# MOLT SEQUENCES IN AN EXTRALIMITAL GREAT GRAY OWL DETECTED OVER TWO WINTERS IN NORTHWESTERN CALIFORNIA

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ABSTRACT: In California, the Great Gray Owl (Strix nebulosa) has a very small population and is considered endangered. The Coast Range of northwestern California is not considered part of the species' regular range, and prior to January 2016 there were only three records for the region. During the winters of 2015–2016 and 2016-2017, however, a Great Gray Owl occurred in Humboldt County at locations separated by about 50 km. We evaluated photographs from both winters to assess whether they were of the same individual owl. Patterns of retained juvenile wing feathers and replaced feathers of the definitive basic plumage were consistent with the owl photographed in winter 2016-2017 (likely in its fourth cycle) being one year older than the one photographed in winter 2015–2016 (likely in its third cycle). Furthermore, during both years, the same primary feather on the right wing showed an irregularity along the inner web near the tip, including a notch and additional damage to the barbs, evidence that the observations in both years were of the same individual. Feather-replacement patterns in this individual during these two winters, along with those of another specimen from Humboldt County from 2007, imply that the sequences of molt of the remiges in the Great Gray Owl parallel those of other Strix but that the rate of molt may be slower than previously reported.

The Great Gray Owl (Strix nebulosa), listed as endangered in California by the California Department of Fish and Wildlife since 1980 (https://nrm. dfg.ca.gov/FileHandler.ashx?DocumentID=109405&inline), is one of the rarer breeding bird species in the state. Wu et al. (2016) collated and assessed all records of confirmed nests or detections of fledglings in California between 1973 and 2015 and estimated a current population of approximately 79 pairs. The core of the California population occurs on the western slope of the Sierra Nevada from Mariposa County north to El Dorado County (Beck and Winter 2000, van Riper and van Wagtendonk 2006, Hull et al. 2014, Wu et al. 2015, Polasik et al. 2016). Isolated breeding and occurrence records extend south in the Sierra Nevada to Tulare County and north in the Sierra Nevada, southern Cascades, and Modoc Plateau to Modoc County, just south of the Oregon border (Wu et al. 2015, 2016). While in other portions of the species' range Great Gray Owls are known to migrate or disperse hundreds of kilometers during irruptions (Nero and Copland 1997), those in Oregon and California have never been documented to undertake large-scale movements, beyond facultative downslope migration in winter over observed distances up to 25 km (Winter 1986, Bull et al. 1988, Bull and Duncan 1993, Skiff 1995, van Riper and van Wagtendonk 2006, Jepsen et al. 2011).

The Coast Range of northwestern California is not known as part of the regular range of the Great Gray Owl, with no evidence of nesting documented for the region (Bull and Duncan 1993, Hull et al. 2014, Wu et al. 2015, 2016). In rare instances, however, individual birds have been reported in the region during winter, including three from coastal north-

western California prior to January 2016. The most recent such report was from Humboldt County in December 2007, when an emaciated owl was discovered in the Freshwater area of Eureka. This individual survived only a few hours after discovery, and the specimen, recovered by M. Mitchell, is preserved at Humboldt State University (HSU 8960). In January 1982, a Great Gray Owl was observed foraging over a period of a week at Prairie Creek Redwoods State Park. On 22 January it was struck and killed by a vehicle: the specimen, recovered by R. Adams, is also preserved at Humboldt State University (HSU 5029). Prior to these two records, a Great Gray Owl was observed near Endert's Beach just south of Crescent City, Del Norte County, in March or April of 1974 (Winter 1980). The nearest area where Great Grav Owls are detected somewhat more consistently lies >100 km to the east, in Siskiyou County, a region with multiple winter and summer records since the 1970s (Fetz et al. 2003). Slightly farther to the north, there are multiple breeding records from southern Oregon, in southeastern Jackson County and southwestern Klamath County (Bull and Henjum 1990).

On 16 January 2016, Emily Christian and Danielle Westberg discovered a Great Gray Owl in Prairie Creek Redwoods State Park (Figure 1), foraging along roadways and forest edges surrounding a large meadow. The owl was observed and photographed by many birders for a period of about 7 weeks (last reported on 29 February 2016; www.eBird.org; detailed data accessed by permission May 2017). The following winter, on 24 December 2016, O. and S. Peterson (pers. comm.) discovered a Great Gray Owl near Alder Grove Road on the outskirts of Arcata, approximately 50 km south of the previous winter's observation at Prairie Creek Redwoods State Park (Figure 1). The Alder Grove owl, which was identified as female by its vocalizations (O. and S. Peterson pers. comm.), used meadows and pasture on private land within a forested matrix <1 km from a largely urban area. Birders reported seeing the owl through 30 March 2017 (O. and S. Peterson pers. comm.).

The rarity of detections in Humboldt County and more generally in the Coast Range of northwestern California suggest that detections in two consecutive winters could have been of the same individual. On the other hand, the substantial distance between the two locations suggests the contrary. If there were two individuals, their discovery might signal a recent range expansion or a previously undiscovered population of wintering or even permanently resident owls. While it may seem unlikely that a population of such a charismatic species, sought after by birders, could have gone heretofore undiscovered, the Great Gray Owl's nocturnal and cryptic habits make the species surprisingly hard to detect. Indeed, in 2006 a previously unknown cluster of nesting Great Gray Owls was discovered in uncharacteristic habitat in the lower montane zone of the central Sierra Nevada (Polasik et al. 2016).

The most reliable way to determine if multiple detections of a bird represent the same individual is with extrinsic markers, such as leg bands. For unmarked individuals, however, it may be possible to glean substantial information from intrinsic markers. Although the term "intrinsic marker" usually denotes genetic (e.g., Ruegg et al. 2014) or isotopic features (e.g., Coiffait et al. 2009) that carry information about an individual or its source population, certain plumage characteristics may also be thought of as intrinsic markers. At a minimum, patterns of molted and retained feathers may indicate the

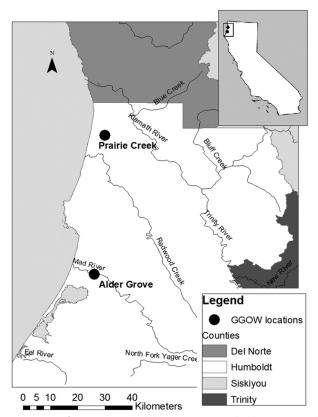


Figure 1. Locations of Great Gray Owl detections in Humboldt County, California, between 16 January and 29 February 2016 at Prairie Creek Redwoods State Park and between 28 December 2016 and 18 February 2017 near Alder Grove Road on the outskirts of Arcata.

plumage cycle and age class of a bird (Pyle 1997a, b). We examined such patterns in considering whether the sightings in 2016 and 2017 pertained to the same individual owl. For example, molt patterns indicating that the bird in 2017 was one year older than the one in 2016 would be consistent with its being the same bird. If the owl in 2017 was younger than, the same age as, or more than one year older than the one in 2016, the detections would represent distinct individuals. In some cases, individual birds may also have unique or unusual plumage characteristics (e.g., distinctive notches on particular feathers) that can differentiate them from other individuals of the same age class. Along with consistent molt patterns and age, such notches or irregularities on specific feathers can confirm that two or more observations pertain to the same bird (Pyle and Sullivan 2010, Nelson and Pyle 2013).

In owls, sequences of molt of the remiges are complex. In some species, molt commences from a node among the middle primaries and proceeds

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both inward and outward (Pyle 1997a, b). Additional study by Pyle suggests that these nodes may be consistent within a genus. For example, molt of the primaries begins with p7 among species of Bubo and Tyto, p5 among species of Strix (see also Suopajärvi and Suopajärvi 1994), and p3 among species of Athene (e.g., Trefry and Holroyd 2012). In Aegolius, molt appears to proceed distally from a node among the medial primaries, while in other North American genera it may proceed in typical sequence from p1 outward. but confirmation of these molt sequences and their consistency within all owl genera is needed. In all owls, replacement of the secondaries appears to proceed as is typical of diastataxic species (those having evolutionarily lost a secondary between what we now call s5 and s6: Bostwick and Brady 2002). bilaterally from the second tertial, proximally from s5, and proximally from s1 (Pyle 2008, 2013). In the Spotted (Strix occidentalis) and Barred (S. varia) owls, as well as other Strix species in Europe (Pietiäinen et al. 1984, Cramp 1985, Suopajärvi and Suopajärvi 1994), the sequence of molt of the remiges has been reported as irregular (Pyle 1997a, b), but recent study by Pyle indicates that replacement proceeds consistently bilaterally from a node at p5 (or possibly p6 in some cases) and that secondaries are replaced as indicated above, at least in the Barred Owl. The sequence of molt of the remiges in the Great Gray Owl is not well known but may be similar to that of other species of Strix (Cramp 1985, Pyle 1997a, b), whereas rectrix molt has been observed to be synchronous (Gura et al. 2017). In larger owls (e.g., Bubo, Strix, and Tuto) molt can proceed very slowly relative to other species of birds, in some individuals replacement of all remiges taking up to six years or more. Understanding these patterns and distinguishing juvenile feathers from those of the basic plumage following each molt can allow the age of owls to be determined up to at least their fourth plumage cycle (Pyle 1997a, b).

Our objective was to assess whether plumage characteristics could provide evidence that the 2016 and 2017 detections in Humboldt County represented the same individual Great Gray Owl and, if the owl was the same, to assess its age and trace its molt patterns during the intervening summer.

# **METHODS**

We examined >230 photographs of the owls, taken during both winters (over 70 from each winter), which were accessible in Cornell University's Macaulay Library or were provided directly to us by the photographers (see Figures 2–4). In reviewing the photographs, we focused particularly on feather generation, molt patterns, and notches on individual feathers. By the standard convention, the Great Gray Owl's ten primaries are numbered distally from the innermost (p1) to the outermost (p10), the 14 secondaries are numbered proximally from the outermost (s1) to the innermost (s14, s12–s14 representing the tertials), and the 12 rectrices are numbered from the innermost (r1) to the outermost (r6) on each side of the tail (Pvle 1997b).

# **RESULTS**

Molt patterns in the Great Gray Owl photographed at Prairie Creek Redwoods State Park in 2016 are shown in Figure 2. Among the primaries



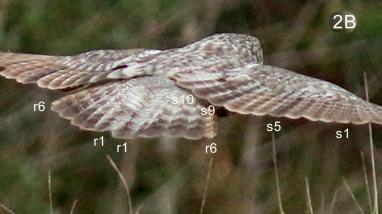


Figure 2. Great Gray Owl, photographed in Prairie Creek Redwoods State Park, California, on 21 January 2016. Note that the all primaries appear to be juvenile except for p5 and p6 in both wings, with p6 appearing a year newer than p5 (A). On both wings, s1–s4 and s6–s8 appear to be juvenile, the tertials and innermost secondaries (s11–s14) appear to have been replaced at the same time as p5, and s5, s9, and s10 appear to have been replaced at the same time as p6. Among the rectrices, the outermost (r6) appears to be juvenile, while those in the middle of the tail (among r1–r5) represent two later generations matching p5 and p6 in freshness.

Photos by Sean McAllister



Figure 3. Great Gray Owl, photographed near Alder Grove Road on the outskirts of Arcata, California, during winter 2016–2017. Patterns of feather replacement parallel those of the bird in 2015–2016 (Figure 2), except for the replacement of several additional feathers. These include the primary coverts corresponding to p7 on both wings, the left s2 (growing), s6, s8, s13, and perhaps additional tertials on both wings, the left r2, and r6 on both sides of the tail. The pattern of juvenile and older feathers is consistent with the bird of 2015–2016 having replaced these feathers, in sequence, during the intervening summer.

Photos by Michael Lang (A, 16 January 2017) and Rob Fowler (B, 6 January 2017) (Figure 2A), all feathers appear to be of the same generation except for the newer p5 and p6 on both wings. Primary 5 appears more worn and faded than p6, consistent with its being replaced a year before p6. The remaining eight primaries on each wing are older still, thinner, more pointed at the tips, and show consistent bar patterns across all feathers, indicating that they are of the juvenile plumage (Pyle 1997a, b). The primary coverts corresponding to each primary show the same patterns of replacement (Figure 2A). Among the secondaries (Figure 2B), s5, s9, and s10 on both wings are newer and appear to have been replaced at the same time as p6. The inner secondaries (s11-s14, including the tertials) appear to be a year older and of the same generation as p5, and the remaining seven secondaries on each wing (s1-s4 and s6-s8) appear to be older still and with wear and bar patterns consistent with juvenile feathers. In comparison with what is known about molt in Strix (Pyle 1997a, b), this evidence suggests that p5 and s11-s14 were replaced during the summer and fall of 2014, and that p6, s5, and s9-s10 were subsequently replaced during the summer and fall of 2015. The rectrices are not fully analyzable in the photos from 2016 (Fig. 2B), but the outermost rectrices (r6 on each side) are old, narrow, and juvenile, while the remaining rectrices are newer, potentially with r1, the right r3, and r4 and r5 being a year newer than r2 and the left r3.

Molt patterns in the Great Gray Owl photographed in 2017 at Alder Grove (Figure 3) are similar to those of the one in 2016 except that a few more feathers are new. As in 2016, p5 and p6 are the only replaced primaries on both wings, p5 is older looking than p6, and the remaining primaries appear juvenile. Notably, the primary coverts corresponding to p7 on both wings are new (Figure 3A), a difference from 2016. In 2017 the secondaries also show the same patterns as in 2016, except that the left s2 is new and appears to be growing (being shorter than both s1 and s3), s6 and s8 are new on both wings, and s13 is newer than a very worn s12 on the left wing, at least (as seen in Figure 3B). Among the rectrices (Figure 3B), r6 on both sides and the left r2 appear new; r1, r5, and r4 on both sides and the right r3 appear to have been replaced the year before this, and the right r2 and left r3 appear to be browner and of yet an older generation. Thus in 2017 the bird was very similar in molt-sequence pattern to that of 2016, but with s6, s8, s13, r6, and the primary covert corresponding to p7 replaced on both wings, s2 replaced on the left wing, s13 replaced on at least the left wing, and r2 replaced on the left side of the tail. Wear patterns are consistent with these feathers being replaced during the summer and fall of 2016, following those feathers replaced in 2014 and 2015 as described above.

In general, the primaries, secondaries, and rectrices do not show distinctive notches at the tips during either year. This is not surprising, as the softness of owl plumage minimizes this kind of imperfection. However, during both years, the right p7 shows an irregularity along its inner web near the tip, including a notch and additional damage to the barbs, suggesting impact with a branch or other object (Figure 4). These notches are similar enough to confirm, along with the similarity in molt patterns, that the 2016 and 2017 birds were the same individual.

Pyle's examination of photos of the 2007 specimen from Humboldt County (HSU 8960), right wing, revealed molt patterns similar to those of the

owl of 2016–2017. All primaries and secondaries appear juvenile except s5 and s10–s14, with s5 and s10–s11 appearing one year newer than s12–s14. The primary covert corresponding to p5 has also been replaced. Among the rectrices, the left r5–r6 and right r6 appear juvenile and the central two rectrices appear one year newer than the other replaced rectrices. Thus the tertials and most rectrices were apparently replaced during the summer of 2006, and s5, s10–s11, the primary covert corresponding to p5, and the central rectrices were replaced during the summer of 2007.

### DISCUSSION

Analysis of molt patterns and notching in the primaries indicates that the Great Grav Owl detections in Humboldt County during the winters of 2015-2016 and 2016-2017 were of the same bird. In addition, new information on the species' molt patterns and age-determination criteria can be inferred from this individual and the 2007 specimen from Humboldt County. The pattern of replacement of the primaries of both wings of the owl in 2016-2017 indicates that the molt began a node at p5 in this individual, after which it proceeded distally to p6, consistent with the pattern previously recorded in the Barred Owl and possibly prevailing in all other Strix species (Pyle 1997a, b; unpubl. data). The replacement of the primary coverts corresponding to p7 on both wings during the summer of 2016, without concurrent replacement of p7 on either wing, is of interest, as few birds are known to molt primary coverts without molting their corresponding primaries, the woodpeckers being the only broad exception of which we are aware (Pyle 1997b, Siegel et al. 2016). The replacement of the primary covert corresponding to p5 in the 2007 specimen is another example of this, and may further support a node at p5, provided that the replacement of this primary covert portends the subsequent replacement of its corresponding primary.

Our observations of replacement of the secondaries on both the bird photographed in 2016–2017 and the specimen picked up in 2007 also support a conclusion that the Great Gray Owl follows the pattern typical for diastataxic species, with molt proceeding distally from the tertials and proximally from s5 (Pyle 2008, 2013). We were unable to ascertain the sequence of replacement of the inner secondaries, on either bird, whether or not it proceeded bilaterally from a node at the second tertial (s12), but the replacement of this feather during the summer of 2016 on that individual is at least consistent with there being a node at s12. Both this bird and the 2007 specimen also establish that several secondaries between s5 and s14 can be replaced before replacement inward from s1 commences. We infer that the replacement of the left s2 during the fall or winter of 2016–2017 was adventitious, as no node is known here in any other large bird (Pyle 2008. 2013) and the feather appeared still to be growing in January 2017. Finally, in both individuals, replacement of the rectrices appeared to proceed from r1 to r6 on each side of the tail, with some asymmetry between the two sides. Such asymmetry is also known in raptors and other birds in which the flight feathers are not completely replaced each year (Pyle 2008). The patterns we observed differ from the synchronous molt of all rectrices recorded by

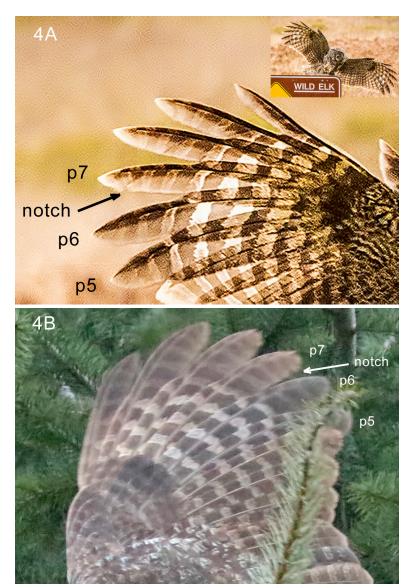


Figure 4. Great Gray Owl, photographed in Prairie Creek Redwoods State Park on 27 January 2016 (A) and near Alder Grove Road on the outskirts of Arcata on 5 January 2017 (B). Note the notch to the inner web of p7 in both images, suggesting damage from impact with a branch or other object. We believe that this, along with the consistent molt patterns (Figures 2-3), confirms that these two images are of the same individual.

Photos by Mark Larson (A) and Elias Elias (B)

Gura et al. (2017) on the basis of 20 Great Gray Owls in western Wyoming, during which 34 of 34 molts of rectrices were recorded as synchronous.

On the basis of Pyle (1997a, b) and because the older outer primaries and other flight feathers of the 2016–2017 Humboldt County Great Grav Owl appeared to be juvenile, we might infer that p5, s11-s14, and r1-r2 or r1-r3 were replaced during the second prebasic molt in the summer and fall of 2014; that p6, s5, s9-s10, r1, and r3-r4 or r4-r5 were replaced during the third prebasic molt in the summer and fall of 2015: and that s6. s8, s13, r6, and at least one of r2 or r3 were replaced during the fourth prebasic molt in the summer and fall of 2016. This would result in the owl's being in its third cycle (fourth calendar year) in January 2016 and in its fourth cycle (fifth calendar year) in January and February 2017, having hatched in 2012. However, its having molted no primaries during 2016 suggests that it could have skipped primary molt in previous years and may be older than this by a year or two (hatched in 2011 or before). Snowy Owls (Bubo scandiacus) are known to not molt any primaries during the second prebasic molt (Pyle 1997a, 1997b), and if this was so in the Great Gray Owl it would have been a year older than inferred above. Similarly, from its molt patterns the 2007 specimen may have been its third cycle, or it could have been an older individual that had skipped replacement of remiges or rectrices during its first two prebasic molts.

In any case, replacement of only two primaries during the owl's first four or five years represents molt slower than known in any other North American bird, with the possible exception of the California Condor (Gymnogyps californianus; Pyle 2008). Given that previous literature on the Great Gray Owl suggests that each annual molt encompasses more feathers (Cramp 1985, Suopajärvi and Suopajärvi 1994, Pyle 1997a, b), we suggest that this individual's being out of range could have contributed to its being in poor condition nutritionally, leading to a rate of feather replacement slower than typical of this species. In the 2007 specimen, molt also appears slower than reported in the literature, which could be related to the bird's emaciated condition when collected. Alternatively, the similarity of the patterns in both individuals could indicate that molt of the Great Gray Owl's remiges is much slower than is currently known, entirely possible given how little molt has been studied in this species. That both Humboldt County owls appeared to have replaced their rectrices incompletely each year also indicates an abnormally slow molt of these feathers, by comparison with the synchronous and complete tail molts that Gura et al. (2017) observed in Wyoming.

In any event, we believe the sequence of remex and rectrix molt we report here is typical of the Great Gray Owl and *Strix* in general, although more study is needed on the extent of molt in relation to food resources and nutritional stress. Finally, we suggest that systematic survey effort in northwestern California would be worthwhile for assessing whether additional Great Gray Owls may winter or even breed in the area.

### **ACKNOWLEDGMENTS**

We thank the numerous photographers and birders who obtained photographs for this analysis, Tamar Danufsky for providing information and images of the 2007

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specimen, Jerry Cole for obtaining and processing eBird data, and Elias Elias, Rob Fowler, Mark Larson, Michael J. Lang, and Sean McAllister for permission to publish their images of the owl seen in 2016 and 2017. We additionally thank Rob Fowler and Sue Leskiw for helping us locate and procure photographs, and Owen and Shelby Peterson for providing additional information about the 2016–2017 Alder Grove Great Gray Owl, which wintered near their home. Bryce Robinson, Daniel Ruthrauff, Dave Quady, and Philip Unitt provided helpful comments on an earlier draft of the manuscript. This is contribution 575 of The Institute for Bird Populations.

### LITERATURE CITED

- Beck, T. W., and Winter, J. 2000. Survey protocol for the Great Gray Owl in the Sierra Nevada of California. U.S. Department of Agriculture, Forest Service, Vallejo, CA.
- Bostwick, K. S., and Brady, M. J. 2002. Phylogenetic analysis of wing feather taxis in birds: Macroevolutionary patterns of genetic drift? Auk 119:943–954; doi 10.1642/0004-8038(2002)119[0943:PAOWFT]2.0.co;2.
- Bull, E. L., and Duncan, J. R. 1993. Great Gray Owl (Strix nebulosa), in The Birds of North America (A. Poole and F. Gill, eds.), no. 41. Acad. Nat. Sci., Philadelphia; doi 10.2173/bna.41.
- Bull, E. L., and Henjum, M. G. 1990. Ecology of the Great Gray Owl. U.S. Forest Service Gen. Tech. Rep. PNW-GTR-265.
- Bull, E. L., Henjum, M. G. and Ronald, S. 1988. Home range and dispersal of Great Gray Owls in northeastern Oregon. J. Raptor Res. 22:101–106.
- Coiffait, L., Redfern, C. P. F., Bevan, R. M., Newton, J., and Wolff, K. 2009. The use of intrinsic markers to study bird migration. Ringing Migration 24:69–174; doi 10.1080/03078698.2009.9674388.
- Cramp, S., ed. 1985. The Birds of the Western Palearctic, vol. 4. Oxford Univ. Press, Oxford, England.
- Fetz, T. W., Janes, S. W., and Lauchstedt, H. 2003. Habitat characteristics of Great Gray Owl sites in the Siskiyou Mountains of southwestern Oregon. J. Raptor Res. 37:315–322.
- Gura, K. B., Bedrosian, B., and Mendelsohn, B. 2017. Synchronous tail molt in Great Gray Owls (Strix nebulosa). J. Raptor Res. 51:190–192; doi 10.3356/ JRR-16-59.1.
- Hull, J. M., Englis, A., Jr., Medley, J. R., Jepsen, E. P., Duncan, J. R., Ernest, H. B., and Keane, J. J. 2014. A new subspecies of Great Gray Owl (Strix nebulosa) in the Sierra Nevada of California, U.S.A. J. Raptor Res. 48:68–77; doi 10.3356/JRR-13-35.1.
- Jepsen, E. P. B., Keane, J. J., and Ernest, H. B. 2011. Winter distribution and conservation status of the Sierra Nevada Great Gray Owl. J. Wildl. Mgmt. 75:1678–1687; doi 10.1002/jwmq.239.
- Nelson, K., and Pyle, P. 2013. Distribution and movement patterns of individual Crested Caracaras in California. W. Birds 44:45–55.
- Nero, R. W., and Copland, H. W. R.. 1997. Sex and age composition of Great Gray Owls (Strix nebulosa), winter 1995/1996, in Biology and conservation of owls of the Northern Hemisphere: 2nd International Symposium (J. R. Duncan, D. H. Johnson, and T. H. Nicholls, eds.), pp. 587–590. U.S. Forest Service Gen. Tech. Rep. NC-190, North Central Forest Experiment Station, St. Paul, MN.
- Pietiäinen, H., Saurola, P., and Kolunen, H. 1984. The reproductive constraints on moult in the Ural Owl Strix uralensis. Ann. Zool. Fenn. 21:277–281.
- Polasik, J. S., Wu, J. X., Roberts, K., and Siegel, R. B. 2016. Great Gray Owls nesting in atypical, low-elevation habitat in the Sierra Nevada, California. J. Raptor Res. 50:194–206; doi 10.3356/rapt-50-02-194-206.1.

# MOLT SEQUENCES IN AN EXTRALIMITAL GREAT GRAY OWL

- Pyle, P. 1997a. Flight-feather molt patterns and age in North American owls. Monogr. Avian Biol. 2:1–32.
- Pyle, P. 1997b. Identification Guide to North American Birds, part 1. Slate Creek Press, Bolinas, CA.
- Pyle, P. 2008. Identification Guide to North American Birds, part 2. Slate Creek Press, Point Reyes Station, CA.
- Pyle, P. 2013. Evolutionary implications of synapomorphic wing-molt sequences among falcons (Falconidae) and parrots (Psittaciformes). Condor 115:593–602; doi 10.1525/cond.2013.120173.
- Pyle, P., and Sullivan, B. L. 2010. Documenting repeated occurrence of individual birds with digital images. W. Birds 41:261–265.
- Ruegg, K., Anderson, E., Paxton, K., Apkenas, V., Lao, S., Siegel, R. B., DeSante, D. F., Moore, F. and Smith, T. 2014. Mapping migration in a songbird using high-resolution genetic markers. Molec. Ecol. 23:5726–5739; doi 10.1111/mec.12977.
- Siegel, R. B., Tingley, M. W., Wilkerson, R. L., Howell, C. A., Johnson, M., and Pyle, P. 2016. Age structure of Black-backed Woodpecker populations in burned forests. Auk 133:69–78; doi 10.1642/AUK-15-137.1.
- Skiff, S. 1995. Winter ecology of Great Gray Owls (Strix nebulosa) in Yosemite National Park, California. M.S. thesis, Univ. of Calif., Davis.
- Suopajärvi, P., and M. Suopajärvi, 1994. Lapinpöllön iän määrittäminen. (English summary: Ageing of Great Grey Owls). Linnut 29:27–30.
- Trefry, H. E., and Holroyd, G. L. 2012. Molt in Burrowing Owl (Athene cunicularia). N. Am. Bird Bander 37:4–1.0
- Van Riper, C., and J. van Wagtendonk. 2006. Home range characteristics of Great Gray Owls in Yosemite National Park, California. J. Raptor Res. 40:130–141; doi 10.3356/0892-1016(2006)40[130:HRCOGG]2.0.CO;2.
- Winter, J., 1980. Status and distribution of the Great Gray Owl in California. Calif. Dept. of Fish and Game, Sacramento.
- Winter, J. 1986. Status, distribution, and ecology of the Great Gray Owl (Strix nebulosa) in California. M.A. thesis, San Francisco State Univ.
- Wu, J. X., Siegel, R. B., Loffland, H. L., Tingley, M. W., Stock, S. L., Roberts, K. N., Keane, J. J., Medley, J. R., Bridgman, R. and Stermer, C. 2015. Diversity of nest sites and nesting habitats used by Great Gray Owls in California. J. Wildl. Mgmt. 79:937–947; doi 10.1002/jwmg.910.
- Wu, J. X., Loffland, H. L., Siegel, R. B., and Stermer, C. 2016. A conservation strategy for Great Gray Owls (Strix nebulosa) in California, interim version 1.0. The Institute for Bird Populations and California Partners in Flight, Point Reyes Station, CA; http://birdpop.org/docs/pubs/IBPConservationStrategy Version1.0.pdf.

Accepted 23 October 2017