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A NEW SUBSPECIES OF GREAT GRAY OWL (*STRIX NEBULOSA*) IN THE SIERRA NEVADA OF CALIFORNIA, U.S.A.

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KEY WORDS: *Great Gray Owl*; *Strix nebulosa*; *California*; *owl*; *phylogenetic*; *Sierra Nevada*; *subspecies*.

The Great Gray Owl (*Strix nebulosa*) has a holarctic distribution with two previously described subspecies: *S. n. nebulosa* in North America and *S. n. laponica* in Eurasia (Bull and Duncan 1993). *Strix n. nebulosa* is differentiated from *S. n. laponica* by slightly smaller size and generally darker plumage (Cramp 1985, Bull and Duncan 1993). The North American breeding range of the species is extensive, and the species occurs throughout the boreal forests of Canada and the northern United States. The winter range of *S. n. nebulosa* is similar to the breeding range, with irregular irruptive movements from the northern portion of the range southward as far as New York and Pennsylvania (Brunton and Pittaway 1971, Bull and Duncan 1993). In western North America, the breeding range extends

southward through the montane coniferous forests of Washington, Idaho, Montana, Wyoming, Oregon, and reaches a southern terminus with a geographically isolated population occurring in the central Sierra Nevada of California (Bull and Duncan 1993).

Great Gray Owls from the central Sierra Nevada are primarily found within Yosemite National Park and the adjacent Sierra and Stanislaus national forests, but rare breeding occurrences have been documented south to Tulare County and north to Plumas County (California Natural Diversity Database [CNDDDB] 2010). This population is estimated to have between 100–200 breeding individuals (Winter 1980, Rich 2000) and is listed by the state of California as an endangered species. This species does not occur in the Klamath Basin and thus there is a gap of several hundred kilometers between the central Sierra Nevada population and the next-nearest breeding population in the Cascade Range of southern Oregon (Bull and Duncan 1993). Although birds from the northern

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populations of Great Gray Owls are known to migrate/disperse hundreds of kilometers, birds from neither the Oregon nor the Sierra Nevada populations have been observed to move such distances (Bull and Duncan 1993).

Whereas morphometric data and plumage differences have historically been used to describe avian subspecies, such descriptions have often been found to mislead taxonomic inference (Zink 2004). Although the use of mitochondrial data to describe subspecies is still debated (see Ballard and Whitlock 2004), mitochondrial data provide valuable insights into avian subspecific taxonomy (see Zink and Barrowclough 2008), particularly for subspecies with small population sizes and allopatric distributions (Phillimore and Owens 2006). Because the Sierra Nevada population of Great Gray Owls is both limited in number and isolated by hundreds of kilometers from the nearest northern population, the use of mitochondrial data for subspecific delineation is appropriate.

A phylogenetic analysis using 1920 base pairs of mitochondrial *control region* and *NADH dehydrogenase subunit 2* (*nad2*) revealed the central Sierra Nevada population as a distinct clade separate from other breeding populations of Great Gray Owls in western North America (Hull et al. 2010a, Fig. 1). This clade is defined by unique mitochondrial haplotypes that form a highly supported monophyletic clade that was isolated during Pleistocene events, approximately 26 700 yr before present (Hull et al. 2010a). In contrast, haplotypes recovered from other sites in North America did not form geographically supported clades. Similarly, data collected from 30 nuclear microsatellite loci revealed a distinct central Sierra Nevada population of Great Gray Owls. The patterns of divergence revealed in these two data sets are consistent with two distinct geographically isolated lineages of Great Gray Owls in North America: one restricted to the central Sierra Nevada and a second found throughout the remainder of the North American range. These molecular genetic results are comparable with those of the Spotted Owl (*Strix occidentalis*) in western North America where the phylogenetic structure and genetic differentiation observed at both mitochondrial and microsatellite loci among three described subspecies (*S. o. caurina*, *S. o. occidentalis*, and *S. o. lucida*; Barrowclough et al. 1999; Haig et al. 2004) are similar to those seen between the northern and central Sierra Nevada populations of Great Gray Owls (Hull et al. 2010a). In contrast to the allopatric distribution of Great Gray Owl populations, the recognized subspecies of the Spotted Owl exhibit a hybrid zone in northeastern California associated with post-glacial secondary contact (Barrowclough et al. 2011). Because of the extremely small size of the Sierra Nevada population, insufficient museum specimens exist ($n = 6$) to allow for a rigorous morphological comparison with other North American Great Gray Owl populations. For the purposes of qualitative comparison, Table 1 provides morphometric data from these 6 specimens and 47 specimens from the northern portion of the range.

DISCUSSION

The process of population divergence and speciation is often prolonged (de Queiroz 2005) resulting in an extended period of time when different attributes of species distinction (e.g., morphological differentiation, phylogenetic divergence) are discordant (Omeland et al. 2000, Hull et al. 2008). Among avian species, morphology can frequently mislead taxonomic inference (Zink et al. 2000, Johnson et al. 2007, Hull et al. 2010b). Use of molecular genetic techniques has recently resulted in the recognition of cryptic species and subspecies within wide-ranging, morphologically similar avian populations (Ash et al. 2005, Christidis et al. 2008, Irwin et al. 2011) and can result in an improved recognition of extant biodiversity (see Lohman et al. 2010). Based on recent phylogenetic and population genetic findings (Hull et al. 2010a) and recognizing that identification of distinct evolutionary lineages is central element in taxonomic classification (de Queiroz 2005) and conservation of biodiversity (Faith 1992, Moritz 2002), we consider that the isolated central Sierra Nevada population of Great Gray Owls warrants recognition as a new taxon, which we name:

Strix nebulosa yosemitensis spp. nov.

Holotype. This specimen is an adult female found dead on 20 May 2005 by Kristine Hutchinson. The specimen was killed by a collision with a motor vehicle in California, Mariposa County, Yosemite National Park, on Highway 41, 1.1 km south of Wawona Hotel Road (37°31.848'N, 119°38.307'W) at an elevation of 1280 m. This specimen is deposited in the University of California, Davis Museum of Wildlife and Fish Biology; catalog number WFB-8692. The specimen was prepared by Andrew Engilis, Jr. (AEJr 4200) as a round skin + partial skeleton + tissues. The total length of the specimen is 625 mm; tail length is 295 mm; wing length is 670 mm; unflattened wing chord is 445 mm; flattened wing chord is 460 mm; culmen/nares is 27.6 mm; exposed culmen is 44.6 mm; and diagonal tarsus is 26.0 mm. No brood patch was present. The largest follicle in the ovary was 2.0 mm, indicating the bird was in a nonreproductive condition at the time it was killed. The stomach contained remains of a northern alligator lizard (*Elgaria coerulea*).

Description and diagnosis. Genetically distinct from *Strix nebulosa nebulosa* occurring to the north, *Strix nebulosa yosemitensis* (new subspecies) is defined by a unique mitochondrial haplotype for *nad2* (a transition from C to T at position 673) and two unique mitochondrial haplotypes for *control region* (a transition from T to C at position 202 and a transition from C to T at position 345; Appendix 1). These three transitions result in the monophyly of *Strix nebulosa yosemitensis* with respect to *Strix nebulosa nebulosa*. Supporting this designation, *Strix nebulosa yosemitensis* is further distinguished from other *Strix nebulosa* subspecies by microsatellite data in which the Sierra Nevada population comprises a genetically distinct Bayesian cluster based on 30 nuclear microsatellite loci (see Hull et al. 2010a).

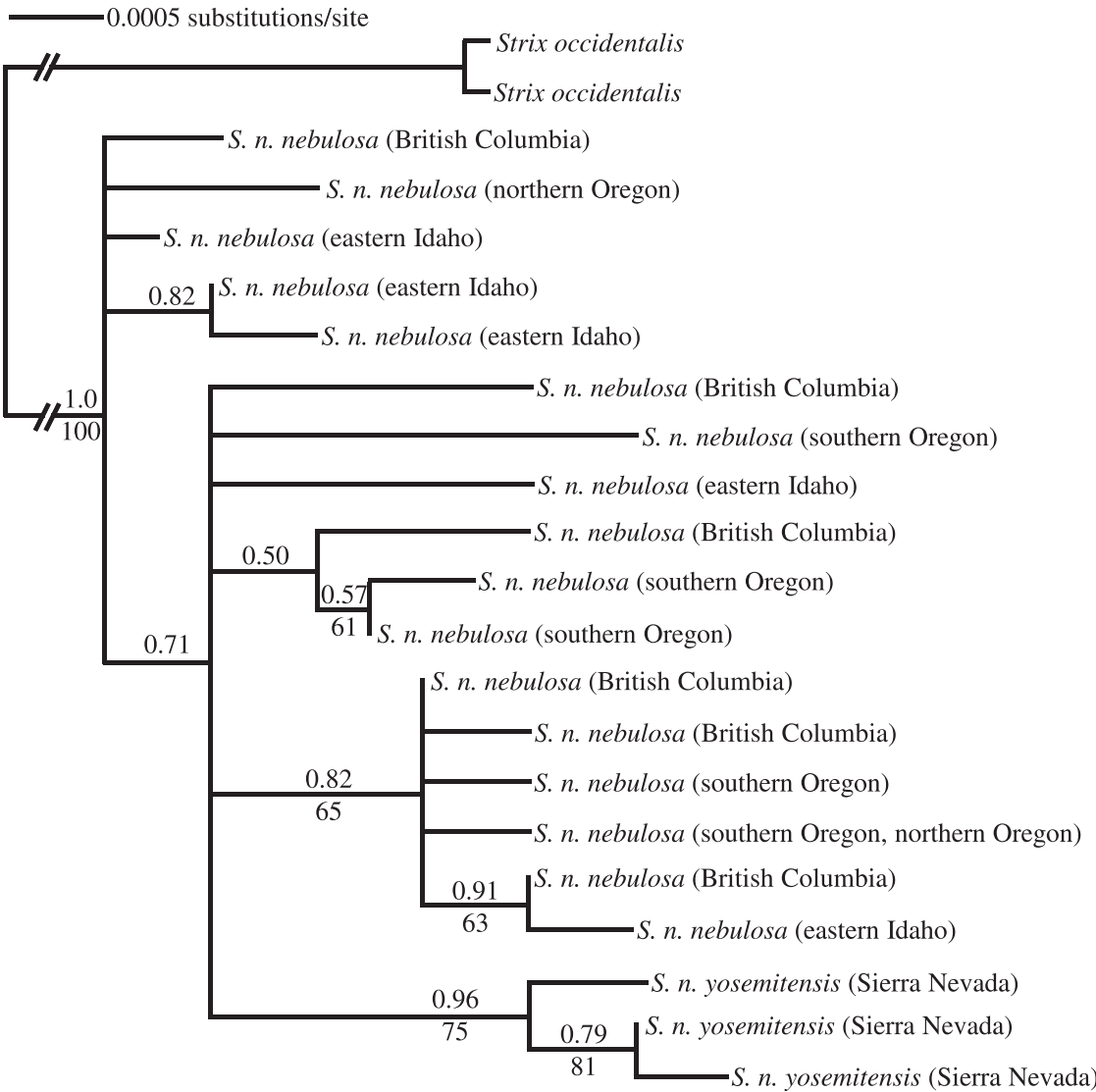


Figure 1. Phylogenetic relationships of *S. n. nebulosa* and *S. n. yosemitensis* based on 1938 base pair alignment of *nad2* and *control region* sequence. The Sierra Nevada samples are monophyletic, whereas the remaining 17 *S. n. nebulosa* haplotypes show no geographic structure. Numbers below branches are bootstrap values (Maximum-likelihood); numbers above branches are Bayesian posterior probabilities. Figure adapted from Hull et al. 2010a.

Morphometric measurements taken from the limited number of museum specimens and banded birds provide a preliminary qualitative description of the size of individuals from each subspecies (Table 1). This preliminary description includes morphological data from 37 Great Gray Owls in the central Sierra Nevada and 47 Great Gray Owls outside of the central Sierra Nevada range (Alaska, $n = 8$; Alberta, $n = 9$; British Columbia, $n = 1$; Maine, $n = 3$; Manitoba, $n = 9$; Massachusetts, $n = 3$; Minnesota, $n = 4$;

Northwest Territories, $n = 4$; Oregon, $n = 1$; Wyoming, $n = 1$; Yukon, $n = 4$). We collected morphological data for three characters: (1) tail length (the length of the tail from the insertion point of the number one rectrices to the tip of the longest rectrix, taken with the ruler between the number one rectrices), (2) wing chord (straight line length of the chord from the carpal joint to the tip of the longest primary; this measurement is taken without flattening the natural curve of the wing), and (3) length

Table 1. Mean and range from *S. n. nebulosa* and *S. n. yosemitensis* for wing chord (mm), tail length (mm), and culmen length (mm). *S. n. nebulosa* live specimens of known sex were sampled during the breeding season in Manitoba, Canada. *S. n. nebulosa* museum specimens were collected during the nonbreeding season from Alberta, British Columbia, Manitoba, Northwest Territories, Yukon (all in Canada), and Alaska, Maine, Massachusetts, Minnesota, Oregon, and Wyoming (U.S.A.); the breeding origin of these birds was unknown. All *S. n. yosemitensis* specimens were sampled from the central Sierra Nevada in California; live specimens were sampled during the breeding season whereas the museum specimens were collected during the breeding and nonbreeding season.

SUBSPECIES	SEX	SOURCE	n	WING CHORD	TAIL LENGTH	CULMEN LENGTH
<i>S. n. nebulosa</i>	F	Live	42	422 (405–441)	294 (281–311)	Unavailable
		Museum	26	442 (410–466)	286 (255–310)	41.5 (36.6–43.7)
	M	Live	20	405 (382–425)	284 (262–304)	Unavailable
		Museum	21	425 (404–446)	279 (260–300)	41.0 (38.9–42.9)
<i>S. n. yosemitensis</i>	F	Live	17	431 (400–465)	288 (271–306)	39.5 (36.6–45.5)
		Museum	3	425 (405–445)	294 (286–300)	44.3 (44.0–44.6)
	M	Live	14	408 (397–422)	281 (263–295)	37.4 (34.7–41.8)
		Museum	3	408 (396–425)	285 (272–305)	40.9 (38.9–42.5)

of culmen (Golden Gate Raptor Observatory 1998). A larger, comparable sample size is needed to determine whether mitochondrial divergence is associated with divergence in morphometric measurements. Data for such a comparison do not currently exist and will be difficult to collect due to the low number of individuals in the Sierra Nevada.

In addition to the eight available museum specimens from *S. n. yosemitensis*, we examined photographs taken from banding efforts of Sierra Nevada Great Gray Owls (17 females and 14 males) for comparison with *S. n. nebulosa*. This preliminary survey suggested that adults of *S. n. yosemitensis* appear overall grayer than *S. n. nebulosa*. Additionally, the pattern of the facial disc may be more muted in Sierra Nevada birds, with the facial disc rim more intensely marked in northern birds. Hatch-year (HY) individuals of *S. n. yosemitensis* possess an overall brighter-speckled “necklace” (feathers around the lower rim of the facial disc) than do hatch-year *S. n. nebulosa*, but sample sizes were too small to determine whether this is a consistent character distinguishing the two subspecies. Figure 2 provides an illustration of ventral and lateral views of typical *S. n. yosemitensis* adult plumage. Examination of 47 museum skins of *S. n. nebulosa* collected throughout North America shows considerable variation in tones of grays and browns and may be related to age of the feathers, and possibly sex. Due to limited sample size we did not attempt to determine the differences in plumages between hatch-year and adult Sierra Nevada birds.

Etymology. The name for the new subspecies is derived from the location, Yosemite, where it was collected in the central Sierra Nevada.

Distribution. The breeding distribution of Great Gray Owl ranges from 700–2600 m in elevation in the Sierra Nevada. The core breeding range is located in Fresno, Tuolumne, Madera, and Mariposa counties, California (Winter 1986, Quady 2008, CNDDDB 2010; Fig. 3). Outside of the core breeding range, records in the Sierra Nevada have been documented to the north and south of the

core breeding range in El Dorado, Placer, Plumas, and Tulare counties, California. Within their breeding range Great Gray Owls in the Sierra Nevada occur in conifer forests and oak (*Quercus* spp.) woodlands usually associated with meadows. Meadows at higher elevation sites may be intermittently to seasonally flooded, semi- to permanently flooded, or upland herbaceous systems. At lower elevations upland herbaceous meadows may be interspersed within oak and pine (*Pinus* spp.)-oak woodlands. Great Gray Owls are facultative elevational migrants in winter and migrate to elevations as low as approximately 500 m in response to prey, weather, and snow conditions (Jepsen et al. 2011)

Conclusions. *S. n. yosemitensis* is both monophyletic and allopatric with respect to *S. n. nebulosa* in the core range of the species in North America. *S. n. yosemitensis* is vulnerable to extirpation due to low abundance (Winter 1980, Rich 2000), as well as habitat loss or degradation due to human development and management practices (grazing, timber harvest, fire suppression/wildfire), and landscape conversion, particularly at lower elevations (see Millar 1996, Dull 1999, Jepsen et al. 2011). Other documented threats to this subspecies include mortality due to vehicle strikes (J. Mauer, Yosemite National Park pers. comm., J. Keane unpubl. data) and potential mortality from West Nile virus (see Gancz et al. 2004, Hull et al. 2010c). In light of past and continuing threats to its persistence and the importance of peripheral populations in conservation of biodiversity and maintenance of evolutionary processes (Lesica and Allendorf 1995), *S. n. yosemitensis* may require continued monitoring and conservation attention.

UNA NUEVA SUBESPECIE DE *STRIX NEBULOSA* EN LA SIERRA NEVADA DE CALIFORNIA, EEUU

RESUMEN.—Brindamos un diagnóstico para una nueva subespecie de *Strix nebulosa* para el centro de la Sierra

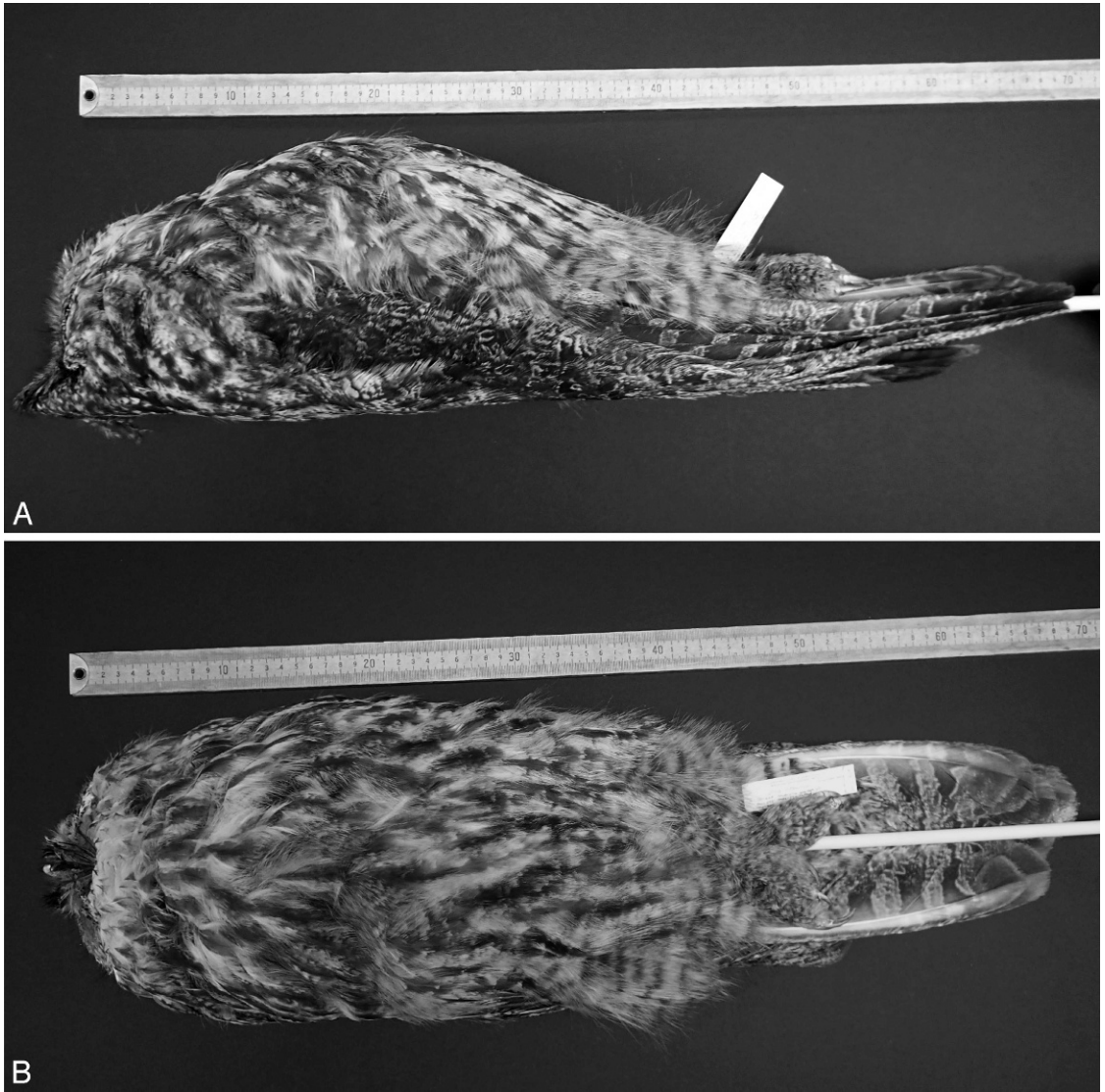


Figure 2. Lateral (A) and ventral (B) views of typical adult *Strix nebulosa yosemitensis* plumage. The specimen shown is the holotype housed at the Museum of Wildlife and Fish Biology at the University of California, Davis. See text for description of morphological characters.

Nevada de California basados en análisis filogenéticos y genéticos poblacionales previos y en la distribución alopatrica. La nueva subespecie está definida por análisis filogenéticos de 1920 pares de bases de una *región de control* y en la subunidad 2 de la NADH deshidrogenasa de una secuencia de ADN mitocondrial y respaldada por una diferenciación genética poblacional en 30 marcadores de ADN microsatelital nuclear. La distribución de esta subespecie incluye ecosistemas boscosos y forestales y praderas asociadas entre los 700 m y 2600 m en el centro de la Sierra

Nevada en California, EEUU. Esta subespecie de *S. nebulosa* está amenazada por numerosos factores y justifica esfuerzos de conservación continuos.

[Traducción del equipo editorial]

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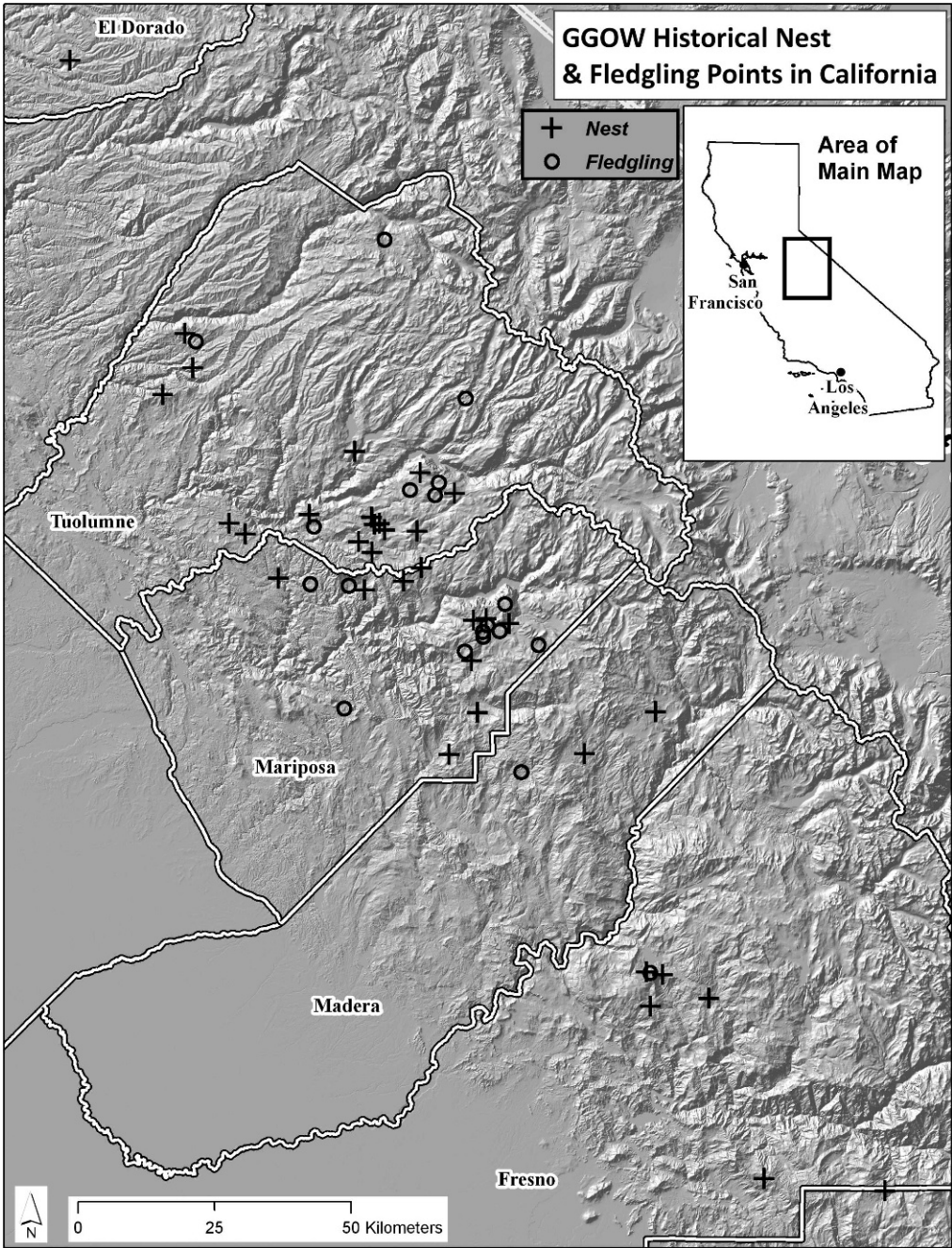


Figure 3. Breeding distribution of *Strix nebulosa yosemitensis* (GGOW) in the central Sierra Nevada as inferred from historic nesting and fledging points. Crosses indicate nesting records and open circles indicate fledging records. These data were taken from previously published research (Quady 2008; Winter 1980, 1985, 1986), unpublished records from ongoing research conducted by the U.S.D.A. Forest Service Pacific Southwest Research Station, and personal communications with district biologists in the Sierra, Sequoia, and Stanislaus national forests. Data are current as of October 2013.

the following museums for access to their specimens: Museum of Comparative Zoology (J. Trimble), U.S. National Museum – Bird Division (J. Dean), Museum of Vertebrate Zoology (C. Cicero) and Museum of Wildlife and Fish Biology (I. Engilis). E. Harper provided photographs of northern birds from Montana and Wyoming and A.M. Engilis provided assistance in recording data from specimens. We also thank the Editor and three peer reviewers for their thoughtful comments and guidance. Financial support for this study was provided by the U.S.D.A. Forest Service-Pacific Southwest Research Station-Sierra Nevada Research Center, Region 5-U.S.D.A. Forest Service.

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Appendix 1. Unique *nad2* and control region sequences for *Strix nebulosa yosemitensis*. The consensus *Strix nebulosa nebulosa* sequences and above with unique *Strix nebulosa yosemitensis* mutations indicated in bold below at *nad2* position 673 (transition from C to T) and at control region positions 202 (transition from T to C) and 345 (transition from C to T).

<i>nad2</i> :					
1	11	21	31	41	51
CATGGGGGAG	AGCGGTAGGA	GTAGGATTGA	TGAGGAGGTG	AGGGGGGCGA	TGATGGTGT
-----	-----	-----	-----	-----	-----
61	71	81	91	101	111
TGCTGGGCTA	TTGGTGTGTC	AGTGCTTTAT	ATGGGTGCG	GAGTTTGGTG	GGAGGGTGAT
-----	-----	-----	-----	-----	-----
121	131	141	151	161	171
TGTTGAGTAG	TATGCGAGTC	GTAGGTAGAA	GAATAGTCCT	AGAAGTGATA	GTATAGCGAT
-----	-----	-----	-----	-----	-----
181	191	201	211	221	231
GAGTGTGGCT	GTGGGGGTTA	GTTCTGGTT	GGTTAGTTCT	TGGAGAATGA	GTCATTTTGG
-----	-----	-----	-----	-----	-----
241	251	261	271	281	291
TAGAAAGCCG	GTTAGGGGTG	GTAGTCCTGC	TAGTGAGAGT	AGGGTTAATA	TAAAGGCTGT
-----	-----	-----	-----	-----	-----
301	311	321	331	341	351
GTTCAGTATG	GGGGCTTTTG	TTCATGTAAT	TATCATTGTC	TGTAGGTTCA	TGGTCTTGGT
-----	-----	-----	-----	-----	-----
361	371	381	391	401	411
TGTGTTTAGG	GTTAGGAATA	CGGTGGCGGT	TATTATAGTG	TAGAGGTAGA	AGGTTAGTAG
-----	-----	-----	-----	-----	-----
421	431	441	451	461	471
TGTGAGCTTA	GGGTAGTAGA	GGATGATAGC	AGCTATTCAG	CCTAGGTGTG	AGATGGATGA
-----	-----	-----	-----	-----	-----
481	491	501	511	521	531
GAAGGCCAGG	ATTTTTCGAG	TTTGTGTTTG	GTTTAGCCCC	ATTCAGCCTC	CTAGGGCGGT
-----	-----	-----	-----	-----	-----
541	551	561	571	581	591
TGAAGAGATG	GCTATGGCGG	TTAGTAGGGT	GGGGTTTAGT	GAGTGCGATG	TTAGTAAGAG
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601	611	621	631	641	651
GAGGGTAAGT	GGAGGGAGTT	TTATTAGTGT	TGAGAGTAGG	AGGGCCGTGG	TGAGGGATGT
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661	671	681	691	701	711
TCCTTGAGAG	ACCTCTGGGA	ATCAGAAAGTG	GAATGGGACT	AGTCCTAGTT	TTATTGCAAT
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721	731	741	751	761	771
TGCTATTGTT	ATGAGTAGGC	AAGGTACGGT	GTGGGTATT	TGAGTGACAT	CTCATTGTCC
-----	-----	-----	-----	-----	-----
781	791	801	811	821	831
TGAGGATCAT	GCATTGGCTA	TGCTTGAGAA	GAGCAATAGG	GCGGAGGCGG	TTGCTTGTA
-----	-----	-----	-----	-----	-----
841	851	861	871	881	891
TAGAAAGTAT	TTGATTGTAG	CTTCGATGGC	TCGGGGGTGG	TGTGATTGG	CAATTATAGG
-----	-----	-----	-----	-----	-----
901	911	921	931	941	951
GATGATGGCT	AGAGTGTTGA	TTTCTAGTCC	GGTTCAGGCT	ATTAGTCAGT	GGTTGCTTGA
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961	971	981	991	1001	
GATGGTGATG	GTTGTTCCTA	ATAGGAGACT	AAGGGAGGTA	AGTAG	
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Appendix 1. Continued.

Control region:					
1	11	21	31	41	51
CCCCCCCTTA	CCCCCCCGGC	CTCTGGGATT	GCCCTTTATG	CCGTTTGGGA	TGTATAATTG
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61	71	81	91	101	111
CACATCACAC	TATCTACCCC	ATACACATAC	CATTAATGTA	CTAAACACAT	ACTATCCATG
-----	-----	-----	-----	-----	-----
121	131	141	151	161	171
TACAAACTCC	ATACCATTAA	TGTACTATAA	ACACCCTAAT	CCATGACAAA	CCGACACACT
-----	-----	-----	-----	-----	-----
181	191	201	211	221	231
ATCCATGTCC	TATAAACATA	CTATGCATGT	ACCAAAAACA	TCCTAATCCA	TGACAAACCG
-----	-----	- C -	-----	-----	-----
241	251	261	271	281	291
ACACACTATC	CATGCTCTCT	AAATATGAAC	TGTATGTACC	AAGAATACTC	TAATTCATGC
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301	311	321	331	341	351
CAGCCGAATA	TACTATCCAT	GCCCTATAAA	ACATACCATC	CATGCTCTTC	ACCTAGGCCA
-----	-----	-----	-----	- T -	-----
361	371	381	391	401	411
TTCATGTCTA	AATCACAATC	CATCCATGTA	CTTCACCTCA	CCCTACCAAC	AAGGCATTCC
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421	431	441	451	461	471
CTTCCCATCA	ACAGCTCTAC	TTTCAAGTAT	TGTTTCAAGT	AATAGTCCCA	CCTAAAGTAA
-----	-----	-----	-----	-----	-----
481	491	501	511	521	531
GCCAACTTCT	CTCGTACCTA	AACCATACCC	TCTCTAATCT	GTAATAAACA	ATGTCCCTAT
-----	-----	-----	-----	-----	-----
541	551	561	571	581	591
ATACGGATAT	GCTTGCACAT	AACTGGCGCA	GCGGTAACAC	CCCATATAGC	TACGATATTC
-----	-----	-----	-----	-----	-----
601	611	621	631	641	651
TCGTTGTACC	GGCTCCCAAG	GTACTGGGTT	ATTTATTAGT	CGGACTCCTC	ACGTGAAATC
-----	-----	-----	-----	-----	-----
661	671	681	691	701	711
AGCAACCCGG	TGTTAGTAAG	ATCCTAAGAC	CCTAGCTTCA	GGCTCATTCT	TTCCCCCTAC
-----	-----	-----	-----	-----	-----
721	731	741	751	761	771
ACCCCTCGCC	CTACTTGCAC	TTTTCGCGCT	CTGGTTCCTC	GGTCAGGGCC	ATCTCTCTAC
-----	-----	-----	-----	-----	-----
781	791	801	811	821	831
GCATCCTCTC	AACTTGCTCT	TCACCGATAC	ATCTGGTTGG	CTATTAATCA	CCATCGTCTC
-----	-----	-----	-----	-----	-----
841	851	861	871	881	891
TCTTAATCGT	ATCACCGACA	GCCTTTTCTC	TTTTCTTCTT	TTTTTCTCTC	TCGTCTTCAC
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901	911				
TTTGCCCTTC	AAGTG				
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