable.

We thank Kristie Nelson and Daniel D. Gibson for reviewing the manuscript.

LITERATURE CITED


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California Condors (Gymnogyps californianus) feed on a variety of wild and domestic carrion, but are not known to take live prey in the wild (Snyder and Snyder 2000, Snyder and Schmitt 2002). There exists, however, an historical account (Townsend 1848) of a California Condor apparently attempting to take a live salmon along a river bank in the Pacific Northwest. However, the bird was collected before the fish was killed, and it is not clear if feeding was observed. A sister species, the Andean Condor (Vultur gryphus), has, however, been reported to take live prey (Murphy 1925), and smaller species of New World vultures, the Black (Coragyps atratus) and Turkey (Cathartes aura) Vultures have also been reported to take live prey occasionally (Parmalee 1954, Kirk and Mossman 1998, Buckley 1999, Paves et al. 2008). While not providing clear evidence of taking live prey, Townsend's account indicates the opportunistic foraging by California Condors is not confined to dead animals. Nevertheless, occasions for documenting California Condors with live prey have been limited, because, historically, few individuals have been available for observation. Even with intensive conservation efforts during the past 20 years that have resulted in increased numbers of birds in the wild, the practice of provisioning carcasses at designated feeding sites limits opportunities for observation of natural foraging, especially rare events such as attempts to take live prey.

In 1997, Ventana Wildlife Society began releasing captive-reared California Condors along the central California coast. The restored population of this region, including condors released by the National Park Service at Pinnacles National Park, numbered 66 birds as of 2012. This population continues to be fed supplementally, like populations reintroduced in southern California, Arizona, and Baja California. Although in each region condors have been observed feeding on carcasses of land mammals other than those provided through the reintroduction program, the central California population is unique among reintroduced populations because it also feeds on carcasses of marine mammals naturally occurring along the ocean shore (Burnett et al. 2013). Because at least several hundred California Sea Lions (Zalophus californianus) congregate most days in a single rocky cove near Big Sur (36° 12' N, 121° 43' W), condors regularly find and consume sea lion carcasses at this site. We first observed condors feeding on sea lion carcasses at this location in 1999. Since then, the site has provided numerous opportunities for observation of condors foraging, not only of birds feeding on carcasses but also of interactions between condors and live sea lions.

On 20 June 2010, Mike Tyner witnessed a California Condor attempting to forage on a live sea lion at the Big Sur site. The observation began at 11:05 PDT with four condors perched on a large rock on the beach near a dozen or more sea lions. These birds, identified by numbered wing tags, had been feeding on carcasses at this location almost daily for more than a month. On the ground about 1 m below the condors was a live sea lion pup appearing weak and malnourished. One of the condors (#222, Figure 1), a 10-year-old breeding female, approached the sea lion and began pecking at the posterior of the pup. The condor grasped the pup with its beak as the sea lion struggled slowly in the direction of the water, leaving a trail of blood. The sea lion then turned toward a shady spot closely overhung by a second large rock about 1 m away. The pup did not strike back at the condor during the observation, and none of the adult sea lions in the area defended the pup. Eventually, both the sea lion and
the condor were under the rock where the condor could be seen tugging at the sea lion pup. A few minutes later, the condor dragged the now lifeless pup from under the rock and began reaching with its head into the anal orifice. After feeding for 20 minutes, her crop appeared full, and she left the carcass. During the next hour, 11 other condors fed on the sea lion pup, reducing the carcass to mostly bones.

Species of the vulture family are primarily scavengers, but many can kill live prey, as supported by our observation, those of Black Vultures feeding on live seal pups in Chile (Paves et al. 2008), and even observations of California Condors killing and eating live rats and mice in captivity at the Los Angeles Zoo (M. Clark pers. comm.). Nevertheless, special circumstances likely fostered the observation reported here. In June 2010, an unusually large number of sea lion pups was abandoned along the central California coast. Many of these were emaciated, a condition attributed by Melin et al. (2010) to anomalous oceanographic conditions in 2009, warmer sea-surface temperatures reducing the availability of sea lion prey within the normal foraging range of sea lions. This necessitated sea lions having to make longer foraging trips (Melin et al. 2010) under conditions that persisted through the period of pupping. The consequences were seen in females giving birth before reaching normal offshore pupping areas, females abandoning pups, and, ultimately, a nutritional deficit in many pups (Melin et al. 2010). The end result was an unusual abundance of malnourished pups in a predictable location that provided condors with consistent and easy opportunities for foraging (Figure 2).

Our observation has at least one important implication for condor management, namely, in further documenting the ability of condors in recovered populations to locate prey independent of human intervention and demonstrating their ability to take advantage of unusual circumstances opportunistically. For populations supported
by conservation management, such ability can be interpreted as a positive sign that condors will be able to forage successfully if supplemental feeding is scaled back in the future. However, as long as lead poisoning threatens the sustainability of condor populations (Finkelstein et al. 2012, Rideout et al. 2012), providing carcasses is important not only to ensure a source of uncontaminated food but also to facilitate other necessary management, such as trapping for health exams, providing treatments for lead exposure, and maintaining equipment for tracking. The risk of lead exposure for condors feeding on marine mammals along the central California coast is likely reduced, but other harmful contaminants might be present in marine carcasses (Burnett et al. 2013), and the threat of lead exposure persists for these birds when they forage on carcasses of land mammals (Sorenson and Burnett 2007). Our observation need not prompt changes in condor management but provides more information on the condor’s capabilities to take advantage of opportunities for foraging.

On 30 November 2011, lead author Mike Tyner (age 35) was killed by a falling branch while monitoring a newly released California Condor at Big Sur. Mike was best known for his unassuming leadership, his love of outdoor adventure, and his dedication to avian conservation. In five years as a field crew leader for Ventana Wildlife Society, Mike played an important role in the California Condor recovery program, by supervising releases, assisting with condor-rescue efforts during a major wildfire, training young field biologists, and contributing field observations that have advanced our knowledge of condor biology.

LITERATURE CITED


Accepted 14 March 2013
IN MEMORIAM

RICHARD W. STALLCUP, 1944–2012

On 15 December 2012, during the compilation of the Point Reyes Christmas Bird Count in Point Reyes Station, Rich Stallcup passed away in a San Rafael hospital from complications of leukemia. Rich was a co-founder of that count in 1970 and had participated in it every year until 2012. The birding community in California lost a soul of incalculable value as a teacher, naturalist, tour leader, and indefatigable cheerleader for the natural world. His reputation extended far beyond the borders of California; he was well known in birding circles across North America. An ordinary memorial cannot express the depth of his influence on people and how many lives he touched during his time on this planet. In January 2013, more than 500 people, some from as far away as the east coast, attended a memorial service for Rich.

Born Richard William Stallcup in Oakland, California, on 19 December 1944, Rich was educated in the Oakland public school system and attended California State University, Hayward. He had a single sibling, his older brother Kenneth. Married once, he had one daughter, Willow, and eventually two grandchildren. He spent his remaining years with his life partner, Heather Cameron.

His interest in birds began at the early age of six, when his father Leland took him on a field trip to Drake’s Bay on the Point Reyes Peninsula. Throughout his life and international travels, Rich is remembered most for his love of Point Reyes and for living and spending most of his time in that region of California. Although he made over a thousand trips to Point Reyes he never lost his enthusiasm and fascination for the place. As he grew as a naturalist, his interest in things such as reptiles, amphibians, insects, and flora broadened his view of the natural world. He possessed a profound understanding of life on the Point Reyes Peninsula. Even the wandering to the outer point of a bird common only a few miles inland was of major interest to him. Beginning in the 1960s, Rich, along with confederates Guy McCaskie and C. J. Ralph, began to find rare vagrants regularly on outer Point Reyes, a phenomenon that has attracted birders to this area of California ever since. He wrote a field checklist (2000) of the Birds of the Point Reyes Seashore that totaled 470 species, of which well over half were vagrants, nearly all of which Rich had seen personally. Beginning in 1967 he also spent a great deal of time on the Farallon Islands, making frequent 2-week trips there between 1973 and 1978. In 1969, the Farallons became a national wildlife refuge.

Rich’s views of life and nature took on a particular and perhaps inevitable orientation during the counterculture life of the late 1960s and early 1970s. Although drafted and trained as a U.S. marine during the Vietnam War, Rich abhorred the thought of killing another human being, and he was able get a discharge from further service. However, the experience had an indelible impact on his thinking. He realized that the web of life was entirely connected but that mankind had the single greatest influence on life, an influence seriously flawed by greed, ego, and a profound lack of understanding. Rich’s understanding of this principle guided him throughout his life as he sought to...
impart that connection to the many people he taught. As his classroom he preferred the field, where the immediacy of life was all around him. He fought many battles on behalf of wildlife that has no voice in the affairs of mankind.

In 1976 Rich joined the formation of the early tour group *Wings* and led dozens of trips in western North America and Mexico, but being away from Point Reyes and his family for extended periods took its toll, and he began to limit his tour leading mainly to California and Arizona. In 1975 and 1976 I was fortunate enough to co-lead with Rich two trips sponsored by PRBO Natural History Excursions, both of which will be long remembered. His love of Arizona rivaled his love of California.

Rich served as president of Western Field Ornithologists from 1975 to 1978 and was a founding member of the California Bird Records Committee, serving for 8 years. In 1967 he was the first resident bird bander at the fledgling Point Reyes Bird Observatory, set up in a converted chicken coop on outer Point Reyes. From those early days PRBO grew into an international conservation and research organization with a large staff and large annual budget. Rich maintained a close association with PRBO through most of his adult life and joined the staff as a resident naturalist in 1997. In 1982 the American Birding Association bestowed on him the Ludlow Griscom Award for outstanding contributions to American ornithology. In that same year he began a regular column in PRBO’s newsletter (later called the *Observer*) that covered a vast range of topics relating to his personal observations and offering readers a unique personal perspective. He also served for 11 seasons as a co-editor of the quarterly report for the Middle Pacific Coast region in *American Birds*. The entire winter 2013 issue of the *PRBO Observer* (number 171) was dedicated to Rich and offers enriching glimpses of his life and legacy. It is a must read for everyone who knew him.

In 1966, when the *Guide to the Field Identification of Birds of North America* by C. S. Robbins, B. Bruun, and H. S. Zim was published by Golden Press, it was the first such field guide beside the Peterson series to appear since the early 1940s. As did a number of his contemporaries, Rich found that much of the book did not represent birds he knew in life and took to correcting the plates with a felt-tip pen. The guide was ultimately revised in 1983, but problems persisted. Rich then set about detailing the flaws in the Golden Nature Guide, and the result was a slim volume titled *Birds for Real*, which Rich published himself in 1985. Not only did this book reveal how much Rich knew about the species he covered, it also set the stage for field guides to follow and what would be demanded to cover the subject of bird identification adequately. The market for field guides became very competitive, and today most publishers are keenly aware of what a successful book must deliver. Today we have a plethora of excellent field guides that cover North America, Mexico, and South America that met this challenge. The entire ornithological community owes a debt to Rich for taking the time to raise the standard with something that went far beyond a typical book review.

Rich had a natural fascination with the sea and spent as much time as possible on boat trips off the shores of California. He was well known for his understanding of bird life at sea as well as of marine mammals. Yet for his first 25–30 boat trips he had a hard time with sea sickness. He eventually learned to control it without drugs, preferring to remain alert and vigilant, never knowing what might fly across the bow of the boat. Rich’s enthusiasm was infectious, and he was often as excited at seeing a bird he had seen many times as he was the first time he encountered it. No one ever left one of his boat trips without feeling enlightened about something. His experience in the coastal waters of California resulted in *Ocean Birds of the Nearshore Pacific* (1990), in which he described the mechanics of seabirding and addressed the species’ identification with descriptions and photographs, including some species not formally recorded in California at the time. *Ocean Birds of the Nearshore Pacific* is also an excellent primer on coastal oceanography and includes marine mammals, sea turtles, and some fish. It remains useful to this day. He was a senior or junior author or a contributor on dozens of reports, papers, checklists, and books during his life.
IN MEMORIAM

Rich’s connection to the natural world was nearly mystical, and he imparted deep insights to his many followers. That was his true legacy, not a list of publications. He followed in the steps of many 19th century naturalists who were guided by their interest in natural history but who lacked a formal education in a given discipline, education that did not exist in the 19th century. When natural history became a “science,” a great deal of what animates the natural world was lost at the expense of examining how the individual pieces worked and could be described. Rich never lost the importance of a wider connection, yet he understood and integrated the approach that “science” took. He had the soul of a poet, the mind of a scientist, and the spirit of a shaman—a combination of talents not often found in anyone, let alone a naturalist.

Rich’s ability to find rare or uncommon birds was legendary. He often found birds where it seemed none were present, and for those who were fortunate to be in the field with him, this happened too often to be due merely to luck or chance. It was well beyond something that could be attributed to so mundane or trivial an explanation. There are too many such stories to be recounted here, but his ability was extraordinary. Some have said that he was the most gifted field ornithologist of his generation.

Rich was a dear friend for 46 years, a colleague, co-author, and fellow birder. He will be greatly missed by all who were fortunate enough to know him. He was one of a kind, with a staggering talent that few of us can ever hope to imagine.

Jon Winter
BOOK REVIEWS


As the title suggests, this book reviews the birds of prey regularly occurring in New Mexico with additional information on the vagrant species that occasionally appear in the state. This is no small task given that New Mexico is the fifth largest state in the U.S. and boasts the fourth highest number of avian species recorded, so raptors are well represented in the Land of Enchantment. Forty-four documented raptor species, including breeding species as diverse as the Boreal Owl and Aplomado Falcon, make it unique among the 50 states. Each of the 37 regularly occurring species of raptors has its own lengthy section, ranging from 10 to 28 pages, that contains a detailed analysis of the species within New Mexico. Besides Cartron, the chapters are written by a number of authors who have studied a particular species in depth. Additionally, contributions of photographs came from over 100 individuals, so this book is truly a collaboration. This is a landmark publication for New Mexico ornithology as the first publication to take on only the raptors. For each species account and migration data the book pulls an enormous amount of information from the peer-reviewed literature, but it is worded in a fashion that amateur ornithologists and birders can easily follow.

The editor breaks the book into the introduction and two main parts, the introductory chapters and the species accounts. Each section is extremely detailed, and the editor sets the stage for the species accounts well. The introduction and introductory chapters address the origin and definition of the term “raptor,” the plant communities of New Mexico, and long-term data on raptor migration from monitoring sites within the state. “Raptor” has a seemingly new meaning in the wake of new hypotheses about the birds’ relationships arising from recent molecular studies. It is essential then that Cartron introduces the definition of the term “raptor,” where it came from, and how it is applied in this book. He does a nice job of this by introducing the first ornithologists to use “raptor” and the criteria they used to define one. The introduction also speculates about the potential phylogenetic relationships of the raptors and how these relationships may affect our understanding of their evolutionary history.

The plant communities of New Mexico provide raptors a wide variety of habitats. The section addressing them provides a clear overview of their distribution, valuable for the reader interpreting habitat descriptions in the species accounts. For instance, it is important to know the difference between “montane conifer forest” and “Great Basin conifer woodland” because their avifaunas differ.

The migration data presented in this section are impressive. Thirty-five pages are dedicated to long-term banding and observation of migrating raptors, primarily in the Sandia and Manzano mountains of central New Mexico. Migration timing, temporal shifts in abundance, mark-and-recapture studies, satellite-transmitter data, and measurements of birds captured in the field are just some of the topics covered in this section. A good example of the data in this chapter is Figure 2.5 (p. 43), which depicts the movements of 11 individual Golden Eagles that were fitted with satellite transmitters in the Manzano Mountains and subsequently found to move as far north as Alaska and south to Mexico. Such information makes this chapter valuable for anyone who wants to understand the movements of raptors through or within New Mexico.

The 37 species accounts of raptors regularly occurring in New Mexico make up the bulk of this book, nearly 600 pages. They present detailed information on distribution, habitat associations, life history, status, and management. Also, each account has a large map of the species’ distribution in New Mexico, with clear symbols representing breeding, migration, etc. Each species account is carefully constructed so that each presents roughly parallel information, but some accounts lack information that others
have. For instance, the account for Cooper’s Hawk has a section “Migration” under “Life History” while a similar section is lacking in the account for Swainson’s Hawk. As one might expect with many authors, the writing style differs noticeably from account to account, but this in no way takes away from the information presented to the reader. Each account is well written, and it is obvious that the authors have a passion for their respective species. For example, in the account for Harris’s Hawk are several photographs of author James C. Bednarz holding fledglings or monitoring a nest. The species accounts end with ten pages dedicated to seven species of vagrants that have been confirmed in New Mexico. Each of these accounts contains information on the records from the state and speculation on population trends for the species as a whole. Some include photographs of the species from New Mexico, such as of the rufous morph of the Eastern Screech-Owl in Portales in 2003.

It is hard to imagine a bookshelf of anyone interested in ornithology in New Mexico or the Southwest without *Raptors of New Mexico*. With detailed information on migration dynamics, 44 in-depth species accounts, and over 700 color photographs it is a major contribution to New Mexico ornithology and sets the bar for future publications dedicated to raptors.

Matthew J. Baumann


J. Stokley Ligon (1879–1961) was a New Mexico ornithologist and conservationist during one of the most dynamic periods in the state’s history. Dale Zimmerman noted that Ligon “Probably … covered New Mexico more thoroughly than any other naturalist before or during his lifetime.” Born and raised on a ranch in Texas, Ligon was a self-trained ornithologist who spent his twenties drilling wells and fixing windmills in west Texas and southern New Mexico. He was well acquainted with trapping predators and fur-bearers from his time on the ranch and family hunting trips. Later in life he was paid to manage teams of trappers that extirpated the Mexican wolf and grizzly bear from New Mexico. He eventually softened his views on predator control and in 1927 successfully lobbied the state legislature to designate bears as game animals, rather than pests to be shot on sight. Ligon is probably best known to contemporary ornithologists and birders from his *New Mexico Birds and Where to Find Them* (1961), an ambitious but relatable work that describes the state’s bird life and birding locations, along with more general topics such as life zones and bird conservation.

*Twelve Hundred Miles by Horse and Burro* is an account of a little-known period of Ligon’s life: his first job as a professional biologist working for the U.S. Biological Survey (USBS), to assess breeding waterbirds around New Mexico in the summer of 1913. The book begins by describing Ligon’s life prior to the start of his survey and his appointment to the USBS. The bulk of the book consists of day-by-day accounts of the survey, which contain many excerpts from Ligon’s field diary and an unpublished report on his work. As the book notes, Ligon’s diary entries are usually brief and fairly vague. Although Ligon likely kept a personal account of his travels, it seems to have been lost to history (Ligon sent his field diary and report to the USBS, and they are currently housed at the Smithsonian). In the diary he rarely mentions events that do not directly relate to the survey and does not provide complete species lists for each day. Most of his entries are focused on waterbirds, as per his instructions, so references to land birds are often scant. The authors compensate for the lack of detail by providing meticulously researched narration that retraces Ligon’s route as closely as possible while providing a historical context to the locations he visited. In addition to
Ligon’s personal writings, over a dozen of his pictures from the survey are included, and many are compared to current photos of the same location. The authors note that the book is meant to be not only an account of Ligon’s travels but also an exploration of the changes in the way of life and landscape of New Mexico over the past century. In order to accomplish this aim they revisited a number of sites along Ligon’s route and compared the habitats and wildlife Ligon reported to what they observed.

One of the most appealing aspects of the book is its extensive use of primary sources. The authors faithfully transcribed seemingly every entry from Ligon’s diary and much of his formal report, including errors and edits made by Ligon and his supervisors. The authors infer that Ligon did not have access to any field guides before and during the survey because of frequent misspellings and the incorrect use of bird names in the diary. Besides the diary and report, details of Ligon’s correspondence with the USBS and other naturalists are also included. Descriptions of the letters or the letters themselves offer unique perspectives; in one instance, Ligon is chided for the poorly prepared and improperly labeled specimens he sent to the USBS. The authors also explore the occasionally amateur and naïve nature of Ligon’s writings, due to his lack of formal scientific training. These shortcomings were apparently evident to his supervisors, who rejected some of his observations, including an April report of a Scarlet Ibis near the Gila River at close to 7000 feet elevation.

The book generally does a good job correcting Ligon’s errors, but it does contain a number of its own. Although most are minor, some are puzzling. For example, under the species accounts it suggests that Scissor-tailed Flycatchers reached New Mexico by following forests along the Canadian River (the Scissor-tailed Flycatcher is just now expanding its range to the Canadian River basin), and refers to brood parasitism by cowbirds on Willow Flycatchers as “nest predation.” The authors specify that 20 species of shorebirds nest at Bosque del Apache National Wildlife Refuge, and that a similar number nest at Bitter Lake National Wildlife Refuge (the correct total is about five). The attempts to describe changes in habitat and birdlife in the time since Ligon’s journey are commendable but often fall flat. Ornithologists and serious birders will find many of the book’s reports uninformative (e.g., “I observed perhaps fifty coots… so they are still in the area”; p. 154) or too brief to be useful.

This work provides a firsthand account of New Mexico’s first breeding bird survey and contains valuable insights to the development of one of the state’s first modern ornithologists. Those familiar with the region are not likely to gain new information on bird distributions, but the many photographs and writings from over a century ago make it a vivid and entertaining read for anyone interested in the history of ornithology in New Mexico and the southwestern United States.

Cole J. Wolf
WFO PRESIDENT’S MESSAGE:
THE FUTURE OF FIELD ORNITHOLOGY

When it comes to deciding which of the many worthy organizations we should support, the number of options seems overwhelming. None of us can afford to belong to all of them, so we try to choose those focused on the areas we care most about. While we hope WFO members appreciate direct benefits such as first option on special field trips and conference registration, we know that most of you belong to WFO because we work to promote field ornithology in a variety of ways. Among those, none is more important than fostering, encouraging, and teaching the next generation of field ornithologists.

WFO has a substantial Scholarship Fund (thanks in large part to a generous gift from Pasadena Audubon Society). This fund provides young field ornithologists the opportunity to attend our conferences and to participate in field expeditions led by top ornithologists such as Ken Able, Jon Dunn, and Kimball Garrett. We think this is an ideal way to support their growing interest and to give them models to emulate. In recent years we have provided scholarships to seven very impressive young people:

• **John Garrett**, now majoring in Ecology and Evolutionary Biology at the University of California, Santa Cruz, has been making contributions to the field since age 9, when he wrote the “Kid’s Corner” feature for the Pasadena Audubon newsletter. He has served as an eBird editor for Los Angeles County.
• **Kimberlyann Harvey**, an aspiring bird artist and one of our youngest recipients at 13, won a scholarship to attend last year’s conference in Petaluma. She is committed to becoming an ornithologist and recently read Proctor and Lynch’s *Manual of Ornithology* (a substantial tome) cover to cover.
• **Joyce Realegeno** received a scholarship to attend our Sierra Vista conference. She has studied habitat preferences of corvids around Baldwin Hills, California.
• **Ioana Seritan** also earned a scholarship to our Petaluma conference and was voted an ABA Young Birder of the Year in 2013.
• Seventeen year-old **Marcel Such** will participate in the upcoming field expedition to northeastern California. Marcel is a co-editor of *Colorado Birds* and founded the Boulder City Teen Naturalists organization.
• **Ray VanBuskirk** began banding birds at age 12 and created and runs a project studying rosy-finch ecology in New Mexico.
• **Cole Wolf** joined the board of the Central New Mexico Audubon Society at 16 and has studied the nesting requirements of the Pinyon Jay.

All of these recipients have in common participation in hands-on field research in ornithology, involvement in local ornithology/birding organizations, a commitment to teaching other young people about birds and nature, and an abiding interest in and dedication to conservation. For anyone concerned about the future of field ornithology, these young people should give cause for optimism.

We would like to continue and even expand our scholarship offerings. If this is something you care about, you can help by encouraging young people you know to become WFO members and apply for a scholarship (www.westernfieldornithologists.org/scholarship.php). You can also donate to WFO, requesting that your donation go directly to our Scholarship Fund, or simply give a promising young person a gift membership to WFO. A student membership is only $10!

Edward R. Pandolfino
The Song Sparrow (*Melospiza melodia*) is one of the most morphologically variable birds of North America. As many as 52 subspecies have been named, 39 of which were recognized by the American Ornithologists’ Union (AOU 1957) and Paynter (1970) from Canada, the United States, Baja California, and central Mexico. In the latest taxonomic revision of the Song Sparrow, Patten and Pruett (2009) recognized 25 subspecies. The subspecies vary from small and pale in the desert Southwest (*fallax*) to large and dark in the Aleutian Islands (*maxima*), with a wide range of intermediates and other variations. Although the Song Sparrow has little or no prealternate molt, the appearance of the basic plumage, especially in subspecies of more open and drier habitats, is affected by wear. The upperparts generally become paler (grayer or browner) and less distinctly streaked from fall to spring, while the underparts become whiter (less buff or brownish) and more distinctly streaked in spring. The subspecies are migratory to various degrees, with some being resident, while others are short-distance or medium-distance migrants (AOU 1957, Arcese et al. 2002).

Grinnell and Miller (1944) detailed the distribution of 18 subspecies of the Song Sparrow in California, including 12 characterized as “permanent residents,” four found only in winter, and two that breed in California and show at least some evidence of seasonal movement. Subspecies *santaecrucis* was synonymized with *gouldii* in the fifth edition of the AOU checklist (1957) and by Pyle (1997), on the basis of information from Aldrich (1984) and other sources. Pyle (1997) categorized the remaining 17 subspecies into four subspecies groups, the northwest coastal Pacific (*rufina*) group, the California mainland (*gouldii*) group, the California island (*clementae*) group, and the interior western (*montana*) group. Two other subspecies groups occurring north of Mexico, the Alaska island (*insignis*) and eastern (*melodia*) groups, contain subspecies without records in California at the time. Arcese et al. (2002) and Patten and Pruett (2009) synonymized five additional subspecies recognized in California by Grinnell and Miller (1944), realigned some of the subspecies according to subspecies groups, and recognized just five groups overall. Here we follow the subspecies taxonomy of Patten and Pruett (2009) with the exception of recognizing *fisherella* (see below). We also maintain the interior western subspecies group of Pyle (1997), which was lumped with the eastern group by Patten and Pruett.

Finding and identifying wintering or migrant subspecies of the Song Sparrow in California can be confounded by the presence and variability of local resident subspecies. Southeast Farallon Island, part of the Farallon National Wildlife Refuge, located 32 km off the coast of Marin County, lacks a resident population of the Song Sparrow and thus provides a unique opportunity for investigation of its migration and identification along the central California coast. PRBO Conservation Science (formerly known as the Point Reyes Bird Observatory) has censused birds and operated a banding station on the island since 1967 (DeSante and Ainley 1980, Richardson et al. 2003), allow-
ing banders to obtain detailed data on many of the migrant Song Sparrows reaching
the island, including measurements and photographs. From 1967 to 2012, 97 Song
Sparrows were recorded on the island, with 70 of those arriving from August to
November, 25 from February to June, and one each in December and January. Four
fall migrants remained through the winter, but none has oversummered. Of these 97
individuals, attempts were made to identify 36 to subspecies, either by biologists in
the field or retrospectively by us from photographs and banding data. Twenty-five
Song Sparrows were caught and banded, of which nine were photographed in hand,
and two additional birds were preserved as specimens. We have used photographs
and measurements of Song Sparrows from the island and compared them to series
of specimens, published measurements, and morphological descriptions. We have
also reviewed all specimens of the Song Sparrow collected in central California and
 housed at the California Academy of Sciences (CAS) and the Museum of Vertebrate
Zoology (MVZ). Here we summarize the subspecies of the Song Sparrow on South-
east Farallon Island and in central California on the basis of our best identifications.

Subspecies of the northwest coastal Pacific group breed from coastal Alaska to
Oregon, migrate to coastal northwestern and central California (Grinnell and Miller
1944, Patten and Pruett 2009), and were reported by DeSante and Ainley (1980) to
be the most common subspecies group to reach the island. *M. m. morphna* breeds
from coastal southwestern British Columbia to central western Oregon (Swarth 1923,
Patten and Pruett 2009). Grinnell and Miller (1944) characterized *morphna* as a fairly
common winter visitant to California, primarily to the northern half of the state west
of the Sierra Nevada, with records as far south as San Bernardino and Los Angeles
counties. Patten and Pruett (2009), however, indicated *morphna* to be less migratory,
with only a few individuals moving into northwestern California. It appears that Patten
and Pruett (2009) referred most of the birds identified as *morphna* by Grinnell and
Miller (1944) to *merrilli*, which breeds primarily from mainland southeastern Alaska
and interior central British Columbia south to eastern Washington and northern Idaho
and occurs in winter as far south as southern California and Arizona (Phillips et al.
1964, Patten et al. 2003).

*M. m. morphna* is characterized by its medium size, rufous upperparts with indistinct
darker streaks on the back, and heavy diffuse rufous streaking on the breast; its
appearance does not vary as much between fall and spring as does that of some other
subspecies, perhaps because of its preference for shaded habitats. *M. m. merrilli* is
a variable subspecies and may represent an intergrade swarm among the northwest
coastal Pacific (where placed by Patten and Pruett 2009), interior western (where
placed by Pyle 1997), and eastern subspecies groups, similar to subspecies *Passerella
iliaca altivagans* of the Fox Sparrow and *Junco hyemalis cismontanus* of the Dark-
eyed Junco, which breed in this same region of British Columbia (Pyle 1997). Along
the western boundary of its range, *merrilli* appears to grade into *morphna* (Patten
and Pruett 2009), having the upperparts reddish but slightly grayer than in *morphna*
toward the interior western group; see below) and with the dark streaks more distinct
toward the eastern group; see below). The underpart streaking of *merrilli* tends to
be finer than that of *morphna*, toward the interior western group. Seasonally, *mer-
rilli* appears to wear from redder in fall to grayer in spring, so it could be more easily
confused with *morphna* when in fresher fall and winter plumage.

At Southeast Farallon Island, 31 Song Sparrows were identified at the time of ob-
servation as of the northwest coastal Pacific group, and 19 of the 31 were identified as
*morphna*. Our examination, however, indicates that only three records from the island
have been satisfactorily documented as *morphna*, including a specimen collected 11
October 1969 (PRBO 330; Figure 1) and individuals photographed on 21 September
1983 and 20 September 2010 (see the lower photo on this issue’s back cover). Several
Song Sparrow records from Southeast Farallon that have been referred to *morphna*
appear instead to represent *merrilli*. These include a specimen collected 12 October
1969 (PRBO 331; Figure 1) and individuals photographed 21–22 September 1989, 30 March 1990, and 22 October 2008–12 April 2009 (Figure 2).

In a review of 107 specimens collected in California and labeled “morphna” at CAS and MVZ, Pyle found that only 15 individuals appeared to fit pure morphna; these were collected along the coast south to Santa Cruz County (MVZ 92895) and east to Yolo (CAS 51542) and Alameda (CAS 51569) counties. The remainder appeared
to be either pure merrilli, intergrades between morphna and merrilli, or in one case, an intergrade between morphna and rufina (see below). A specimen collected at Carmel, Monterey County (CAS 21554), was either morphna or a morphna × merrilli intergrade. Thus, on the basis of records from Southeast Farallon Island and this review of specimens, we agree with Patten and Pruett (2009) that merrilli rather than morphna is the more common migratory subspecies reaching most of California and that the winter range of morphna is restricted primarily to moister coastal habitats.
of northwestern California, south to Santa Cruz and perhaps Monterey counties. We suspect that many of the Song Sparrows on Southeast Farallon identified as *morphna* may in fact have been *merrilli*.

Pyle (1997) and Patten and Pruett (2009) placed three additional subspecies of the Song Sparrow in the northwest coastal Pacific group. These include *kenaiensis*, which breeds on the Kenai Peninsula of the south coast of Alaska, *caurina*, which breeds on the northern coast of the Gulf of Alaska, and *rufina*, which breeds in coastal British Columbia and southeastern Alaska. Some individuals of all three of these subspecies migrate south along the coast for the winter (Patten and Pruett 2009) and could show up in central California, though Grinnell and Miller (1944) recorded only *caurina* in California and primarily along the immediate coast in Del Norte and Humboldt counties. A specimen from Alameda County reported by Grinnell and Wythe (1927; Univ. Calif. Los Angeles 12148) as *caurina* is *merrilli*, as we confirmed by examining photos of the specimen.

The subspecies *caurina* is very dark, larger and longer-billed than *morphna*, with colder gray-brown rather than rufous upperparts and darker and browner underparts; it also has a shorter bill than the otherwise similar *kenaiensis*. In fall, the darker back streaking of *caurina* is even less distinct than that of *morphna*, and it practically disappears in spring, at which point the upperparts become duskier. Although similar to *caurina*, *rufina* is slightly smaller with an equally long bill and with more rufous tones to the plumage; *rufina* appears intermediate between *caurina* and *morphna* and intergrades with each.

On Southeast Farallon Island, DeSante and Ainley (1980) identified two fall migrants as “cf. *caurina*,” one banded on 16 October 1970 and another observed 23–24 October 1972, but no photographs or descriptions were recorded to assess the identifications, and the wing chord of the former (64 mm) is small for *caurina* (Pyle 1997). We have identified two large and dark Song Sparrows from the island as either *caurina* or *rufina*. An individual banded and photographed on 4 October 1986 (see the lower photo on this issue’s inside back cover) was dark dusky brown above, suggestive of *caurina*, but had some reddish tones below and a short wing chord (63 mm), both suggesting *rufina*, and is thus probably best identified as *caurina/rufina*. Another individual banded and photographed 26–27 September 1980 was similarly dark overall but showed significant reddish tones both above and below, and its small size (wing chord 63 mm) is more suggestive of *rufina* (Figure 3). A large individual banded on 13 September 1987 was likely *caurina* on the basis of a combination of the relatively long wing chord (73 mm; see Pyle 1997) and large mass (33.2 g), but no plumage characters were noted.

Review of specimens from California at CAS and MVZ revealed only one individual closest to *caurina*, collected in Humboldt County (MVZ 87445), one individual closest to *rufina*, collected 14 December 1904 in Alameda County (CAS 60331), and one individual that appeared to be an intergrade *rufina* × *morphna*, collected 8 December 1901 in San Benito County (CAS 51580). In addition, we have examined photographs of individuals closest to *caurina* from San Francisco County (Figure 4), and closest to *rufina* from Mendocino County (Figure 5). Although Grinnell and Miller (1944) did not record *rufina* in California, records for coastal Oregon (Marshall et al. 2006) and the evidence we report here suggest it regularly, if rarely, reaches Southeast Farallon and coastal northern California in fall and winter, expected since both *caurina* and *morphna* do so. It should be noted, however, that the systematic relationships and morphological variation of the subspecies in this group are particularly poorly known (L. DeCicco pers. comm.), so any identification of these three subspecies out of range should be regarded as provisional.

In central California, the subspecies *gouldii* of the California mainland group breeds in upland habitats along the California coast opposite Southeast Farallon from Lake and coastal southern Mendocino counties through Santa Cruz County. Grinnell and
Miller (1944) considered it a permanent resident, although Patten and Pruett (2009) reported a single vagrant *gouldii* south of its normal range, on Santa Cruz Island, Santa Barbara County, 31 October 1988 (San Diego Natural History Museum 45418); we agree with this identification after examining photos of the specimen. To the north of *gouldii* the subspecies *cleonensis* breeds from coastal southwest Oregon to central Mendocino County. Although Grinnell and Miller (1944) considered it essentially a resident, they noted an individual of *cleonensis* collected at Olema, Marin County, 17 September 1909 (Grinnell and Wythe 1927; MVZ 10570); we have examined this specimen and agree that it is *cleonensis*. Another individual at Bolinas, Marin County, November–December 2010 was identified in the field by Pyle as closest to *cleonensis*. The remaining five resident California subspecies in this group (*heermanni, pusillus, maxillaris, samuelis*, and *graminea*) noted by Grinnell and Miller (1944) and recognized by Patten and Pruett (2009) occur as residents in specific bioregions such as San Francisco Bay marshes and in southern California, including on the Channel Islands. We consider these subspecies unlikely to reach Southeast Farallon Island and do not consider them further here.

The subspecies *gouldii* has olive-brown upperparts with distinct dark brown back streaks in fall, becoming grayer on the face and redder on the wings with wear through spring. Its underpart streaking is darker brown and more distinct than in subspecies of the northwest coastal Pacific group. *M. m. cleonensis* is intermediate between *morphna* and *gouldii* in most respects, with more gray on the face and more distinct back streaks than in *morphna* but with more rufous in the plumage than in *gouldii*. It was considered part of the California mainland group by Pyle (1997) and part of the northwest coastal Pacific group by Patten and Pruett (2009), but given that it is intermediate between the two groups it could reasonably be placed with either. We have identified as closest to *gouldii* a Song Sparrow present on Southeast Farallon Island 31 March–1 April 1991 (see the upper photo on the inside of this issue’s back cover and Figure 6). Another individual on 17 October 1974 was described at the time of observation as representing a California coastal subspecies (i.e., *gouldii*), but was not photographed or measured extensively enough to confirm the subspecies. A Song Sparrow photographed on the island 11 November 2012 (Figure 7) was small, tinged brownish, and more heavily streaked on the back and underparts than *merrilli*. We have tentatively identified it as *cleonensis*, and it is possible that some of the other individuals on the island identified as *morphna* or *gouldii* were actually *cleonensis*. Thus, despite *gouldii* and *cleonensis* being considered resident or nearly so by Grinnell and Miller (1944), there does appear to be some propensity for these two subspecies to disperse or migrate. We suggest that *gouldii* is like some resident coastal species thought unlikely to reach the island by DeSante and Ainley (1980:77), including the American Crow (*Corvus brachyrhynchos*), Bewick’s Wren (*Thryomanes bewickii*), and Western Bluebird (*Sialia mexicana*), that have been recorded since.

The interior western group, including *merrilli* (see above), *fisherella*, and *montana*, breeds in drier inland habitats from central British Columbia south to northern California and east through the Great Basin; it can be distinguished from other groups by relatively pale grayish upperparts and muted pale reddish to brownish streaking on the upperparts and underparts. Grinnell and Miller (1944) separated *fisherella* as occurring in inland northern California south to Tehama and Inyo counties, whereas Patten and Pruett (2009) synonymized it with *montana* of the Great Basin. On the basis of our examination of specimens we recognize *fisherella* but suspect its boundary with *montana* might be better defined biogeographically (see Pyle 1997:28) as along the crest of the Cascade Range and Sierra Nevada, rather than to the east of Oregon and California as considered by Grinnell and Miller (1944). *M. m. fisherella* is darker and browner above and has darker and browner (less reddish) and more distinct upperpart and underpart streaking than *montana*; like *merrilli*, it appears to be heavily influenced by intergradation with surrounding subspecies *montana*,
merrilli, cleonensis, Gouldii, and heermannii, showing characters of each of these subspecies where ranges approach one another (cf. Grinnell and Miller 1944). The pale reddish fallax, a resident of the desert Southwest (Grinnell and Miller 1944, Patten and Pruett 2009), could also be considered part of this group.

Both fisherella and montana are migratory and have been recorded in winter as far south in California as Los Angeles and Imperial counties (Grinnell and Miller 1944, Patten and Pruett 2009). In the eastern San Francisco Bay region, specimens of fisherella have been taken in Sonoma, Napa, and eastern Alameda counties (Grinnell and Wythe 1927, Grinnell and Miller 1944), and it appears to be regular in winter along the east flank of the coastal range south at least to Monterey County (CAS and MVZ specimens; D. Roberson pers. comm.). In coastal central California, a specimen closest to fisherella was collected at Berkeley, Alameda County (MVZ 124699), and a specimen that appears closest to montana was collected at Santa Cruz, Santa Cruz County (MVZ 95042), although Grinnell and Miller (1944:543) cautioned that such individuals may represent variants of fisherella or intergrades between fisherella and montana. We have identified from Southeast Farallon Island no Song Sparrows as fisherella or montana (but see Figure 6); however, these other records from the San Francisco Bay area and elsewhere suggest a potential for these two subspecies to occur there.

The eastern group of the Song Sparrow contains two subspecies: the highly migratory nominate melodia, including several subspecies synonymized by Patten and Pruett (2009), and atlantica, which is largely resident in salt marshes on the middle Atlantic coast and is not expected to reach the West. Nominate melodia breeds across much of eastern North America, west to northeastern British Columbia, and winters across much of the eastern United States east of the Rocky Mountains (AOU 1957, Arcese et al. 2002, Patten and Pruett 2009). Vagrants have occurred in Washington, where a specimen was collected in King County, 27 February 1978 (Paulson 1992), and twice in Arizona (Phillips et al. 1964). M. m. melodia is characterized by small to medium size, a short thick bill, medium brownish dorsal coloration largely lacking gray or reddish tones, heavy dusky dorsal streaking, a broad dark malar stripe, heavy and distinct dark brown ventral streaking, and a buff wash across the chest when fresh.

Song Sparrows banded on Southeast Farallon Island on 3 November 1993 (see upper photo on this issue’s back cover; wing 70 mm, weight 19.5 g) and 15–16 October 1995 (Figure 8; identified by Richardson et al. 2003 as keniensis; wing 70 mm, weight 19.7 g) match nominate melodia. Both individuals had distinct black streaking both dorsally and ventrally that contrasted strikingly with the ground color, much buff in the supercilium and chest, a contrasting dark malar stripe, and a short conical bill; both were on the large end for melodia and so may have come from western populations (i.e., juddi, synonymized with melodia by Patten and Pruett 2009). Moreover, these individuals lacked the gray face of the somewhat similar California mainland group and were darker and more heavily streaked than montana of the interior western group (see above). A third individual on the island, photographed at a distance on 6 November 1992, also appears closest to nominate melodia, but the photograph is not detailed enough for us to be certain. We have also examined photographs of a Song Sparrow at Clatsop County, Oregon, 23 November 2010 (M. Patterson pers. comm., Figure 9) that represents nominate melodia. To our knowledge, these individuals represent the first records of the eastern subspecies group for California and Oregon. Given these records, others documented from Washington and Arizona, and the regularity with which many migratory eastern passerines occur on Southeast Farallon Island and the Pacific coast, we suggest that melodia may occur rarely but regularly in California and Oregon in fall and winter.

Our analysis indicates that Song Sparrows can reach Southeast Farallon Island from a broad range of areas, representing at least seven subspecies: at least three records of morphna; three of caurina/rufina, possibly including at least one each of
Figure 8. Although published by Richardson et al. (2003) as kenaiensis, this Song Sparrow banded on Southeast Farallon Island, 15 October 1995 represents nominate melodia, perhaps of the western populations or an intergrade with merrilli or montana. The very contrasting plumage, buff wash on the chest, and short conical bill are typical of melodia. The gray dorsum, however, is unusual for at least the eastern populations of melodia (D. A. Sibley pers. comm.).

Photo by Peter Pyle

caurina and rufina; at least four of merrilli; one of cleonensis; one closest to Gouldii; and at least two of melodia. Our records of rufina and melodia from Southeast Farallon and elsewhere in coastal central California represent the first records of these subspecies from the state. Although no individuals of fisherella or montana have been documented from Southeast Farallon, fisherella, at least, appears to be uncommon in fall and winter in the eastern San Francisco Bay area and should be expected to occur on the island. The uncertainty evident in the identification of many

Figure 9. Song Sparrow of subspecies M. m. melodia photographed at Warrenton, Clatsop County, Oregon, 23 November 2010. Note the contrasting plumage, thick bill, and broad dark malar stripe typical of melodia.

Photo by Mike Patterson
of the birds we discuss underscores the fact that identification of subspecies can be difficult and it may not be realistic to identify all individuals to subspecies with certainty, particularly those outside of their normal range. The unique situation on Southeast Farallon Island has provided insight into the movements of the Song Sparrow, and we hope that this analysis will help others locate and document migratory subspecies in coastal central California.

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Song Sparrow (*Melospiza melodia*) of the coastal California group, Southeast Farallon Island, San Francisco County, California, 31 March 1991. The small size, gray ground color of the head, and whitish underparts with black streaks in spring (worn) basic plumage are consistent with subspecies *gouldii* found along the coast of central California opposite the Farallon Islands.

*Photo by Peter Pyle*

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Song Sparrow (*Melospiza melodia*) of the Alaska group, Southeast Farallon Island, San Francisco County, California, 4 October 1986. The large size, long narrow bill, and very dark and sooty coloration are consistent with the subspecies *caurina* or *rufina*, breeding in southern and southeastern Alaska. The rusty tone in the streaking of underparts suggests *rufina* (not yet confirmed in California), but in lack of a specimen *caurina* (regular in winter along the coast of northern California) cannot be excluded.

*Photo by Odvin Lund*