Flight-feather Molt Patterns and Age in NORTH AMERICAN OWLS

Peter Pyle

American Birding Association
Monographs in Field Ornithology No. 2

Flight-feather Molt Patterns and Age in

NORTH AMERICAN OWLS

by Peter Pyle

All flight feathers (primaries, primary coverts, secondaries, and rectrices) are retained by owls during the first prebasic molt, after which flight-feather molt patterns vary substantially among genera and individuals. Certain species replace all flight feathers during the second prebasic molt, whereas in others up to five or six years are needed to renew all primaries and secondaries. Patterns of flight-feather replacement and differences in shape, pattern, and wear between juvenal and adult feathers have been used in Europe for precise ageing of owls; in some species, individuals can be aged up to their third or fourth year. In North America, however, similar published information for most species is incomplete, if not erroneous. In this study 2,429 specimens of all 19 North American owl species (north of Mexico) were examined to assess flight-feather molt patterns and differences between juvenal and adult flight feathers, and the utility of these criteria for ageing. Similar patterns were found among Holarctic genera and related species. Ageing summaries are provided for each North American species, in certain cases up to their third or fourth year of life.

Monographs in Field Ornithology

This series of occasional monographs, published by the American Birding Association, has been established for original scholarly contributions to field ornithology. Possible subject matter may include studies of distribution and abundance, population dynamics, identification, behavior, conservation, migration, and life history.

Monographs in Field Ornithology number 2

AMERICAN BIRDING ASSOCIATION

$9.95

Flight-feather Molt Patterns and Age in North American Owls

by
Peter Pyle

Point Reyes Bird Observatory
4990 Shoreline Highway
Stinson Beach, CA 94970 USA

published by:
American Birding Association, Inc.
PO Box 6599
Colorado Springs, CO 80934 USA

Monographs in Field Ornithology

This series of occasional monographs, published by the American Birding Association, has been established for original scholarly contributions to field ornithology. Possible subject matter may include studies of distribution and abundance, population dynamics, identification, behavior, conservation, migration, and life history.

Correspondence concerning manuscripts for publication in the series should be addressed to the Editor, Dr. Kenneth P. Able, Department of Biology, State University of New York, Albany, New York 12222.

Monographs in Field Ornithology, No. 2, 32 pages

Editor of Monographs in Field Ornithology, Kenneth P. Able

Author, Peter Pyle

Manuscript received 3 January 1996; revised 5 February 1997; accepted 6 February 1997; issued, 1 April 1997

Price, $9.95

Library of Congress Catalog Card Number, 97-071955

ISBN: 1-878788-36-1

Additional copies of this monograph are available from:

ABA Sales
PO Box 6599
Colorado Springs, CO 80934 USA
(800) 634-7736 or (719) 578-0607
fax: (800) 590-2473 or (719) 578-9705
e-mail: abasales@abasales.com

Cover photo: *Wing of a third-year Barn Owl found dead near Ensenada, Mexico, on 9 Jan 1994. Note that P6, S2, and S10-S13 have been recently replaced. See figure 1 for more details.*

TABLE OF CONTENTS

1. Abstract 5
2. Introduction 6
3. Methods 7
4. Results and Discussion 9
    A. *Tyto* 12
        1. Key to Ageing North American Barn Owls 12
    B. *Otus* 15
        1. Key to Ageing North American *Otus* Owls 17
    C. *Bubo* 18
        1. Key to Ageing Great Horned Owls 19
    D. *Nyctea* 19
        1. Key to Ageing North American Snowy Owls 20
    E. *Surnia* 21
        1. Key to Ageing Northern Hawk Owls 21
    F. *Glaucidium* and *Micratene* 22
        1. Key to Ageing North American Pygmy-Owls and Elf Owls 22
    G. *Speotyto* 22
        1. Key to Ageing Burrowing Owls 23
    H. *Strix* 23
        1. Key to Ageing North American *Strix* Owls 25
    I. *Asio* 25
        1. Key to Ageing North American Short-eared Owls 26
        2. Key to Ageing North American Long-eared Owls 27
    J. *Aegolius* 27
        1. Key to Ageing North American *Aegolius* Owls 29
5. Conclusions 29
6. Acknowledgements 31
7. Literature Cited 31

8. Tables

1. Totals and Inferred Ages of 2,429 Owls Examined for This Study 7

2. Ranges in Bar Patterns on p9, s1, r1, and r6 in Five Species of Owls 13

9. Figures

1. Wing of a TY Barn Owl 10

2. Specimen of a 4Y Great Horned Owl 10

3. Replacement Patterns in the Wing by Age Group in Great Horned Owl 11

4. Plumage Patterns on p8 and p9 by Age in Long-eared Owl 14

5. Plumage Patterns on s1 in Long-eared Owl 14

6. Plumage Patterns on r6 in Barn Owl 15

7. Variation in the talon flange by age in Barn Owl 15

8. Patterns of Secondary Replacement by Age in Long-eared Owl 16

9. Shape of the Outer Primaries in *Otus*, Northern Hawk, and Burrowing Owls 17

10. Plumage Patterns on the Outer Primary Coverts in Eastern Screech-Owl 17

11. Plumage Patterns on the Outer Primary Coverts in *Strix* Owls 18

12. Plumage Patterns on the Central Rectrix by Age in Northern Hawk Owl 21

13. Shape and Width of the Rectrices in Spotted and Barred Owls 24

14. Replacement Patterns of the Primaries and Secondaries in *Aegolius* Owls 28

ABSTRACT

All flight feathers (primaries, primary coverts, secondaries, and rectrices) are retained by owls during the first prebasic molt, after which flight-feather molt patterns vary substantially among genera and individuals. Certain species replace all flight feathers during the second prebasic molt, whereas in others up to five or six years are needed to renew all primaries and secondaries. Patterns of flight-feather replacement and differences in shape, pattern, and wear between juvenal and adult feathers have been used in Europe for precise ageing of owls; in some species, individuals can be aged up to their third or fourth year. In North America, however, similar published information for most species is incomplete, if not erroneous. In this study 2,429 specimens of all 19 North American owl species (north of Mexico) were examined to assess flight-feather molt patterns and differences between juvenal and adult flight feathers, and the utility of these criteria for ageing. Similar patterns were found among Holarctic genera and related species. Ageing summaries are provided for each North American species, in certain cases up to their third or fourth year of life.

INTRODUCTION

Owls typically have a partial first prebasic molt in June to October or November, which includes the body feathers but not the flight feathers (primaries, primary coverts, secondaries, and rectrices). In adults, this molt is incomplete to complete, with some or all flight feathers replaced (Cramp 1985). The extent of the adult (definitive, or second or later) prebasic molt varies substantially among owls. In some genera (e.g., *Glaucidium* and *Athene*), all flight feathers are typically renewed, whereas in others (e.g., *Tyto, Bubo, Nyctea, Strix*, and *Aegolius*) as few as 0-4 primaries and 3-7 secondaries may be replaced each year. In certain individuals of these species it may take up to 5-6 years to renew all primaries and corresponding primary coverts (Cramp 1985, Hornfeldt *et al.* 1988). Rectrix molt is most often complete, but sometimes incomplete in certain genera, species, or individuals. In the Spotted Owl *(Strix occidentalis)* a complete tail molt every other year has been documented (Forsman 1981, Moen et al. 1991). This unusual molt pattern has not been found in other owls, although in many species the extent of rectrix molt is poorly known or undescribed.

When the adult prebasic molt is incomplete, certain consistent patterns of primary and secondary replacement typically occur. In *Tyto, Bubo*, and *Nyctea*, for example, the second prebasic molt usually includes just 1-3 primaries within the outer portion of the wing, and the third prebasic molt includes 2-5 primaries on either side of those replaced during the second prebasic molt. Similar consistent patterns of replacement occur among the secondaries. By 4-5 years of age, however, the pattern and number of primaries and secondaries replaced become irregular, individuals or pairs of feathers from several molt series along the wings being renewed each year. By examining the pattern of replaced feathers, therefore, many individuals of these species can be aged reliably through their third or fourth years. By contrast, in those species with a complete second prebasic molt, the only clues to separate first-year birds from older birds are differences in shape and/or color pattern of the flight feathers, as body plumage is indistinguishable after the first prebasic molt and the extent of skull pneumatization presumably cannot be used to age owls (Canadian Wildlife Service [CWS] and U.S. Fish and Wildlife Service [FWS] 1991), probably because full pneumatization is not achieved in these species.

In the Western Palearctic, molt patterns in owls and their applicability to ageing have been investigated for most species (Piechocki 1974, Haarhaus 1983, Cramp 1985, Pietiäinen and Kolunen 1986, Hornfeldt *et al.* 1988). In North America, however, molt schemes in several species have been erroneously reported or are undescribed, and for other species accurate information exists but its full applicability for ageing has not been examined. Past authors (e.g., Forbush 1927, Bent 1938, Karalus and Eckert 1974, Oberholser 1974) mistakenly assumed that complete adult prebasic molts occurred annually in all North American owls. More recently, the presence of one vs. two generations of flight feathers has been used indiscriminately to separate first-year from older owls (Slack *et al.* 1987, Grigg 1989, CWS and FWS 1991, Duffy and Kerlinger 1992, Loos and Kerlinger 1993). But in species or individuals with complete second prebasic molts this may lead to misclassifications, and in those with incomplete molts, attempts to age third-year, fourth-year, and older birds based on patterns of flight feather replacement have not been made. Furthermore, only sporadic information has been published to document differences in shape, condition, or color pattern between juvenal and adult flight feathers of North American owls.

The purposes of this monograph are to 1) summarize published information on flight-feather molt patterns in owls of North America north of Mexico, 2) outline inferred molt patterns in North American species based on detailed specimen examination, and 3) propose more detailed, molt-related ageing criteria than have previously been published in the North American literature. I hope that the information outlined here will provide a basis upon which further investigation and understanding of these useful ageing criteria can develop.

METHODS

Specimens of 2,429 owls housed at the California Academy of Sciences (CAS), San Francisco, Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, and Point Reyes Bird Observatory (PRBO), Stinson Beach, California, were examined (Table 1). This examination included all specimens at CAS and PRBO and most (79%) of those at MVZ. Specimen tag data (sex, subspecies, date and location of collection, and any indication of age) were noted. Although a disproportionate number of specimens were collected in California, individuals from all regions of North America were represented. To ensure wider geographic representation, all MVZ specimens from states other than California were included in the samples. A few owls were excluded from consideration due to broken or extremely worn flight feathers, precluding accurate assessment of age.

Flight feathers were examined for multiple generations and differences in shape, condition, and color pattern between juveniles and adults. Using criteria established for Long-eared Owls *(Asio otus)* in Cramp (1985), measurements were taken on the bar patterns of flight feathers in five larger species to help assess variation in feather patterns (see Table 2). Based on body plumage and flight feathers, each owl was assigned an age code following the calendar-based system of the Bird Banding Laboratory (CWS and FWS 1991), as modified by Pyle *et al.* (1987). Codes include: **HY/SY** and **AHY/ASY** for birds in and beyond their first basic plumage, respectively; and **SY/TY** and **ASY/ATY** for birds in and beyond their second basic plumage. Here, **TY/4Y** and **ATY/A4Y** are used for birds in and beyond their third basic plumage, and **4Y/5Y** indicates birds in their fourth basic plumage. In each case the codes represent birds in the one-year period between molts (usually September to August); the code before the slash applies until the end of the year and the code after the slash applies between the beginning of the year and the next molt. Juveniles, here defined as fully-grown birds with juvenal body plumage, or still retaining nesoptile down on the tips of body feathers, were also examined. Primaries (p1-p10) and rectrices (r1-r6) were numbered distally (toward the outside) and secondaries (s1-s18; including the tertials) proximally (toward the inside). The total number of secondaries varies among species, from 12-18 (not including the innermost feather which is questionably a secondary), as mentioned for each genus. Statistical data on feather replacement were taken from the right wing, although both wings of all specimens were examined to assess age.

For most owl species some information on flight-feather molt patterns and ageing criteria have been published on which to base age-code determinations of examined specimens. For a few species, however, little or nothing was found in the literature, and age classes were inferred by comparing patterns to those in congeners or related species. Reliable age information on specimen labels coincided with age-code determination in virtually all cases. However, it should be noted that, except for juveniles, the ages of the owls were inferred rather than absolutely known. Thus, confirmation of the information presented here through study of captive or recaptured, known-aged birds is desirable.

Table 1: Totals and inferred ages of 2,429 owls examined for this study. Note that numbers of juveniles (Juv) and HY/SYs are probably disproportionately large in the specimen collections due to the accession of many inexperienced, road-killed birds. See text for scientific names.

Species	*Total*	*Juv*	*U/ AHY*	*HY/ SY*	*AHY/ ASY*	*TY/ 4Y*	*ASY/ ATY*	*TY/ 4Y*	*ATY/ A4Y*
Barn Owl	171	10	0	68	0	30	8	19	36
Flammulated Owl	104	3	3	41	5	21	31	0	0
Eastern Screech-Owl	143	14	21	48	60	0	0	0	0
Western Screech-Owl	237	32	25	92	88	0	0	0	0
Whiskered Screech-Owl	61	4	11	16	30	0	0	0	0
Great Horned Owl	285	46	0	115	0	47	19	21	37
Snowy Owl	70	3	0	29	0	7	0	6	25
Northern Hawk Owl	69	3	0	49	0	7	10	0	0
Northern Pygmy-Owl	236	22	194	0	20	0	0	0	0
Ferruginous Pygmy-Owl	114	8	50	0	56	0	0	0	0
Elf Owl	110	11	83	0	16	0	0	0	0
Burrowing Owl	251	17	40	79	115	0	0	0	0
Spotted Owl	72	7	0	26	3	13	23	0	0
Barred Owl	60	0	0	26	8	8	18	0	0
Great Gray Owl	26	0	0	13	1	2	10	0	0
Long-eared Owl	145	17	5	59	28	21	15	0	0
Short-eared Owl	148	0	118	0	10	11	9	0	0
Boreal Owl	23	0	0	14	0	3	6	0	0
Northern Saw-whet Owl	104	30	2	43	0	9	13	7	0

RESULTS AND DISCUSSION

In many species of owls, juvenal flight feathers average narrower and more tapered at the tip than adult feathers (Forsman 1980, 1981, Cramp 1985, Pietiäinen and Kolunen 1986, Moen *et al.* 1991). Juvenal feathers, especially outer primaries, tertials, and rectrices retained for more than one year, also tend to be more worn and frayed than adult feathers. However, there is overlap between age groups in flight-feather shape and wear, and distinctions can be difficult to determine, especially when feathers are very fresh or very worn. In many owl species, juvenal flight feathers have paler, less mottled base coloration (especially at feather tips), and narrower, more abundant, and more distinct dark and light barring than adult feathers. However, there is also overlap between age groups in these features. The light markings on the primary coverts of many species tend to be smaller and rounder on juvenal feathers vs. larger, squarer, or more bar-like on adults (see Pietiäinen and Kolunen 1986). All of these distinctions were found during specimen examination, but relative differences of each criterion varied substantially among species. The usefulness of these differences for ageing, based on this specimen examination, is outlined in the following genus accounts.

Molt in North American owls appeared to be confined to the summer and early fall; few specimens from other times of year were taken in active molt. Tropical American forms of these and other owls, however, may have more extended or year-round molting seasons, which could complicate age-code assignment. Nine of 19 species showed evidence of incomplete annual primary molt in adults; these and four other species showed incomplete annual secondary molt. In previous studies, newer feathers have been distinguished from older feathers by carefully looking for contrasts in age, wear, and luster (Piechocki 1974, Evans and Rosenfield 1987, Taylor 1993). In the Barn Owl *(Tyto alba)* and Snowy Owl *(Nyctea scandiaca)*, newer flight feathers tend to be whiter than older ones. In the other species, newer feathers are darker and have a pinkish wash (when fresh) that juvenal feathers lack (Evans and Rosenfield 1987). Differences in specimens may be more difficult to detect. With practice, however, juvenal and adult feathers were usually distinguished using the above criteria (except for the pinkish wash which could not be assessed on the closed wings of specimens), along with feather shape and color pattern (see Figs. 1-2). Inner primaries (p1-p4) and outer secondaries (s1-s4) of most species averaged fresher (darker and less abraded), due to less exposure, than outer primaries and inner secondaries of the same generation (see Fig. 1). Thus, caution was applied when assessing relative differences between these feather groups. Fault bars, which have been used by some to help age owls (CWS and FWS 1991), were found on only a small percentage of specimens and, except where noted, did not add as much to reliable ageing as did the presence or absence of contrasts between feather generations.

Most owls showed patterns of wing-feather replacement that allowed confident age-code assignment; however, a few had patterns that were anomalous or ambiguous. Some owls showed primary replacement indicating one age and secondary replacement indicating another. Individual variation was also found within age groups, and it is possible that the most advanced individuals of one age group (e.g., SY/TY) overlapped in pattern with the slowest individuals of another (TY/4Y; see Fig. 3). For these reasons, age codes were assigned conservatively in ambiguous cases or when primary and secondary replacement indicated different ages. See Table 1 for totals of ambiguous cases—those aged U/AHY, AHY/ASY, or ASY/ATY where more precise older age codes were also assigned. Pre-

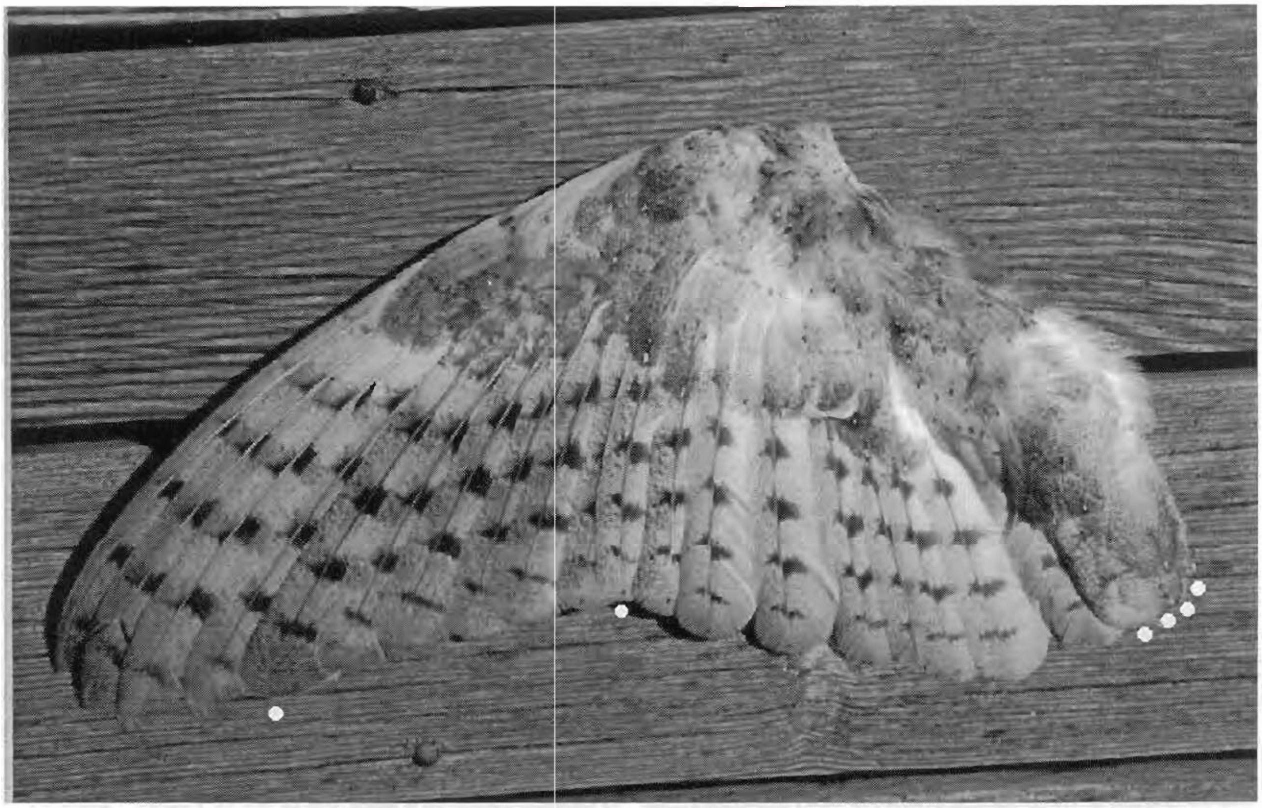


Figure 1. Wing of a TY Barn Owl found dead near Ensenada, Mexico, on 9 January 1994. This same wing is shown, in color, on the cover. Note that p6, s2, and s10-s13 (indicated with white dots) are fresher, broader, and more mottled than the other, juvenal wing feathers. This pattern is typical of SY/TY Barn Owls (see text).

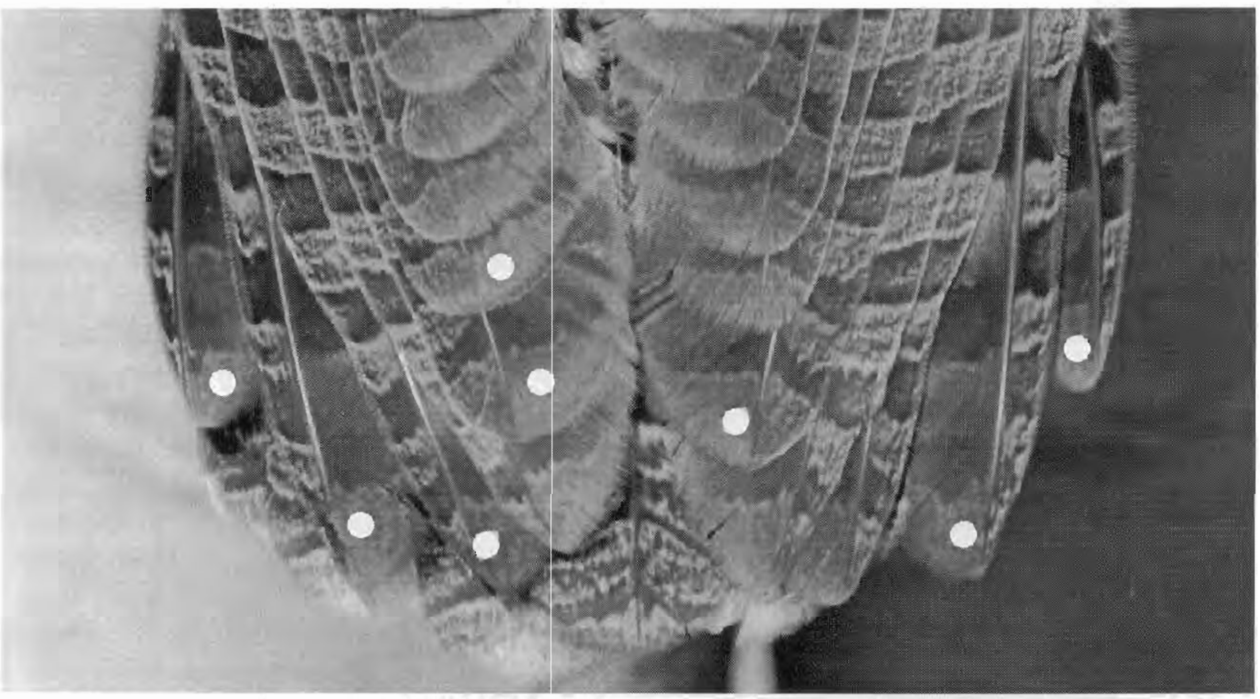


Figure 2. Specimen of a 4Y Great Horned Owl (CAS 16950) collected in January in Guerrero, Mexico. Contrasting feather generations indicate that the bird had recently replaced p9-p10 and p6 on the right wing and p8-p10 and p5-p6 on the left wing (white dots). The right p7-p8 and the left p7 had been renewed a year previous to replacement of these other feathers. This pattern, including the asymmetry, is typical of TY/4Y Great Horned Owls (see Fig. 3).

sumed adventitiously replaced or anomalously retained flight feathers were also noted on occasion, which complicated age-code assignment. Replacement patterns were not always symmetrical (especially with older birds), thus examination of both wings helped facilitate accurate ageing. Recently published information on molt sequences in owls were confirmed in most cases, and North American forms of holarctic species were found to have similar molt patterns to those documented in Europe and elsewhere. No evidence of normal flight-feather replacement was found in juveniles or inferred HY/SYs of any species. No marked variation in molt patterns or ageing criteria with sex, subspecies, or geographic locality could be detected. In some species, males or certain subspecies averaged paler in general plumage coloration than females or other subspecies, but these differences did not affect ageing criteria greatly. The following accounts summarize, by genera, published information and results of this study for each North American owl species.

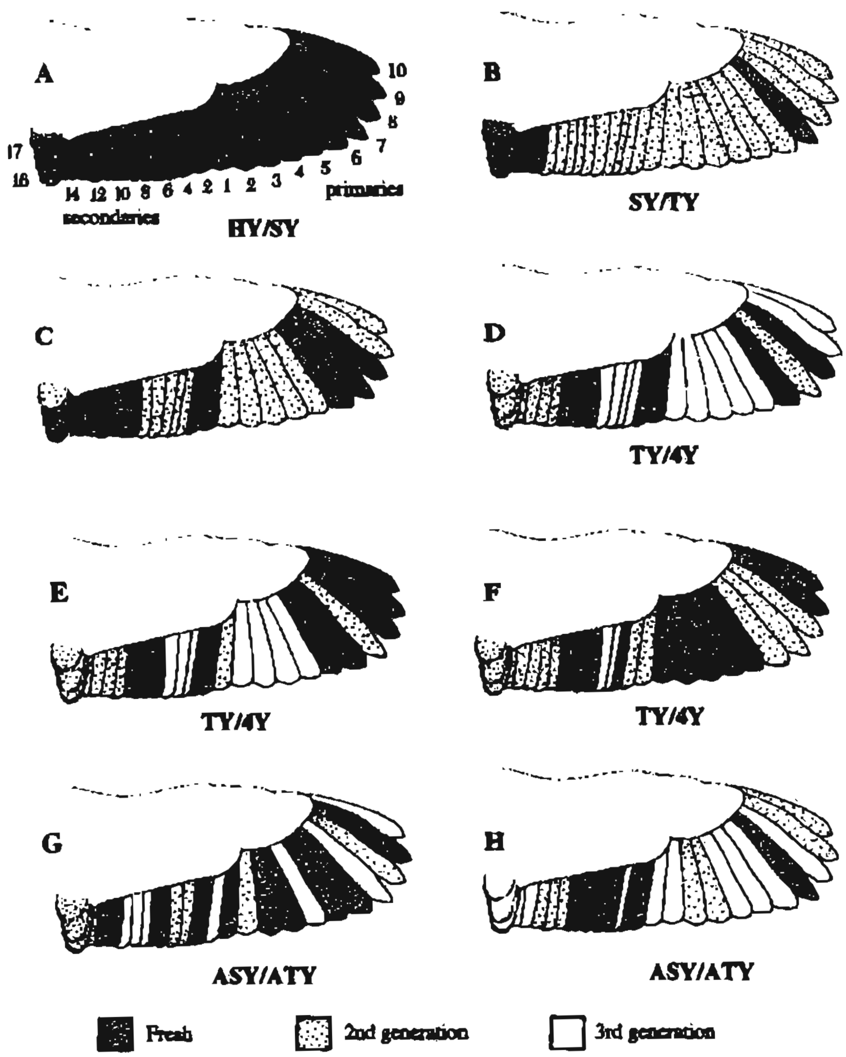


Figure 3. Diagrammatic replacement patterns in Great Horned Owls by age group. Examples near to minimum and maximum replacement, within each group, are shown. Similar, but not identical, patterns of replacement occur in Barn and Snowy Owls (see text).

Tyto

The discovery of incomplete flight-feather molts in owls was first made by R. Piechocki (1961, 1974) based on studies of captive Barn Owls in Germany. Piechocki's findings have been confirmed, refined, and applied to ageing European forms of Barn Owl (mostly *T.a. alba* and *T.a. guttata*) by Stresemann and Stresemann (1966), Cramp (1985), Baker (1993), and Taylor (1993). Cramp (1985) indicated that similar molt sequences and timing were found in other western Palearctic subspecies; however, in four captive birds of Malaysian populations *(T.a. javanica)*, all flight feathers were replaced over the course of a year (Lenton 1984), indicating that wing-feather generation pattern may not be as useful for ageing tropical forms of Barn Owl.

Flight-feather molt sequences and timing in North American Barn Owls *(T.a. pratincola)* appear similar to those found in Europe (P. Bloom in Marti 1992). Results of this study indicate that ages of birds could be confidently assigned through ATY/A4Y (Table 1) according to patterns of primary and secondary replacement (see Fig. 3). During the second prebasic molt, based on inferred SY/TYs and TY/4Ys (Table 1), 28 (57%) owls had replaced p6 only (Fig. 1), 15 (31%) had replaced p6-p7, and six (12%) had replaced p5-p7. Among secondaries, 1-6 ($\bar{x}$=2.7) feathers among s9-s14 had been renewed during the second prebasic molt, with 18 of 30 birds (60%) having replaced just s12-s13, and two birds having replaced just s12. Six SY/TY owls (all with at least four inner secondaries replaced) had also replaced s2 on both wings; otherwise, no symmetrical replacement of outer secondaries was found. No inferred SY/TYs were found that had not replaced at least p6, a pattern that has been reported to occur occasionally in Europe. It is possible that occasional birds may not replace any flight-feathers during the second prebasic molt, resulting in SY/TYs being erroneously coded HY/SY; however, the distribution of replacement patterns observed, e.g., no birds that had not replaced at least two feathers, indicate that this probably occurs in an insignificant proportion of birds. The 19 inferred TY/4Ys had replaced from two (p5 and p7, or p5 and p8 only; 3 specimens) to five (p3-p4 and p8-p10; 1 specimen) primaries ($\bar{x}$=3.1). The number of juvenal secondaries remaining in these birds ranged from 1-5, among s1, s3-s4, and s7-s8. ATY/A4Ys had replaced 3-6 primaries ($\bar{x}$=4.1), and 4-9 secondaries ($\bar{x}$=6.5) during the most recent molt, in patterns that varied substantially from those found above (see Fig. 3). Twenty-three of 30 (76.7%) inferred SY/TYs had renewed all rectrices during the second prebasic molt, a higher proportion than is indicated for European Barn Owls; 0-9 rectrices had been renewed by those with incomplete replacement.

Examination of North American Barn Owls for differences in color pattern between juvenal and adult feathers revealed several average differences, some of which could assist with ageing. Adult flight feathers averaged fewer bars and wider distances between dark bars than juvenal feathers (Table 2; Figs. 4-6). The shapes of the outer primary, secondaries, and rectrices were generally narrower and more tapered in juveniles than in adults (Baker 1993, Figs. 5-6). No substantive differences were found between juvenal and adult primary coverts.

Key to ageing North American Barn Owls

HY/SY (August-July): Primaries, secondaries, and rectrices uniform in shape, wear, and pattern, with no contrasts between adjacent feathers (see Fig. 3A); numbers of bars on primaries, secondaries, and rectrices relatively large and distances between bars on these feathers relatively small (Figs. 4-6, Table 2); secondaries and rectrices relatively narrow (Figs. 5-6); talon

Table 2. Numbers of bars and measurements between bars (see footnotes) on p9, s1, r1, and r6, of juvenal and adult feathers in five species of North American owls. Counts and measurements were based on full dark bars in Barn, Great Horned, and Long-eared Owls, and on pale bars (not including the tip) on Spotted and Barred Owls. Measurements were taken only on confidently aged birds, e.g., fully grown juveniles, birds with reliable age information on specimen labels, or adults showing unmistakable patterns of flight-feather replacement. Sample sizes were 20 for all values. For distance between bars, the tabular values represent the 95% confidence limits; thus, the mean is the midpoint of the range and the standard deviation is ¼ of the range. See also Figs. 4-6, and see Barrows *et. al* (1982) and Carpenter (1992) for more on tail barring in *Strix* owls.

		Primary 9		*Secondary 1*	*Rectrix 1*	*Rectrix 6*
Species		*number*[1]	*distance*[2] *(mm)*	*distance*[3] *(mm)*	*number*[4]	*distance*[5] *(mm)*
Barn Owl						
	Juvenal	3-5	58-84	42-63	3-4	51-72
	Adult	2-4	72-117	53-95	2-4	67-97
Great Horned Owl						
	Juvenal	6-8	65-98	61-85	6-8	58-85
	Adult	4-7	78-146	72-103	5-6	79-123
Spotted Owl						
	Juvenal	5-6	75-122	58-86	5-7	66-83
	Adult	4-6	117-142	75-99	3-6	80-97
Barred Owl						
	Juvenal	4-5	78-113	88-120	4-6	96-104
	Adult	3-4	108-150	97-150	3-5	110-155
Long-eared Owl						
	Juvenal	6-8	55-82	26-40	6-8	28-39
	Adult	5-7	70-100	38-55	5-7	37-49

[1] Number of dark or pale (see above) bars between the tips of primary coverts and the tip of p9.

[2] Distance from the tip of p9 to the proximal (lower) edge of the 4th (Great Horned, Spotted, and Long-eared Owls), 3rd (Barred Owl), or 2nd (Barn Owl) dark or pale (see above) bar on the outer web, where the bar meets the feather shaft.

[3] Distance from the tip of s1 to the proximal (lower) edge of the 4th (Great Horned, Spotted, Barred, and Long-eared Owls) or 2nd (Barn Owl) dark or pale (see above) bar on the outer web, where the bar meets the feather shaft. The number of bars distal to the greater coverts may also be of use on live birds but this was difficult to assess on specimens.

[4] Number of dark or pale (see above) bars between the tips of the uppertail coverts and the tip of r1.

[5] Distance from the tip of r6 to the proximal (lower) edge of the 4th (Great Horned, Spotted, Barred, and Long-eared Owls) or 3rd (Barn Owl) dark or pale (see above) bar on the inner web, where the bar meets or comes closest to the feather shaft. Some adult Great Horned and Barn Owl feathers had fewer bars than indicated; thus, this distance could not be measured.

flange narrow and smooth (May-January) or slightly notched (November-August; Fig. 7A).

SY/TY (August-July): P6, p6-p7, or p5-p7, *and* 1-7 secondaries among s2 and/or s9-s14 glossier, broader, fresher, more mottled, and showing bar patterns of adult feathers (Figs. 1, 4-6, Table 2; see also Fig. 3B,C) vs. all other wing feathers uniformly more faded, narrow, worn, less mottled, and showing bar patterns of juvenal feathers; rectrices uniformly broad and fresh as adult (Fig. 6) or mixed with some to (occasionally) all, more worn and tapered, juvenal rectrices (Fig. 6); middle talon flange wide and deeply serrated (Fig. 7B-C).

TY/4Y (September-August): Like SY/TY except adult p6, p6-p7, or p5-p7 moderately worn, surrounded by 2-5 contrastingly fresh adult primaries among p2-p5 and p7-p10, with the remaining 2-7 primaries juvenal, contrastingly narrow, faded, and worn; *and* secondaries also showing three generations, with 2-7 feathers among s2-s11 contrastingly fresh, and 1-5 secondaries among s1, s3-s4, and s7-s8 still juvenal and very worn (see Fig. 3D-F); rectrices uniformly broad and with pattern of adult (Fig. 6).

ATY/A4Y (August-July): Like TY/4Y but primary and secondary contrasts present but irregular, including varying numbers and positions of new and old feathers, not representing the patterns found in SY/TY or TY/4Y (see Fig. 3G,H).

Remarks: SY/TYs and TY/4Ys should only be aged if both primary and secondary patterns coincide (although a bird with completely juvenal primaries but a secondary pattern indicating SY/TY can be reliably aged SY/TY). With more study, some birds may be reliably aged 4Y/5Y, e.g., CAS35611 which had p3-p4 and p8-p10 new, p7 and p5 moderately worn, p6 older, and s1, s4, s8, s12, and s13 new (this specimen was here considered ATY/A4Y). On the other hand,

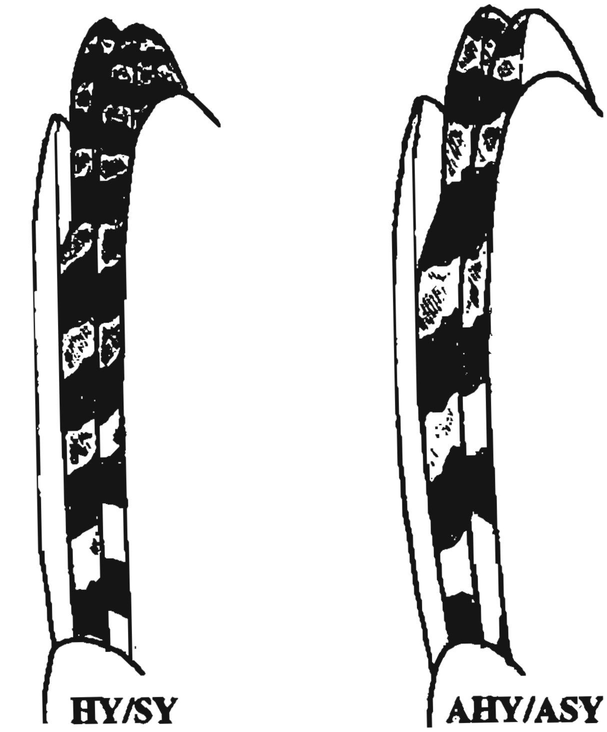


Figure 4. Plumage patterns on p8 and p9 in Long-eared Owls, showing general differences in barring density between the juvenal feathers of HY/SYs and the adult feathers of AHY/ASYs. Similar patterns by age occur in Barn, Great Horned, Spotted, and Barred Owls (see text and Table 2). These should be looked for on confirmed, known-aged *Otus* and *Speotyto* owls, as well.

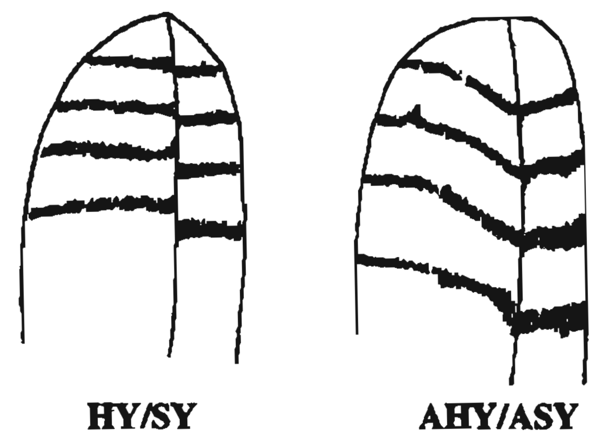


Figure 5. Plumage patterns on s1 in Long-eared Owls, showing general differences in barring density between the juvenal feathers of HY/SYs and the adult feathers of AHY/ASYs. Similar patterns by age occur in Barn, Great Horned, Spotted, and Barred Owls (see text and Table 2). These should be looked for on confirmed, known-aged *Otus* and *Speotyto* owls, as well.

some ATY/A4Ys may coincidentally show replacement patterns like SY/TYs or TY/4Ys; some of these birds are probably best aged AHY/ASY. It is possible that 2nd-generation feathers show bar patterns (Figs. 4-6; Table 2) intermediate between juvenal and adult feathers (probably closer to adult) and, with more study, this might be helpful in more precise ageing of older birds.

Otus

European species of *Otus* owls usually molt all primaries and rectrices each year but retain some secondaries during the adult prebasic molts (Cramp 1985). Here, this was found to be the case for Flammulated Owl *(O. flammeolus)* but not, typically, for Eastern *(O. asio)*, Western *(O. kennicottii)*, or Whiskered *(O. trichopsis)* Screech-Owls. Of 178 AHY/ASY screech-owls examined (Table 1) only one, a Western Screech-Owl collected in January (CAS84589), had undergone incomplete secondary molt, having retained s1, s2, s4, and s7 on one wing and s3,

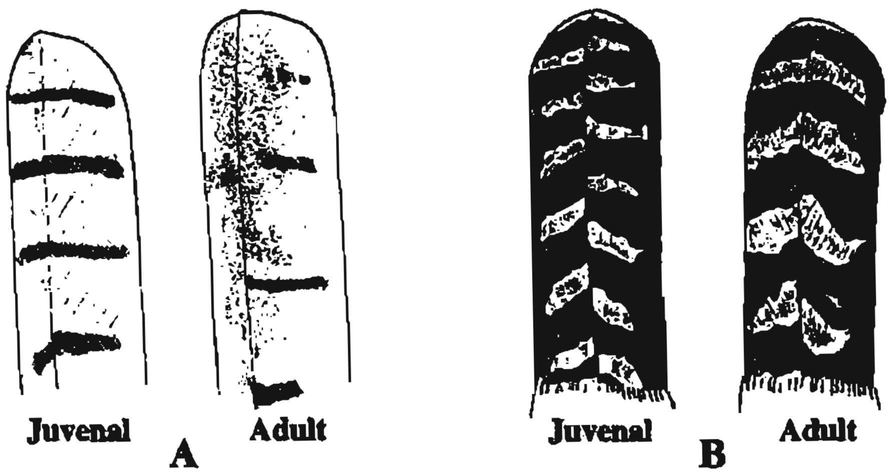


Figure 6. Plumage patterns on the outer rectrix (r6) in Barn Owl (A) and the central rectrix (r1) in Long-eared Owl (B) showing general differences in barring density between juvenal and adult feathers. Similar patterns by age occur in Great Horned, Spotted, and Barred Owls (see text and Table 2).

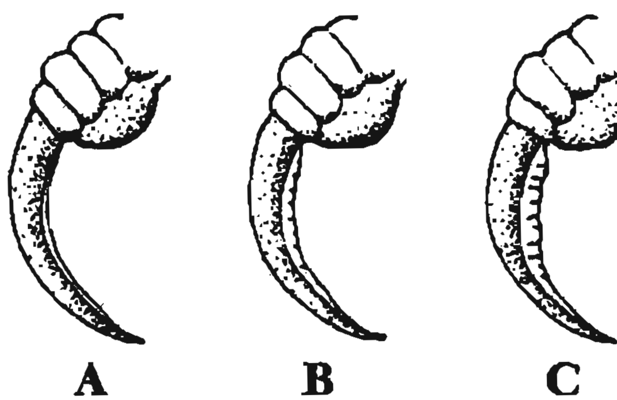
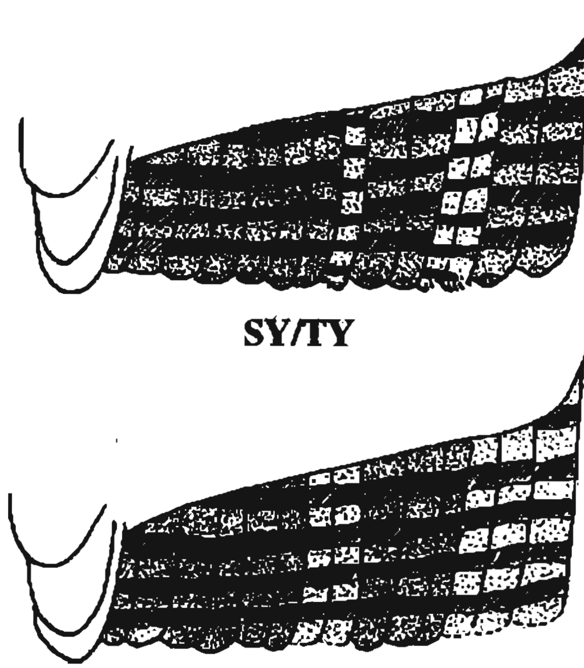


Figure 7. Variation in the width and degree of serration on the talon flange of the middle toe, by age, in Barn Owl. Juveniles have a very thin or no flange (A), after which it slowly thickens and becomes more serrated, such that by SY/TY it resembles illustration C. See Johnson (1991) for details.

s4, s7, and s8 on the other. Because of the pattern of replacement and high contrast of wear this was likely a TY bird. These findings contradict, somewhat, the CWS and FWS (1991) manual, which suggest that adults more regularly have an incomplete molt. Most adult screech-owls in July to November were in the process of wing-feather replacement and could reliably be aged AHY.

Retention of flight feathers by Flammulated Owls allowed separation of SY/TYs from ASY/ATYs (Fig. 8). In 21 SY/TY specimens, 2-5 juvenal secondaries ($\bar{x}$=2.8) among s1-s8 had been retained, most often s1, s3-s4, and/or s7. Interestingly, six owls had also retained from 1-3 juvenal primaries among p2-p5. The 31 ASY/ATYs had retained 1-6 adult secondaries ($\bar{x}$=3.2) and 0-2 adult primaries ($\bar{x}$=0.3). Patterns in adults often showed asymmetry between wings, and were usually not the same patterns as those displayed by SY/TYs. Six specimens (16%) had feather characteristics of adults (see below) but showed no contrasts, suggesting that the adult prebasic molt can be complete. The distribution of replacement patterns in SY/TYs indicates that a complete molt may typically occur only in the third and/or subsequent prebasic molts. The Common Scops Owl (*O. scops*) of Europe often suspends flight-feather molt over migration (Cramp 1985); however, several August specimens of the closely related Flammulated Owl (e.g., MVZ87453) appeared to be completing primary molt on the breeding grounds. More study of molt patterns on migrant and wintering Flammulated Owls (of which few specimens collected off the breeding grounds exist) is needed.



SY/TY

ASY/ATY

Figure 8. Patterns of secondary replacement in SY/TY and ASY/ATY Long-eared Owls. Not all birds of these age groups show two feather generations and these should be aged AHY/ASY. The retention of s3-s4 and s7 (as well as s1-s2 and s8 in some birds) is typical of SY/TY, whereas other feathers are usually retained in ASY/ATYs. Note the higher contrast and density of barring in the retained, juvenal secondaries of the SY/TY (see also Figure 5 and Table 2), whereas the retained, adult feathers in ASY/ATY show less contrast and similar barring density to the replaced adult feathers. Similar patterns of secondary replacement and relative differences, allowing reliable ageing, can be found in Flammulated, Northern Hawk, and some Short-eared Owls.

Examination for differences between juvenal and adult flight feathers in *Otus* revealed two useful criteria. A difference in shape existed in the outer primaries (Fig. 9). This could be used to age some but not all screech-owls (see Table 1) after completion of the prebasic molt. The pattern on the primary coverts also appeared to vary with age in Eastern Screech-Owl and Flammulated Owl, but not in Western or Whiskered Screech-Owls. HY/SY Eastern Screech-Owls tended to have distinct spots or notches on the outer webs of these coverts, whereas in adults the pattern varied but was usually less distinct (Fig. 10). Interestingly, both HY/SY and AHY/ASY Western and Whiskered Screech-Owls appeared to have the pattern of HY/SY Eastern Screech-Owl. In Flammulated Owl the pale spots on the outer webs of the primary coverts appeared to be smaller and rounder in HY/SYs vs. larger and squarer on AHY/ASYs, as is found in *Strix* and other owls (see Fig. 12).

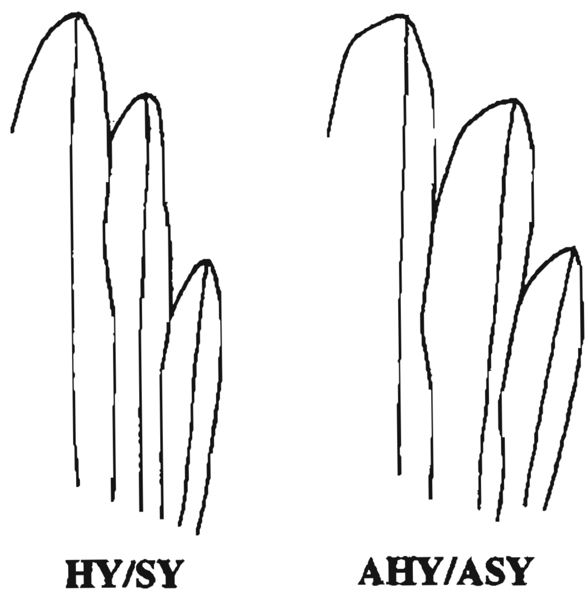


Figure 9. Shape of the outer primaries, by age, in *Otus*, Northern Hawk, Burrowing, and *Aegolius* Owls. Similar but less-indicative differences can be seen in *Glaucidium*, *Micrathene*, and *Strix* owls.

Key to ageing North American *Otus* owls.

HY/SY (September-August): No flight-feather molt present in July-November; p7-p10 relatively narrow, tapered at tip, worn (Fig. 9); outer web of outer primary coverts with distinct notched markings (Eastern Screech-Owl only; Fig. 10) or with small rounded spots (Flammulated Owl only; see Fig. 11).

AHY/ASY (September-August): Flight-feather molt usually present in July-October (to November in many); p7-p10 relatively broad, truncate at tip, fresh (Fig. 9); primaries and secondaries showing no contrasts in shape or wear; outer webs of outer primaries coverts indistinctly patterned (Eastern Screech-Owl; Fig. 10) or with relatively large and squared spots (Flammulated Owl; see Fig. 12).

SY/TY (September-August; regularly found in Flammulated Owl but rarely so in the screech-owls): Like AHY/ASY but 2-5 juvenal secondaries among s1-s8 (typically 2 or more of s1, s3-s4, and/or s7-s8) and occasionally some inner primaries retained, contrastingly narrow, faded, and abraded (see Fig. 8).

ASY/ATY (September-August; Flammulated Owl only): Like SY/TY but retained secondaries and primaries broader, not as contrastingly narrow, worn, and abraded, usually not confined to just s1, s3-s4, and/or s7, and more often lacking symmetry between the wings.

Remarks: Some birds (Flammulated Owls) with contrasting secondaries may be difficult to age precisely and should be considered AHY/ASY. It is also possible that Flammulated Owls with uniform adult flight feathers can be reliably aged ASY/ATY, if the second prebasic molt is rarely if ever complete; more study is needed on known-age birds.

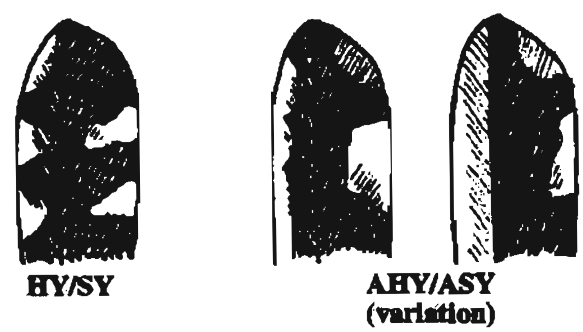


Figure 10. Primary covert patterns by age in Eastern Screech-Owl. The best feathers to examine are those corresponding to p5-p8. Similar but less indicative patterns may occur in Elf Owl. Both age groups of Western and Whiskered Screech-Owls tend to show patterns similar to juvenal (HY/SY) Eastern Screech-Owls.

Bubo

Based on observations of captive, known-age Great Horned Owls *(B. virginianus)*, Weller (1965) suggested that the second prebasic molt began with one or more of p6-p8, and that there may be overlapping feather generations in older birds, but in his words, "more questions concerning molting patterns were raised than were answered" by his observations. Streseman and Streseman (1966) confirmed this sequence, but suggested that all flight feathers were replaced each year. No subsequent information appears to have been published on molt in this species. Specimen examination indicates that the molt pattern in Great Horned Owls is similar to that of Barn Owl and to the Eagle Owl (*B. bubo*) of Eurasia (Cramp 1985) in that four or more years are needed for all primaries and secondaries to be replaced. Thus, individuals can be aged through ATY/A4Y (Table 1, Figs. 2 and 3).

Based on 68 inferred SY/TYs and TY/4Ys examined (Table 1), the second prebasic molt of Great Horned Owls includes 0-3 primaries ($\bar{x}$=1.7) among p6-p8, and 5-12 secondaries ($\bar{x}$=7.7). Secondary replacement includes at least the five innermost, s13-s17, often s12-s11, occasionally s9-s10 and s1, and rarely s8 and s2 (Fig. 3**B**,**C**). The typical order of primary replacement appears to be p7-p8-p6, such that when one primary is replaced, it is p7, and when two are replaced, they are p7-p8. Three of 47 SY/TY individuals (6.3%) were found with secondary replacement (4-5 feathers), but that still had retained all juvenal primaries, indicating that some individuals retain p7 until their third prebasic molt. This pattern is more regularly observed in Eagle Owl (Cramp 1985). Thirteen of 47 SY/TYs (28%) had retained 1-4 juvenal rectrices, usually among r3-r6.

The 21 inferred TY/4Ys examined had replaced 1-5 primaries ($\bar{x}$=3.3) during the third prebasic molt, among p1-p2 and p4-p10, around those not replaced during the second prebasic molt, and 4-8 secondaries ($\bar{x}$=5.6), leaving 2-5 secondaries ($\bar{x}$=3.7) as juvenal, among s1, s3-4, and s6-s8 (Figs. 2 and 3**D**-**F**). One specimen (CAS63658) had replaced just p7 but was aged TY/4Y based on indicative replacement of secondaries. ATY/A4Ys had replaced roughly 3-6 primaries ($\bar{x}$=4.8) and 2-7 secondaries ($\bar{x}$=4.7) in irregular patterns distinct from SY/TYs and TY/4Ys. Rarely, if ever, were three adjacent feathers of the same age, and replacement occurred throughout the wing (Fig. 3**G**,**H**). The pattern of barring on the flight feathers and the shape of the rectrices varied by age, as in other species (Table 2, Figs. 4-6). The shape of the markings on the primary coverts also showed slight variation as in *Strix* owls (see Fig. 12); however, substantial overlap occurred between the ages and this was not considered a useful ageing criterion.

Key to ageing Great Horned Owls

HY/SY (October-September): Primaries, secondaries and rectrices uniform in shape, wear, and pattern, with no contrasts between adjacent feathers (Fig. 3**A**); numbers of bars on primaries, secondaries, and rectrices relatively large and distances between bars on these feathers relatively small (Table 2, see Figs. 4-6); rectrices uniform in wear and relatively narrow.

SY/TY (August-July): P7, p7-p8, or p6-p8 (occasionally no primaries), ***and*** s13-s17, some or all of s8-s12, and/or s1-s2 glossier, broader, fresher, more mottled, and showing bar patterns of adult feathers (Table 2; Figs. 3**B**,**C**, and 4-5), vs. all other wing feathers uniformly more faded, narrow, worn, less mottled, and showing bar patterns of juvenal feathers; rectrices of some birds showing contrasts between worn juvenal and fresh adult feathers.

TY/4Y (October-September): Like SY/TY except p7, p7-p8, or p6-p8 broad and moderately worn, surrounded by 2-5 contrastingly fresh adult primaries among p2-p5 and p7-p10, with the remaining 2-7 primaries juvenal, contrastingly narrow, faded, and worn, *and* secondaries also showing three generations, with 4-8 secondaries among s1-s12 contrastingly fresh, and 2-5 secondaries among s1, s3-4, and s6-s8 still juvenal and very worn (Figs. 2 and 3D-F); rectrices uniformly broad, fresh and with bar patterns of adults (Table 2).

ATY/A4Y (August-July): Like TY/4Y but primary and secondary contrasts irregular, including varying numbers and positions of new and old feathers, not representing the patterns found in SY/TY or TY/4Y (Fig. 3G,H); most or all feathers showing bar patterns of adult feathers (Table 2; see Figs. 4-6).

Remarks: SY/TYs and TY/4Ys should only be aged when both primary and secondary patterns coincide and, with more study, some birds may be reliably aged 4Y/5Y (see Barn Owl). Cursory examination of 36 specimens of Mexican and South American subspecies (e.g., see Fig. 2) indicate that similar replacement patterns occur throughout the range of Great Horned Owl.

Nyctea

Among North American owls, only the Snowy Owl shows marked variation in body plumage, allowing some birds to be aged and sexed through AHY/ASY based on this alone (Josephson 1980). Blackish or brownish-black markings throughout the plumage are more prominent in females than in males and, sex for sex, decrease in thickness and prominence with age. Although the decrease of blackish markings generally continues beyond the second prebasic molt, the best way to age SY/TY and older birds is by contrasts in the wing feathers, the result of incomplete adult prebasic molts (Cramp 1985). Specimen examination indicates that North American and European Snowy Owls have similar molt patterns, as would be expected in this monotypic species. The sequence of replacement is similar to that of Great Horned Owl (Fig. 3) but the timing appears to be slower, taking approximately four years to reach the TY/4Y stage of Great Horned Owl (Fig. 3D-F).

Among 13 specimens of inferred SY/TY and TY/4Y Snowy Owls (Table 1), eight had replaced p7 while five had retained all juvenal primaries during the second prebasic molt. All of these had molted only the innermost secondaries, either s13-s18 (4 specimens), s14-s18 (7), or s15-s18 (2). Although Cramp (1985) indicated that the rectrix molt was complete during the second prebasic molt, four of seven SY/TY specimens collected in North America had retained some, or all (one specimen; CAS44915), juvenal rectrices, most often among r2-r4. The six inferred TY/4Y specimens had replaced 1-3 primaries ($\bar{x}$=1.8), either p7 only, p7-p8, p8 only, or p6 and p8-p9 (the last two cases occurring only when p7 had been replaced during the second prebasic molt), and 4-7 secondaries ($\bar{x}$=5.7) among s9-s14, often s1-s2, and, in one specimen which had replaced three primaries (MVZ4996), s6-s7 as well. ATY/A4Ys had replaced 1-6 primaries ($\bar{x}$=3.9) and 4-8 secondaries ($\bar{x}$=5.6) in irregular patterns similar to those of Great Horned Owl (see Fig. 3G,H). Most ATY/A4Ys showed asymmetrical wing-feather molt patterns, some of them entirely so. Of 25 ATY/A4Ys, six were felt to be 4Y/5Ys, having such patterns as p9, p6, s1, and s7-s9 new (MVZ4982), or p8 new, p7 of 2nd generation, and s1-s2 and s8-s10 new (MVZ4983). More study on known-aged birds is required to assume reliable ageing of 4Y/5Ys and, possibly, of older birds.

Key to ageing North American Snowy Owls

HY/SY (August-July): Primaries and secondaries uniform in shape and wear, with no contrasts between adjacent feathers (see Fig. 3A); central rectrices with 4-6 (♀) or 1-4 (♂) bars (including indistinct ones); body plumage heavily (♀) to moderately (♂) mottled black; nape sometimes with a concealed patch of grayish juvenal down (through January).

SY/TY (August-July): Primaries uniform as in HY/SY or with just p7 replaced *and* 4-6 innermost secondaries (among s13-18) newer and fresher than the other, uniformly more faded secondaries (e.g., see Fig. 3B); rectrices often with mixed juvenal and adult feathers; central rectrices (if adult) with 3-5 (♀) or 0-4 (♂) bars; body plumage moderately (♀) to lightly (♂) mottled black; nape without juvenile down.

TY/4Y (October-September): Like SY/TY except 1-3 primaries among p6-p9 *and* 4-7 secondaries among s9-s14, often s1-s2, and occasionally s6-s7, recently replaced, contrasting with the moderately worn, 2nd-generation feathers (see SY/TY) and the uniformly and heavily worn, remaining juvenal primaries and secondaries (e.g., see Fig. 3D); black mottling averages less extensive, sex for sex.

ATY/A4Y (August-July): Like TY/4Y except primary and secondary contrasts present but irregular, including varying numbers and positions of new and old feathers, not representing the patterns found in SY/TY or TY/4Y (see Fig. 3G,H); black mottling virtually absent (♂) or reduced (♀).

Remarks: See Josephson (1980) for further information on differences between the sexes, within each age group. Most SY/TYs and TY/4Ys should only be aged when both primary and secondary patterns coincide, and it is probable that 4Y/5Ys can be reliably aged (see Barn Owl).

Surnia

Specimen examination indicates that a similar molting scheme applies in both the Northern Hawk Owl of Europe (*S. ulula ulula*; see Forsman 1980, Cramp 1985) and the North American subspecies, *S.u. caparoch*. All primaries are typically replaced during the second and adult prebasic molts, whereas many or all birds retain secondaries during these molts; thus, Northern Hawk Owls can be aged through ASY/ATY. The seven inferred SY/TY specimens (Table 1) had retained 2-6 secondaries ($\bar{x}$=4.1), including s4 and s7 (all examples), s3 (6 specimens), s6 (3), s8 (3), s2 (2), and s1 (1). The ten inferred ASY/ATYs had retained 3-7 secondaries ($\bar{x}$=4.9) with each of s1-s15 retained at least once, but most retained feathers being among s1-s10; the pattern of retained secondaries of ASY/ATYs did not match those of the SY/TYs. Although no owls were found that had completed secondary molt in one year (see also Cramp 1985), as Forsman (1980) points out, most specimens in collections are those that wander south during years of short food supply, and these may be less likely to complete the secondary molt (see also Evans and Rosenfield 1987). Complete second and subsequent prebasic molts might be expected in years of food abundance.

The shape of the tertials and shape and pattern of the rectrices (Fig. 11) also differed by age, as has been documented in Europe. Here it was found that the shape of the outer primaries (see

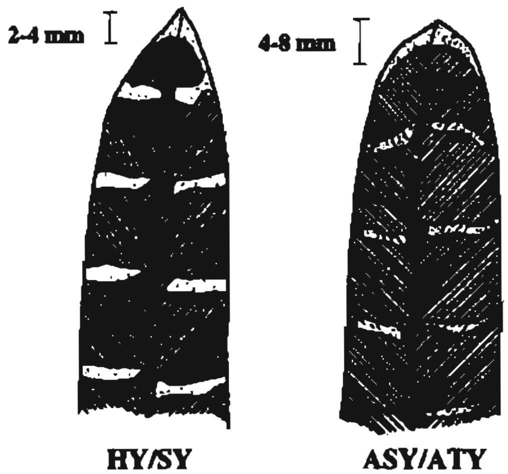


Figure 11. Width and pattern of the central rectrix, by age, in Northern Hawk Owls.

Fig. 9) could also be useful in distinguishing HY/SYs from older birds.

Key to ageing Northern Hawk Owls

HY/SY (August-July): All secondaries juvenal, uniform in shape and wear, narrow, tapered, and with no contrasts between adjacent feathers; p7-p10 narrow, tapered (see Fig. 9); tertials pointed, the whitish markings obscure or worn off (see Forsman 1980); central rectrices narrow, tapered, with bolder and more complete white bars, and with the white at the tip restricted (usually 4-8 mm wide; Fig. 11).

SY/TY (August-July): Secondaries mixed juvenal and adult, typically with s3-s4 and s7, sometimes with s1, s2, s6, and/or s8 (and possibly also s9-s11) narrow, tapered, and worn, contrasting markedly with the other, broader, more truncate and fresher secondaries (see Fig. 8); primaries uniformly broad, p7-p10 truncate at tip (see Fig. 9); tertials and central rectrices like ASY/ATY (below) but tending toward SY/TY in pattern (see Fig. 11).

ASY/ATY (September-August): Like SY/TY but all secondaries adult, showing irregular contrasts in wear, the older feathers broad, truncate, less distinctly worn in comparison with newer secondaries (see Fig. 8); tertials truncate, the whitish markings bold (see Forsman 1980); central rectrices broad, truncate, with less distinct pale bars, and with the white at the tip expanded (usually 2-4 mm wide; Fig. 12).

Remarks: The patterns on the tertials and central rectrices may be intermediate between juvenal and adult feathers (see Fig. 12). A complete secondary molt may occur in some birds (see above), resulting in uniform adult secondaries. These could be either SY/TYs or ASY/ATYs and thus should be aged AHY/ASY.

Glaucidium and *Micrathene*

Specimen examination and the literature indicate that owls of these genera have complete adult prebasic molts. Except for 94 birds collected in active molt in June to September (AHY/ASYs in Table 1), no specimens of Northern Pygmy-Owl *(G. gnoma)*, Ferruginous Pygmy-Owl *(G. brasilianum)*, or Elf Owl *(M. whitneyi)* were found with mixed generations of flight feathers. Cramp (1985) mentions several relative differences in plumage between HY/SY and AHY/ASY Eurasian Pygmy-Owls *(G. passerinum)*, including differences in color pattern in the tertials, primary coverts, and rectrices. Although similar differences were detected in North American pygmy-owls and Elf Owl, there appeared to be too much individual variation to use these differences for reliable ageing. As in other owls, juvenal flight feathers (especially the outer primaries and central rectrices) were, on average, slightly narrower and more tapered than corresponding adult feathers (see Fig. 9), but again, differences were too slight to effectively use these criteria for ageing. In these genera, the presence of fault bars (CWS and FWS 1991) may be the only way to reliably age HY/SYs, while birds without them should be aged U/AHY. Examination of Northern Pygmy-Owl specimens revealed that the distance from the tip of the central rectrices to the center of the third white bar on these feathers averaged shorter in juveniles (range 25-30 mm) than adults (28-34 mm). However, sample sizes were small (Table 1), and further confirmation of this potential ageing criterion is needed. It also appeared that, in the Elf Owl, the primary covert pattern differed slightly by age, approaching the variation shown by Eastern Screech-Owl (Fig. 10), and the central rectrices had more distinct whitish bars on juveniles and less distinct to none on adults. Because only the juveniles and molting birds were of known age, however, these differences need confirmation.

Key to ageing North American pygmy-owls and Elf Owls

Juvenile-HY (June-August): Nesoptile down of juvenal plumage still present; flight feathers not in molt in June-August.

U/AHY (September-August): Nesoptile down not present; flight feathers in molt in June-August.

Remarks: Elf Owls may suspend molt over migration (Ligon 1968), so contrasting wing-feather generations in migrants during August to November, indicating AHY, might also be expected. See above for other subtle differences that may prove useful in separating HY/SY from AHY/ASY; these differences should be examined in known-age birds.

Speotyto

Little Owls *(Athene noctua)* of the Palearctic have complete adult prebasic molts (Cramp 1985) and the same was indicated by specimen examination in the closely related Burrowing Owl *(S. cunicularia)*. Except for individuals in active molt during July to October (17 of 115 AHY/ASYs, Table 1) and a few birds with anomalous retention of single feathers, no mixed generations of flight feathers were found. As in Little Owls (Cramp 1985) the best way to separate HY/SYs from AHY/ASYs was by the shape of the outer primaries, which averaged narrower and more tapered in juvenal feathers (see Fig. 9). Both North American subspecies *(S.c. hypugaea* and *S.c. floridanus)* showed these differences. However, 7% of the specimens (aged U/AHY in Table 1) could not be separated in direct comparison with other specimens because the outer primary shape and wear were intermediate between the two age groups. This proportion of birds in the field, where direct comparison may not be possible, will be considerably greater. No other marked differences between juvenal and adult flight feathers were found. Juvenal tertials and rectrices were slightly narrower and more tapered at the tip, and the white barring on the central rectrices was slightly more distinct and bar-like in HY/SYs than in AHY/ASYs. There was too much overlap in these characters, however, for them to be of use in ageing.

Key to ageing Burrowing Owls

HY/SY (October-September): No flight-feather molt present in July-October; p7- p10 relatively narrow, tapered at tip, relatively worn (Fig. 9).

AHY/ASY (October-September): Flight-feather molt usually present in July- September; p7-p10 relatively broad, truncate at tip, relatively fresh (Fig. 9).

Remarks: Ageing with the above may only be reliable with experience or with extremes only; expect that at least 50% of November to June birds will be intermediates that cannot be aged. Ageing may be further facilitated in a few birds by the patterns of fault bars (see above), if present.

Strix

Forsman (1981) detailed flight-feather molt in the Spotted Owl *(S. occidentalis)* and Cramp (1985) outlined flight-feather molt in the Great Gray Owl *(S. nebulosa)*, but little has been published on molt in the Barred Owl *(S. varia)*. Flight feather molt in this genus shows greater individual variation than in other owls. Adult Spotted Owls usually replace 3-7 primaries and 3-9 secondaries each year, but this can apparently vary from none to all (Forsman 1981). The second prebasic molt is probably incomplete in most if not all cases. It may typically involve p2-p3, and/or one to a block of outer primaries within p4-p10, and some or all of the innermost secondaries (s10- s13), s5, and s1-s3. The third prebasic molt usually includes those primaries and secondaries not molted during the second prebasic molt (occasionally more and sometimes less) and subsequent prebasic molts are variable. Other *Strix* owls (including Tawny Owl, *S. aluco*, and Ural Owl, *S. uralensis*; Cramp 1985) appear to follow similar wing-feather molt patterns, although they are usually more complete in Tawny Owl and less complete in Great Gray Owl. Except for complete tail molts every other year in the Spotted Owl (Forsman 1981) and every year in the Tawny Owl (Cramp 1985), rectrix molt in this genus is not well documented. It generally appears to vary individually and interannually, being absent, incomplete, or complete.

Results of specimen examination agree with what is known in Spotted Owls, and suggest that wing and tail molt in the Barred Owl parallels that of the Spotted Owl. The 13 inferred SY/TY

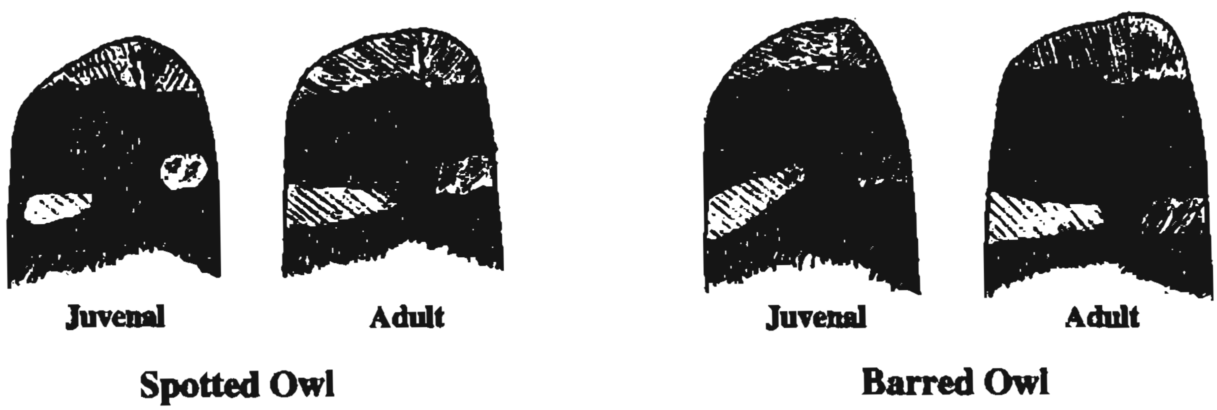


Figure 12. Primary covert patterns by age in Spotted and Barred Owls. The best feathers to examine are those corresponding to p5-p8. Note that all feathers of HY/SYs will be juvenile, and that SY/TYs will have mixed retained, juvenal and replaced, adult feathers. Similar but slightly less indicative patterns occur in Flammulated, Great Horned, Great Gray, and Long-eared Owls.

Spotted Owls (Table 1) had replaced 4-8 primaries ($\bar{x}$=6.4) and 4-10 secondaries ($\bar{x}$=6.8), and inferred ASY/ATYs had renewed 3-10 primaries ($\bar{x}$=6.4) and 4-10 secondaries ($\bar{x}$=6.5). Eleven of the 13 SY/TYs had retained the juvenal rectrices and, with experience, could be aged by this criterion alone (Fig. 13; see Moen *et al.* 1991). Two appeared to have replaced all rectrices at the second prebasic molt but could be aged by wing feather replacement and other criteria (see below). Three adult birds either had molted all flight feathers or had contrasts that were difficult to detect and were aged AHY/ASY. In Barred Owls, inferred SY/TYs had replaced 5-8 primaries ($\bar{x}$=6.9) and 5-9 secondaries ($\bar{x}$=6.9). Inferred ASY/ATYs had replaced 4-9 primaries ($\bar{x}$=6.3) and 3-11 secondaries ($\bar{x}$=6.7). Feather contrasts were either more difficult to detect in adult Barred Owls than in Spotted Owls, or a higher percentage of Barred Owls had complete molts and had to be aged AHY/ASY (Table 1). Seven of the eight inferred SY/TYs had apparently retained all juvenal rectrices and could be aged by these, as in the Spotted Owl (Fig. 13). One bird (MVZ164332) appeared to be an SY/TY by wing-feather replacement but had fresh, adult-like rectrices.

As in Europe (Cramp 1985), too few specimens were available for a thorough evaluation of flight-feather molt in the Great Gray Owl. Of two inferred SY/TYs (Table 1), one (MVZ82188) had replaced just p5 on both wings, and the other (MVZ32324) had replaced p1-p3 and p6-p10 on both wings. Both of these birds had secondary replacement patterns typical of SY/TYs in this genus, with eight secondaries replaced among s1-s3 and s10-s15. One worn October bird (MVZ75633) was possibly an SY/TY that had not molted any flight feathers during the second prebasic molt but it was aged AHY/ASY here. In addition to color pattern differences in the rectrices (Fig. 13), juvenal and adult primary coverts differ in Spotted and Barred Owls (Fig. 12), as they do in Ural Owl (Pietiäinen and Kolunen 1986). This was a useful criterion for ageing. Mixed juvenal and adult primary coverts (corresponding with old and renewed primaries) indicated SY/TY whereas mixed old and new adult coverts indicated ASY/ATY. As in other owls, the pattern of barring on the primaries, secondaries, and rectrices (Table 2; Figs. 5-6), and the shape of the secondaries and rectrices (Figs. 5-6), varied by age in Spotted and Barred Owls (Table 2, Figs. 4-6).

Juvenal

Adult

Figure 13. Width and pattern of the rectrices, by age, in Spotted and Barred Owls. Both species usually retain the juvenal rectrices for two years, hence SY/TYs usually show the juvenal pattern; however, the tips to the feathers are heavily abraded and less acuminate (bracket-shaped) at the tip (see Moen *et al.* 1991).

These two species also showed slight age-related variation in the shape of the outer primaries, as in screech-owls (Fig. 9), but not as marked. Available specimens of Great Gray Owl indicated that these differences in plumage patterns were not as indicative for ageing but that differences in width and shape of flight feathers (particularly the central rectrices; see Cramp 1985) could be used to distinguish juvenal feathers from adult feathers.

Key to ageing North American *Strix* owls

HY/SY (August-July): Juvenal flight feathers retained; secondaries and primaries uniform in wear, narrow, and tapered; light markings of primary coverts small, rounded (Fig. 12); numbers of bars on primaries, secondaries, and rectrices relatively large and distances between bars on these feathers relatively small (Table 2, see Figs. 4-6); rectrices narrow (Great Gray Owl), acuminate at the tip, and with the terminal band pure whitish (Spotted and Barred Owls, Fig. 13).

SY/TY (August-July): Secondaries *and* primaries showing contrasts between juvenal and adult feathers, often with 3-9 primaries and 4-10 secondaries fresher, broader, more truncate, and having bar patterns of adults (Table 2; Figs. 4-5), contrasting with the narrower, more faded and abraded, and juvenile-patterned other primaries and secondaries; some juvenal primary coverts (corresponding to the older primaries) retained, showing small rounded spots, in contrast to the replaced, adult feathers, with larger and squarer bars (Fig. 12); rectrices usually as in HY/SY (occasionally as in ASY/ATY) but very abraded, the tip not acuminate (Fig. 13).

ASY/ATY (August-July): Secondaries and primaries with irregular and less distinct contrasts in wear between adjacent feathers, all feathers being broad, truncate and showing bar patterns of adult (Table 2; Figs. 4-5); all primary coverts showing the square bars of adult feathers (Fig. 12); rectrices broad (Great Gray Owl) and rounded, with the terminal band mixed whitish and brown (Spotted and Barred owls, Fig. 13).

Remarks: The above can be used to distinguish age groups in most Spotted and Barred Owls and probably many Great Gray Owls. A small proportion of *Strix* owls can probably be aged ATY/A4Y, having two generations of adult flight feathers plus one to a few very worn, retained juvenal flight feathers. Retained primary coverts (Fig. 12) may be the easiest juvenal feathers to detect on these birds.

Asio

In Europe, both Long-eared *(A.o. otus)* and Short-eared *(A. flammeus)* Owls have adult prebasic molts that vary from incomplete to complete, being more often complete in Short-eared than in Long-eared Owl (Piechocki 1968, Haarhaus 1983, Wijnandts 1984, Cramp 1985, Baker 1993). When adult prebasic molts are incomplete, typically, only some secondaries (and rarely p10) are retained. A similar replacement pattern has been documented in North American Long-eared Owls *(A.o. wilsonianus)* by Evans and Rosenfield (1987), who found that 50.8% of 394 fall migrant adults in Minnesota showed incomplete molt of the secondaries and primaries. Retained secondaries most often included s1-s4 and s7-s8, less frequently s5-s6 and s9-s10. Only 2.5% of adults had retained p9 and/or p10. Evans and Rosenfield suggested that these birds may complete the flight-feather molt on the winter grounds; however, evidence from Europe and this study indicate that they are retained until the following summer. Little has been published on molt in North American Short-eared Owls.

Several differences between juvenal and adult flight feathers have been documented in European Long-eared Owls (Cramp 1985). These differences applied to North American Long-eared Owls as well (Table 2, Figs 4-6), although numbers of bars on all feathers averaged larger in North America than in Europe. The shape of the pale markings on the primary coverts also varied in Long-eared Owl, as in *Strix* owls (Fig. 12); however, overlap occurred between the ages. Juvenal and adult flight feathers (including pattern differences of the rectrices; see Cramp 1985, Baker 1993) were much harder if not impossible to separate in Short-eared Owls. Similar average differences to those in Long-eared Owl were found in this species but birds could not be reliably aged due to substantial individual variation within all age groups.

In this study, incomplete replacement of secondaries was found in 31.5% of all Long-eared Owl specimens (62.5% of known AHY/ASYs) and 20.3% of Short-eared Owl specimens. The lower proportion of Long-eared Owls than was found by Evans and Rosenfield (1987) likely reflects a disproportionate number of HY/SYs in the collections (see Table 1). Most Long-eared Owls with two generations of secondaries could be readily aged by the pattern of replacement and the condition and pattern of retained feathers (Figs. 5 and 8). The 21 SY/TY Long-eared Owls (Table 1) had retained 1-6 juvenal secondaries ($\bar{x}$=2.7) including s4 in all 21 birds and, in decreasing order of occurrence, s3 and s7 (10 specimens each), s8 (6), s2 and s6 (4), and s9 (2). The 15 ASY/ATYs had retained 1-6 adult secondaries ($\bar{x}$=2.8), usually not involving the same feathers, although one ASY/ATY specimen (MVZ89462) had retained just s4 on both wings. Both SY/TY and ASY/ATY specimens had retained as few as one secondary on one wing, indicating that all feathers can presumably be replaced during both the second and later prebasic molts. Thus, 21 specimens with uniform adult secondaries were aged AHY/ASY. Four additional birds had retained secondaries (in patterns typical of SY/TYs) with intermediate plumage characters (Table 2; Figs. 4-6) and were also aged AHY/ASY.

Short-eared Owls with mixed generations of secondaries were harder to age than Long-eared Owls. The 30 Short-eared Owls showing mixed generations had replaced 1-6 secondaries ($\bar{x}$=2.4). Of these, 11 were cautiously inferred to be SY/TYs and nine to be ASY/ATYs based on the patterns of replacement (similar to that of Long-eared Owl) and relative contrast in wear and shape between new and old secondaries. The remaining ten could not be reliably aged and were called AHY/ASY (Table 1). No birds of either species were found with mixed generations of primaries or rectrices. Thus, ageing criteria differed between the two species.

Key to ageing North American Short-eared Owls

Juvenile-HY (June-September): Nesoptile down of juvenal plumage still present; flight feathers not in molt and uniform in wear and color.

U/AHY (October-September): Nesoptile down not present; flight feathers in molt (June-September) and/or uniform in wear and color.

AHY/ASY (September-August): Secondaries with mixed generations, 1-6 feathers contrastingly abraded and worn.

Remarks: A few AHY/ASYs may be designated SY/TY or ASY/ATY, with experience, by the location, shape, bar pattern, and condition of retained secondaries, as in Long-eared Owl (see Fig. 8). Differences between the two age groups are very hard to infer, however, and most birds with mixed generations of secondaries should be aged AHY/ASY only.

Key to Ageing North American Long-eared Owls

HY/SY (August-July): All juvenal flight feathers retained, the secondaries and primaries uniform in wear, tapered, and lacking a pinkish tinge to the undersurfaces; numbers of bars on the primaries, secondaries, and rectrices relatively large and distances between the bars on these feathers relatively small (Table 2, Figs. 4-6).

AHY/ASY (August-July): All secondaries and primaries adult, uniformly fresh, broad, and with a pinkish wash to undersurface; numbers of bars on the primaries, secondaries, and rectrices relatively small and distances between the bars on these feathers relatively large (Table 2, Figs. 4-6).

SY/TY (August-July): Like AHY/ASY but 1-6 secondaries including s4 and one or more of s2-s3 and/or s6-s9 contrastingly narrow and worn, and showing the bar patterns of juvenal feathers (Table 2, Figs. 5 and 8); patterns often symmetrical or nearly so.

ASY/ATY (August-July): Like SY/TY but retained secondaries adult, broad, truncate, less distinctly worn in comparison with newer secondaries and usually not with the same patterns of replacement as SY/TYs, and showing the bar patterns of adult feathers (Table 2, Figs. 5 and 8); patterns more often asymmetrical between the wings.

Remarks: A few birds with mixed generations of secondaries will show retained feathers with characters intermediate between juvenal and adult feathers. These should be aged AHY/ASY.

Aegolius

Primary and secondary molt patterns in the Boreal Owl of Europe *(A.f. funereus)* were outlined by Cramp (1985) and Hornfeldt *et al.* (1988), and those of the Northern Saw-whet Owl *(A. acadicus)* were detailed by Evans and Rosenfield (1987). In both species adult prebasic molts are reported to be complete in a very small percentage of birds (see also Weir *et al.* 1980, Slack 1992) but the majority of individuals, probably including all SY/TYs, show incomplete flight-feather replacement. The second prebasic molt in both species usually includes consecutive blocks of 3-6 outer primaries (occasionally 7-9, and rarely 10) and 3-9 inner secondaries (occasionally more). Boreal Owls can apparently replace some outer secondaries as well (Cramp 1985), whereas Northern Saw-whet Owls appear to retain these (Evans and Rosenfield 1987). The third prebasic molt appears to differ between the two species (Fig. 14). In Boreal Owls, a second block of *central* primaries, usually among p3-p8, is replaced, leaving juvenal inner primaries (Hornfeldt *et al.* 1988). Northern Saw-whet Owls, in contrast, replaced 3-4 *inner* primaries, leaving 3-4 central primaries among p3-p7. In both species, the secondaries show patterns of replacement corresponding to the primaries (Fig. 14). In contrast to what is assumed in Northern Saw-whet Owls, captive Boreal Owls can retain p1 (and sometimes p2) for up to 4-5 yrs (Hornfeldt *et al.* 1988). Rectrix molt in Boreal Owl is usually complete (but occasionally incomplete). Little has been published about extent of rectrix molt in Northern Saw-whet Owls (see Mayr and Mayr 1954, Collins 1961).

An insufficient number of Boreal Owl specimens was available (Table 1) to assess flight-feather molt patterns, but it appears that replacement patterns in North American birds *(A.f. richardsoni)* are consistent with those in

Europe. The three inferred SY/TYs had each replaced p7-p10 and s8-s13 or s9-s13. Inferred ASY/ATYs had irregular molt patterns not matching those of the SY/TYs. One specimen (MVZ39765) had replaced p4-p6 and s4-s7 on each wing (Fig. 14) and could have been a TY/4Y; however, because the innermost primaries are fresher due to less exposure, it could not be determined whether or not these were juvenal feathers. Another specimen (CAS19436) had molt patterns consistent with TY/4Y Northern Saw-whet Owls (see below), with p6-p10 of second generation, p4-p5 very old, and p1-p3 new. This bird was aged ASY/ATY.

Replacement patterns in Northern Saw-whet Owl specimens also matched those documented by Evans and Rosenfield (1987). In the 16 inferred SY/TY and TY/4Y specimens (Table 1) the second prebasic molt included 3-7 outermost primaries ($\bar{x}$=4.9; among p4-p10) and 4-9 innermost secondaries ($\bar{x}$=6.8; among s5-s13). The seven inferred TY/4Ys had replaced 2-4 inner primaries and 2-4 outer secondaries, leaving 2-4 old juvenal primaries among p3-p7 and 1-5 old juvenal secondaries among s5-s9 (Fig. 14). In these, the newly-replaced innermost primaries and outermost secondaries contrasted greatly with the central block of juvenal primaries and secondaries and were not just slightly less worn due to decreased exposure. Adults showed mixed patterns consistent with those found by Evans and Rosenfield (1987). One specimen (CAS84289) appeared to have uniformly adult feathers, a pattern that may have resulted from a complete molt (see above), or the owl may have been an older individual in which contrasts were hard to detect (see Cramp 1985 on Boreal Owl). None of these owls showed evidence of incomplete molt among the rectrices.

The identification of juvenal vs. adult primaries and secondaries might help clarify some of the complexity of wing-feather molt in *Aegolius*. Cramp (1985) noted that the juvenal primaries of Boreal Owl can have whitish tips (that soon wear off) whereas adult primaries are uniformly dark, that juvenal tertials are more pointed, worn, and russet-colored than adult tertials, and that the white bars on the tail are shaped more like chevrons on juvenal feathers and straighter on adults. These differences were noted in North American specimens, but sufficient overlap in these characters precluded confident ageing. More useful in Northern Saw-whet Owl (at least) seemed to be the width and shape of the outer primaries (see Fig. 9) and width of the central rectrices, both being broader and the primaries being more squared at the tip in AHY/ASYs than in HY/SYs. More study is needed on known-

Figure 14. Diagrammatic patterns of wing-feather replacement in TY/4Y Boreal and Northern Saw-whet Owls. SY/TYs renew only the outer primaries and inner secondaries, those indicated as second generation here. Replacement patterns show substantial variation in these species and confirmation is needed on the reliability of ageing to TY/4Y.

age, North American *Aegolius* owls to confirm the above molt patterns and ageing criteria.

Key to ageing North American *Aegolius* owls

HY/SY (September-August): Juvenal flight feathers retained, the secondaries and primaries uniform in wear; p7-p10 tending to be narrow and tapered at tip (see Fig. 9); central rectrices relatively narrow.

SY/TY (September-August): Sequential blocks of outer primaries *and* inner secondaries, including at least p10-p8 and s9-s12 (sometimes some or all of p3-p7 and/or s4-s8) molting or fresh, contrasting with the relatively older and faded, retained, sequential inner primaries (see Fig. 14); replaced p7-p10 tending to be broad and truncate (see Fig. 9); central rectrices relatively broad.

TY/4Y (September-August): Like HY/SY but a block of sequential primaries *and* secondaries, including some or all of p3-p8 and s4-s7 (Boreal Owl) or p1-p4 and s1-s4 (Saw-whet Owl) fresh and new, contrasting with the slightly older sequential primaries and secondaries to the outside (among p5-p10 and s5-s13) and much older, sequential juvenal primaries and secondaries to the inside (among p1-p5 and s1-s5; Boreal Owl) or center (among p3-p7 and s5-s9; Saw-whet Owl) each of the blocks uniform in wear, without gaps of 1-2 feathers contrasting with adjacent feathers on each side (Fig. 14).

ASY/ATY (September-August): Primaries and secondaries showing at least three generations, and showing irregular contrasts in freshness, unlike the patterns of SY/TY or TY/4Y (see Fig. 14), with 1-2 isolated feathers new, molting, or old (see Fig. 3G-H and Evans and Rosenfield 1987, type "C").

Remarks: Occasional birds with uniformly adult-like feathers may be encountered and should be aged U/AHY or AHY/ASY. Classification of TY/4Y should probably only be assigned with experience, as it is possible that occasional ATY/A4Ys may have replacement patterns that match those of TY/4Y. Birds with intermediate characteristics and more than two generations of primaries present should be aged ASY/ATY.

CONCLUSIONS

Patterns of primary and secondary replacement in owls appear to follow similar sequences among species but feather replacement varies greatly as to timing, taking one to six or more years for all feathers to be renewed. Replacement of the primaries often commences with p6 or p7 and concludes with p2-p4, and molt of secondaries often commences with the tertials and concludes with s1, s3-s4, and/or s7-s8. Why replacement of these feathers occurs so slowly in relation to most other birds—whether it is due to the soft quality of the feathers or nocturnal habits of owls, both resulting in relatively little flight-feather wear, the energy demands of producing such feathers, or other factors—would be an interesting topic of study. Also of interest would be the systematic implications, if any, of molt patterns in owls. At any rate, knowledge of these patterns and their timing, along with differences between juvenal and adult flight feathers, can be used to reliably age owls of certain species up to their third or fourth year of life.

With the above information, individuals of many North American owls should be placed in older age categories than are currently being assigned. Reliable ageing of owls, however, requires caution and experience in many cases. In many owls, molt patterns may not be easily distinguished without practice, or may conflict with what would be expected. Responsible ageing always includes the willingness to place a bird in a less-precise age group should any uncertainty exist. It must again be stressed that most ages of owls in this study were inferred, and confirmation of the above information is needed based on examination of known-aged, captive, or marked individuals.

ACKNOWLEDGMENTS

Karen Cebra and Luis Baptista of CAS and Ned K. Johnson and Carla Cicero of MVZ allowed access to specimens under their care. I thank Steve N.G. Howell for preparing the illustrations in the figures, for help in the collections, and for commenting on the manuscript. The manuscript also benefitted from comments by Denver W. Holt (who reviewed two versions), Kenneth C. Parkes, and David L. Evans. I thank Tom Schuster for help in translating German references. This is contribution # 645 of PRBO.

LITERATURE CITED

Baker, K. 1993. Identification guide to European non-passerines. BTO Guide 24. British Trust for Ornithology, Thetford, U.K.

Barrows, C.W., P.H. Bloom, and C.T. Collins. 1982. Sexual differences in the tail barring of Spotted Owls. North American Bird Bander 7:138-139.

Bent, A.C. 1938. Life histories of North American birds of prey. Part 2. U.S. National Museum Bulletin # 170. Washington D.C.

Canadian Wildlife Service and U.S. Fish and Wildlife Service. 1991. North American Bird Banding. Volumes 1 and 2. Environment Canada, Canadian Wildlife Service, Ottawa, Canada and U.S. Fish and Wildlife Service, Washington D.C.

Carpenter, T.W. 1992. Utility of wing length, tail length and tail barring in determining the sex of Barred Owls collected in Michigan and Minnesota. Condor 94:794-795.

Collins, C.T. 1961. Tail molt of the Saw-whet Owl. Auk 78:634

Cramp, S., ed. 1985. Birds of the Western Palearctic. Vol. 4. Oxford Univ. Press, Oxford, England.

Duffy, K. and P. Kerlinger 1992. Autumn owl migration at Cape May Point, New Jersey. Wilson Bull. 104:312-320.

Evans, D.L. and R.N. Rosenfield. 1987. Remigial molt in fall migrant Long-eared and Northern Saw-whet Owls. Pages 209-214 in R.W. Nero, R.J. Clark, R.J. Knapton, and R.H. Hamre, eds., Biology and conservation of northern forest owls. U.S. Forest Service General Technical Report RM-142.

Forbush, E.H. 1927. Birds of Massachusetts and Other New England States. Volume II. Massachusetts Department of Agriculture, Boston.

Forsman, D. 1980. Ageing and moult in western Palearctic Hawk Owls *Surnia u. ulula* L. Ornis Fennica 57:73-75.

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

Grigg, W.N. 1989. Owl banding at Whitefish Point, Michigan - Spring 1988. North American Bird Bander 14:120-122.

Haarhaus, D. 1983. Die Grossgefiedermauser palearktischer Eulen in Gefangenschaft. Beiträge Vogelkund 29:89-102.

Hornfeldt, B., B.-G. Carlsson, and A. Nordstrom. 1988. Molt of primaries and age determination in Tengmalm's Owl *(Aegolius funereus)*. Auk 105:783-789.

Johnson, P.N. 1991. Development of talon flange and serrations in the Barn Owl *Tyto alba*: a guide to ageing. Ringing & Migration 12:126-127.

Josephson, B. 1980. Aging and sexing Snowy Owls. J. Field Ornith. 51:149-160.

Karalus, K.E. and A.W. Eckert. 1974. The Owls of North America. Doubleday and Co., Garden City, New York.

Lenton, G.M. 1984. Moult of Malaysian Barn Owls *Tyto alba*. Ibis 126:188-197.

Ligon, J.D. 1968. The biology of the Elf Owl, *Micrathene whitneyi*. Misc. Pub. Museum of Zoology, Univ. of Michigan 136:1-70.

Loos, G. and P. Kerlinger. 1993. Road-mortality of saw-whet and screech-owls on the Cape May Peninsula. J. Raptor Research 27:210-213.

Marti, C.D. 1992. Barn Owl. *In* The Birds of North America, No. 1 (A.Poole, P.Stettenheim, and F.Gill, Eds.). Academy of Natural Sciences, Philadelphia; American Ornithologists' Union, Washington D.C.

Mayr, E. and M. Mayr. 1954. The tail molt of small owls. Auk 71:172-178.

Moen, C.A., A.B. Franklin, and R.J. Gutierrez. 1991. Age determination of subadult Northern Spotted Owls in northwest California. Wildlife Soc. Bull. 19:489-493.

Oberholser, H.C. 1974. The Bird Life of Texas. Vol 1. Univ. Texas Press, Austin, Texas.

Piechocki, R. 1961. Über die Grossgefieder-mauser der Schleiereule und Waldkranz. J. f. Ornithol. 102:220-225.

Piechocki, R. 1968. Über die Grossgefieder-mauser einer gekäfigten Waldohreule *Asio otus*. Beiträge Vogelkund 13:455-460.

Piechocki, R. 1974. Über die grobgefieder-mauser eines gekäfigten paares der schleiereula *Tyto alba*. J. f. Ornithol. 115:436-444.

Pietiäinen, H. and H. Kolunen. 1986. Age determination of breeding Ural Owls *Strix uralensis*. Ornis Fennica 63:26-27.

Pyle, P., S.N.G. Howell, R.P. Yunick, and D.F. DeSante. 1987. Identification Guide to North American Passerines. Slate Creek Press, Bolinas, California.

Slack, R.S. 1992. Primary molt patterns of Northern Saw-whet Owls *(Aegolius acadicus)* captured during spring migration. North American Bird Bander 17:97-101.

Slack, R.S., C.B. Slack, R.N. Roberts, and D.E. Emord. 1987. Spring migration of Long-eared Owls and Northern Saw-whet Owls at Nine Mile Point, New York. Wilson Bull. 99:480-485.

Stresemann, E. and V. Stresemann. 1966. Die Mauser der Vögel. J. f. Ornithol. (Sonderheft) 107:1-447.

Taylor, I.R. 1993. Age and sex determination of Barn Owls *Tyto alba alba*. Ringing & Migration 14:94-102.

Weir, R.D., F. Cooke, M.H. Edwards, and R.B. Stewart. 1980. Fall migration of Saw-whet Owls at Prince Edwards Point, Ontario. Wilson Bull. 92:475-488.

Weller, M.W. 1965. Bursa regression, gonad cycle, and molt of the Great-horned Owl. Bird-Banding 36:102-112.

Wijnandts, H. 1984. Ecological energetics of the Long-eared Owl *(Asio otus)*. Ardea 72:1-92.