THE LONG-EARED OWL (ASIO OTUS) AND FOREST MANAGEMENT: A REVIEW OF THE LITERATURE

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ABSTRACT.—In North America, 13 of 20 breeding season studies reporting on Long-eared Owl (Asio otus) reproduction were conducted in open country habitats, four in woodland or edge habitats and three in predominantly woodland habitat. Sixteen of 22 nonbreeding season studies that reported communal roost sites were located in forest/edge habitats, five reported locations in open space and one was found within forest habitat. There is currently little data to indicate either a negative or positive effect of forest-management practices on this species. Although there appears to be some evidence of population declines in specific geographic areas, these impacts have been attributed to loss of riparian vegetation, conversion of foraging areas to agricultural fields and reforestation of open habitats. The Long-eared Owl's ecomorphology is suggestive of a species that inhabits open country. Additionally, its primary food is small mammals (e.g., microtine and heteromyid rodents) which inhabit open country. Should the Long-eared Owl be considered a forest owl? Research data would suggest no; however, studies from extensive deciduous and coniferous woodlands are needed.

KEY WORDS: Long-eared Owl; forestry; habitat, diet, ecomorphology; Asio otus.

El búho (Asio otus) y administración forestal: un reviso de la literatura

RESUMEN.—En norte américa, 13 de 20 estudios de tiempos de cría reportadas en el búho Asio otus fueron evaluados en hábitat del campo amplio, cuatro en bosques o orillas de hábitat, y tres en mayoría de hábitat de bosque. Dieciséis de 22 estudios en tiempos sin cría que reportaron sitios de percha comunal fueron localizadas en bosque/hábitat de orilla, cinco lugares reportados en espacio abierto, y uno fue encontrado dentro de un hábitat de bosque. Actualmente poca información indica si los afectos de la administración de bosques son negativo o positivo en el especie. Aunque parece que un poco de pruebas con reducción de poblaciones en áreas específicas geográficamente, estos impactos están atribuido a la falta de vegetación cerca de los ríos, conversión de áreas de forraje a parcela agricolas, y repoblación forestal de hábitat abiertos. La eco-morfología del buho evoca una especie que ocupa el campo abierto. También, su comida principipal es mamíferos pequeños (i.e. microtine y roedor heteronmyid) que ocupan campos abiertos. ¿Debe ser el búho considerado un búho del bosque? Información investigada sugieren que no, sin embargo, estudios de bosque conífero y de hoja caduca extensa es necesaria.

[Traducción de Raúl De La Garza, Jr.]

The Long-eared Owl (Asio otus) is a widely distributed Holarctic species, with six recognized subspecies (Cramp 1985). In the Northern Hemisphere, it ranges from approximately 30–65° latitude, with isolated populations occurring in North and East Africa, the Azores and Canary Islands (Mikkola 1983, Marks et al. 1994). Some aspects of Long-eared Owl natural history have been well studied in the U.S. and some European countries, but most studies have been short in duration, averaging about two seasons.

In North America, two subspecies are currently recognized (A. o. wilsonianus and A. o. tuftsi; see Marks et al. 1994 for further discussion). The

Long-eared Owl has been considered an open country species, inhabiting areas such as grasslands, shrubsteppe, marshes and woodland patches near open areas. Most studies seem to support this. To my knowledge, there have been no attempts to evaluate the affects of forestry practices on this species. Herein, I review the literature and use some inferences from my ongoing 10 yrs of study to address some of the questions concerning the impacts of forest management on Long-eared Owls.

POPULATION TRENDS

Few data exist for population trends of Longeared Owls in North America over the past 10, 25,

Table 1. Status of the Long-eared Owl in North America.

PROVINCE/REGION OR STATE	STATUS	POPULATION TREND ^a		
CANADA (Fyfe 1976)				
British Columbia	Low	Unknown		
Maritime	Low/Medium	Fluctuating		
Northwest Territory/Yukon	Unknown	Unknown		
Ontario/Quebec	Low/Medium	Fluctuating		
Prairie	Low/Medium	Fluctuating		
NORTHEASTERN UNITED STATES (Melv	in et al. 1989)			
Connecticut	Special Concern			
Delaware	Ûnknown			
Massachusetts	Special Concern			
Maryland	Decreased			
Maine	Unknown			
New Hampshire	Special Concern			
New Jersey	Unknown			
New York	Unknown			
Pennsylvania	Decreased			
Rhode Island	Special Concern			
Vermont	Special Concern			
MIDWEST (Petersen 1991)	-			
Illinois	Endangered	Unknown		
Indiana	Uncommon	Declining		
Iowa	Threatened	Unknown		
Kansas	Uncommon	Stable		
Michigan	Special Concern	Unknown		
Minnesota	Regular	Unknown		
Missouri	Special Concern	Unknown		
Nebraska	Unknown	Unknown		
North Dakota	Special Concern	Unknown		
Ohio	Ûnknown	Unknown		
South Dakota	Rare	Declining		
Wisconsin	Special Concern	Unknown		
WEST (Marti and Marks 1989)				
California	Special Concern	Declining		
Colorado	Common	Stable		
Idaho	Common	Unknown		
Montana	Special Concern	Unknown		
Nevada	Common	Stable		
Oregon	Common	Stable		
Utah	Common	Unknown		
Washington	Unknown	Unknown		
Wyoming	Common	Unknown		

^a Trend data not known for northeastern U.S.

50 or 100 yrs, but there are some regional data. The Breeding Bird Survey (BBS) does not include the Long-eared Owl in its data set from 1966–89. For inclusion, a species must have been detected on >10 BBS routes in a physiographic region; 25 or more detections in the three biomes (Eastern, Central, Western); 35 or more detections in Can-

ada; or 50 detections in the U.S. and Canada (Droege pers. comm.).

In Canada, Fyfe (1976) reported population trends and relative abundance of raptors for provinces or specific geographic areas (Table 1). There were no data to support these designations. Also in Canada, Christmas Bird Count (CBC) results

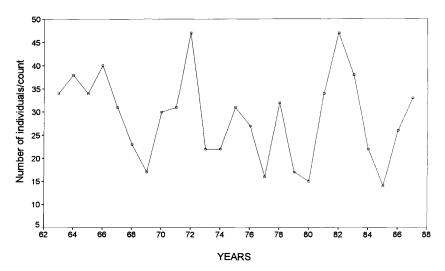


Figure 1. Summary of winter counts of Long-eared Owls from Christmas Bird Counts in the northeastern U.S., 1963–87 (after Melvin et al. 1989).

showed a significant decline in Long-eared Owl numbers, but these data should be interpreted cautiously (Kirk et al. 1994).

In the northeastern U.S., Melvin et al. (1989) reported that the Long-eared Owl was listed as a species of special concern in all the New England states except Maine and decreasing in Maryland and Pennsylvania (Table 1). Within the northeast-

ern states, Melvin et al. (1989) concluded that no clear population trend could be detected for Long-eared Owls, although numbers seemed to fluctuate about every three to six yr (Fig. 1). In New Jersey, Bosakowski et al. (1989, 1989a) analyzed 31 yr (1956–86) of Long-eared Owl Christmas Count Data reporting one or more Long-eared Owls and concluded that the species was declining (Fig. 2).

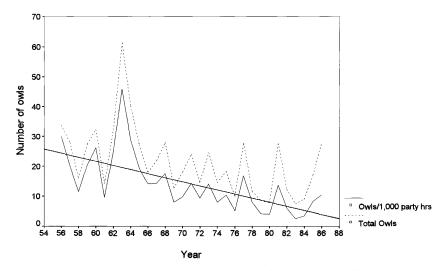


Figure 2. Long-eared Owls reported on New Jersey Christmas Bird Counts (dotted line) and per 1000 party hours (solid line). Regression line (dashed), Y = -0.70x + 25.5, P < 0.0001, r = 0.67 for party hours is significant. Regression line, Y = -0.629x + 31.9, P = 0.005, for total owls had a lower correlation (r = 0.50) (after Bosakowski et al. 1989a).

In the midwestern U.S., Petersen (1991) reported that Long-eared Owls have declined in Indiana and South Dakota, are stable in Kansas and are of unknown status elsewhere (Table 1). This was based on state and regional birding publications and raptor survey forms. In Minnesota, however, Evans (*in* Marks et al. 1994) noted a decline in migrant Long-eared Owls in his study area from 1976–93 (Fig. 3).

In the western U.S., White (1994) reported the Long-eared Owl as stable, but with some local losses in the far west. He did not report how these species designations were assigned. Marti and Marks (1989) reported a Long-eared Owl population decline in California and a stable or unknown population status in the rest of the west (Table 1). In coastal southern California, Bloom (1994) has shown the Long-eared Owl to have been extirpated in some areas, with small remnant populations still occurring inland. The number of historic nesting areas have declined by 55% (Bloom 1994). In Montana, Long-eared Owls were listed as a species of special concern (Marti and Marks 1989). I have shown yearly fluctuations in numbers during CBC counts and breeding seasons (Figs. 4 and 5) with a consistent research effort in the same areas. In Mexico, the status of the Long-eared Owl has not been reported (Enriquez-Rocha et al. 1993).

In summary, realistic population trends for North American Long-eared Owls are difficult to determine. The use of CBC data to determine avian population trends has been controversial, but Root (1988) has presented some of the strengths and weaknesses to this approach.

Population demographics for Long-eared Owls are uncertain because of the paucity of data on mortality, emigration, immigration, migration and other factors. Because Long-eared Owls are highly migratory in some areas, nocturnal, difficult to locate and appear to show food-based nomadism, it is very difficult to determine their status. For example, five notable recoveries of banded owls in Mexico >800 km from banding sites illustrate the Long-eared Owls' high degree of mobility. These long distance recoveries include: one owl banded in Saskatchewan, Canada and recovered 4000 km away in Oaxaca, Mexico; one owl banded in Montana and recovered 3200 km away in Guanajuato, Mexico; and one owl banded in Minnesota and recovered 3100 km away in Puebla, Mexico. Longterm breeding season studies in Montana show little site fidelity by Long-eared Owls. Of 77 breeding pairs intensively monitored for 9 consecutive yr, only 11 males and two females have returned to the same breeding site more than once. Additionally, no mate fidelity has been recorded. These data buttress the argument for highly migratory and nomadic tendencies in Long-eared Owls.

PRIMARY FACTORS RESPONSIBLE FOR LONG-EARED OWL POPULATION TRENDS

In most cases, there were insufficient data to convincingly conclude which factors influence population trends. Population declines have been attributed to habitat alteration, forest succession, urbanization, competition with Great Horned Owls (*Bubo virginianus*), loss of habitat for prey species, rodenticides (Bosakowski et al. 1989a), shooting and habitat loss (Marks et al. 1994) and loss of riparian habitats and grasslands (Bloom 1994).

Some forestry practices are also thought to have affected Long-eared Owls. In New Jersey, Bosakowski et al. (1989a) suggested that forest removal and thinning affected wintering Long-eared Owls and caused them to abandon the area.

On the contrary, many of the nonbreeding and breeding season studies from the eastern U.S. were located at roost sites in plantations of exotic conifers or other man-made habitats such as cemeteries (Tables 1 and 2). In the western U.S., shelter-belts planted for wind and snow breaks, as well as cover and food for wildlife have allowed Long-eared Owls new winter and breeding sites. In other instances, Long-eared Owls have been radiotracked (Ulmschneider 1990) and found to be using forest clear-cuts as foraging areas.

AFFECTS OF PAST AND PRESENT FOREST MANAGEMENT PRACTICES ON LONG-EARED OWLS

There is insufficient information to conclude that forest management has affected Long-eared Owl populations. There is some data from New Jersey, Minnesota and California that show declines. In New Jersey and California, habitat loss or change appears to have affected Long-eared Owls. Bosakowski et al. (1989a) theorized that Long-eared Owls in New Jersey were probably rare breeders prior to European settlement. After the clearing of forests in the 18th and 19th centuries, Long-eared Owl populations increased and expanded in range. When forests were reestablished in the 20th century, Long-eared Owl numbers declined (Bosakowski et al. 1989b). In Minnesota, no explanation for the apparent decline has been given.

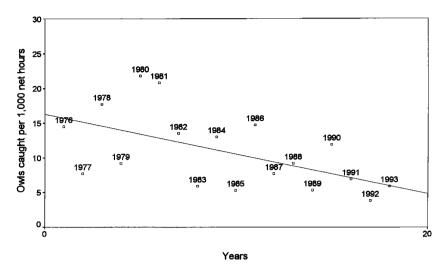


Figure 3. Long-eared Owls caught per 1000 net hours in the fall at Duluth, Minnesota (D. L. Evans, in Marks et al. 1994). Regression line indicates a downward trend (Y = 16.25 - 0.59x).

Many studies, however, indicate that exotic and domestic conifer plantations, wind-rows and shelterbelts planted near or within open areas provide additional nesting and winter roosting habitats that are beneficial to Long-eared Owls.

HOW WOULD LONG-EARED OWLS BE AFFECTED BY SIZE, SHAPE, AND RESIDUALS OF FOREST CUTS?

This is unknown, but a few studies have data which may be relevant. Craig et al. (1988) reported

that two pairs of radio-tagged Long-eared Owls in Idaho avoided scattered areas of juniper (Juniperus spp.) trees within open sagebrush shrubsteppe habitats. The owls generally foraged 1–3 km from their nests, with males using about 240–325 ha and females using about 235–425 ha during nightly forays. Also in southwestern Idaho, Hilliard et al. (1982) reported that one radio-tagged Long-eared Owl (sex unknown) foraged over 70 ha during three consecutive nights in winter, and a second

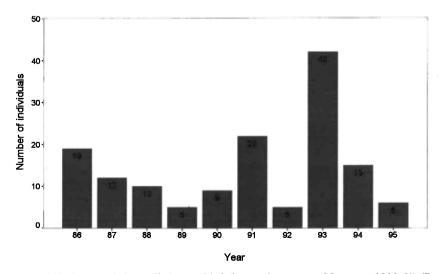


Figure 4. Long-eared Owls recorded on Christmas Bird Counts in western Montana, 1986-95 (D. Holt unpubl. data).

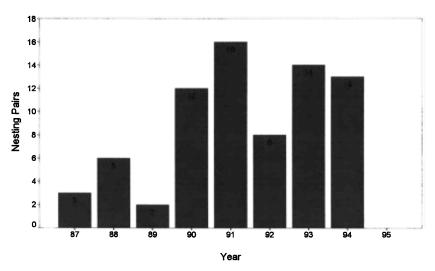


Figure 5. Breeding pairs of Long-eared Owls observed in western Montana, 1987–95 (D. Holt unpubl. data). There were no nests found in 1995.

Long-eared Owl (male) foraged over 190–220 ha each night for five nights in spring. Ulmschneider (1990) reported that seven of 13 radio-tagged Long-eared Owls traveled 73–97 km, and one owl moved 125 km from a shrubsteppe sagebrush breeding area to forested mountains. All the owls were at first in open country and heavily logged areas, four later moved into forest habitat with small openings where three stayed within 1 km of an active logging site and the fourth stayed near a 1-yr-old clear-cut. The three owls near the active logging site stayed for several weeks. She felt the owls had chosen the active logging sites and recently logged sites over older ones.

In Montana, Long-eared Owls nesting in steep mountain hillsides of second growth Douglas-fir (*Pseudotsuga menziesii*) forests and mixed ponderosa pine (*Pinus ponderosa*) forests adjacent to open lands foraged at dusk in nearby clear-cuts and grasslands, respectively (Holt and Hillis 1987). These observations suggest that certain logging practices may benefit Long-eared Owls.

IS THE LONG-EARED OWL A FOREST SPECIES?

I reviewed studies from across North America and tried to address information on habitat associations, diets and ecomorphology of Long-eared Owls. I separated diet into breeding and nonbreeding seasons. Habitat was separated into grassland, edge and forest. For ecomorphology (the relationship between an animal's ecology and morphology), I found only two studies pertaining to Longeared Owls (Poole 1938, Mueller 1986), but then incorporated that into literature directly related to ecomorphology of birds in general and owls in particular.

Habitat Associations. Of 20 studies providing breeding habitat information, only three (Craighead and Craighead 1956, Bull et al. 1989, Bloom 1994) reported that the Long-eared Owl was associated with forest habitat and only Bull et al. (1989) defined the breeding habitat as extensive forest. Four other studies (Wilson 1938, Armstrong 1958, Reynolds 1970, Enriquez-Rocha et al. 1993) described Long-eared Owls as associated with forest or edge, while the remaining 13 studies reported Long-eared Owls to be associated with open habitats (Table 2). Seventeen breeding season studies were conducted in the western Great Plains, Great Basin, Rocky Mountains, West Coast and Mexico; six of these were from Idaho. In general, these studies suggest that Long-eared Owls primarily breed in open spaces (but see Peck and James 1983, in Johnsgard 1988). Other good anecdotal information refers to Long-eared Owls heard calling from extensive forest stands (Hayward and Garton 1988).

Of 22 studies providing nonbreeding season information, 15 reported that edge habitats were occupied and five reported open habitats occupied (Birkenholz 1958, Bosakowski 1984, Marti et al.

Table 2. Breeding and non-breeding season habitat associations for Long-eared Owls in North America.

Навітат	LOCATION	Source		
BREEDING SEASON				
Forest	Michigan	Wilson (1938)		
Total	Michigan	Craighead and Craighead (1956)		
	Michigan	Armstrong (1958)		
	Oregon	Reynolds (1970)		
	Oregon	Bull et al. (1989)		
	Mexico	Enriquez-Rocha et al. (1993)		
	California	Bloom (1994)		
Edge	Michigan	Wilson (1938)		
	Michigan	Armstrong (1958)		
	Oregon	Reynolds (1970)		
	Mexico	Enriquez-Rocha et al. (1993)		
Open	Nevada	Johnson (1954)		
open.	Arizona	Stophlet (1959)		
	Colorado	Marti (1969)		
	Washington	Knight and Erickson (1977)		
	Idaho	Craig and Trost (1979)		
	Idaho	Marks and Yensen (1980)		
	South Dakota	Paulson and Sieg (1984)		
	Idaho	Thurow and White (1984)		
	Idaho	Marks (1986)		
	Idaho	Craig et al. (1988)		
	Idaho	Ulmschneider (1990)		
	Manitoba, Canada	Sullivan (1992)		
	Montana	Holt (unpubl. data)		
MON DREEDING SEAS		Tion (any and and)		
ON-BREEDING SEAS		(1050)		
Forest	Michigan	Armstrong (1958)		
T 1	Mexico	Enriquez-Rocha et al. (1993)		
Edge	Illinois	Cahn and Kemp (1930)		
	Wisconsin	Errington (1932)		
	Michigan	Spiker (1933)		
	Ohio	Randle and Austing (1952)		
	Kansas	Rainey and Robinson (1954)		
	Michigan	Craighead and Craighead (1956)		
	Michigan	Stapp (1956)		
	Michigan	Getz (1961)		
	Iowa	Weller and Fredrickson (1963)		
	New York	Lindberg (1978)		
	Iowa	Voight and Glenn-Lewin (1978)		
	Pennsylvania	Smith (1981)		
	Massachusetts	Andrews (1982)		
	Massachusetts	Holt and Childs (1991)		
	Connecticut	Smith and Devine (1993)		
	Mexico	Enriquez-Rocha et al. (1993)		
Open	Illinois	Birkenholz (1958)		
	New Jersey	Bosakowski (1984)		
	New Mexico	Marti et al. (1986)		
	Washington	Denny (1991)		
	Montana	Holt (unpubl. data)		



Figure 6. Geographic distribution of breeding (●) and non-breeding (◆) season studies in North America.

1986, Denny 1991). One each reported forest (Armstrong 1958) or forest and edge (Enriquez-Rocha et al. 1993) (Table 2). In contrast to the western breeding studies, 18 nonbreeding studies were conducted in the midwest and northeast, except for four: one in New Mexico (Marti et al. 1986), Washington (Denny 1991), Montana (D. Holt unpubl. data) and Mexico (Enriquez-Rocha et al. 1993). The geographic distribution of these studies (Fig. 6) is almost nonoverlapping.

Diet. Of 21 nonbreeding season studies representing 45 671 prey, 17 studies reported a Microtus vole to dominate the long-ear diet. These voles are open country inhabitants (Table 3). The remaining prey species also inhabit open country. Results were similar for the breeding season but with slight differences in prey composition. Of 14 studies representing 13858 prey, all except Bull et al. (1989) reported an open country prey species (Table 4). Bull et al. (1989) reported that Long-eared Owls nested in extensive stands of Grand Fir (Abies grandis) and that the prey species comprising the majority of the diet was the northern pocket gopher (Thomomys talpoides). This species is primarily an open country inhabitant, but also occurs within openings in closed canopy forests and may move into recent clear-cuts (Ingles 1967).

These data are further supported by Marti's (1976) extensive review of the feeding ecology of

Long-eared Owls. He included data from North America, several European countries and Iraq. He concluded that Long-eared Owls feed on small rodents found in open country with *Microtus* voles eaten most frequently, followed by *Peromyscus* mice and Heteromyid rodents.

Ecomorphology. I reviewed the literature to determine if the Long-eared Owl's morphology was consistent with adaptive radiation for particular habitats. Bird groups in general have similar flight morphology, as do birds living in similar habitats. For example, open country bird species like the Long-eared Owl and Snowy Owl (Nyctea scandiaca) have more pointed wings for better agility than forests owls. Forest owls such as the Great Gray Owl (Strix nebulosa) and Boreal Owl (Aegolius funereus) which live in dense vegetation, have short broad wings and a large wing area which aid in maneuverability (see Rayner 1988).

Owls generally exhibit low wing loading and low aspect ratio and are among birds with the lowest wing loading (Norberg 1987). Relative wing loading is defined as the owls' body mass divided by the wing area or; Mg/S (mass M multiplied by the acceleration of gravity g, divided by wing area S), and aspect ratio is defined as wingspan divided by mean chord length, or b^2/S (wingspan b squared, divided by wing area S, or wingspan divided by mean wing chord) (Norberg and Norberg 1986).

Table 3. Non-breeding season diet of Long-eared Owls in North America.

Навітат	DOMINANT GROUP	N	LOCATION	Source
Edge	Peromyscus	1198	Illinois	Cahn and Kemp (1930)
	Microtus	210	Iowa	Errington (1933)
	Microtus	1261	Ohio	Randle and Austing (1952)
	Peromyscus	249	Indiana	George (1954)
	Microtus/Sigmodon	1087	Kansas	Rainey and Robinson (1954)
	Microtus	952	Wisconsin	Craighead and Craighead (1956)
	Microtus	1000	Michigan	Stapp (1956)
	Microtus	2995	Michigan	Armstrong (1958)
	Microtus	2328	Illinois	Birkenholz (1958)
	Microtus	126	Iowa	Weller and Fredrickson (1963)
	Microtus	301	New York	Lindberg (1978)
	Microtus	2112	Iowa	Voight and Glenn-Lewin (1978)
	Microtus	915	Massachusetts	Holt and Childs (1991)
Open	Microtus	3272	Wisconsin	Errington (1932)
	Microtus	199	Michigan	Spiker (1933)
	Perognathus	2821	New Mexico	Marti et al. (1986)
	Microtus	18956	Montana	Holt (unpubl. data)
Unknown	Microtus	108	Iowa	Scott (1948)
	Microtus	1494	Pennsylvania	in Latham (1950)
	Microtus	2495	Nebraska	in Latham (1950)
	Microtus	1622	Pennsylvania	Smith (1984)

Among owls, forest species tend to have much lower aspect ratios than open country species (Norberg 1987), because foraging within vegetation is favored by those species with short wings, large wing area and low wing loading. This enables these species to have slow, maneuverable flight (Norberg 1987). Contrasting this are open country migratory species such as the Long-eared Owl, Snowy Owl and Short-eared Owl (Asio flammeus) which have

long wings for sustained flight, yet have relatively low wing loading (Norberg 1990).

CONCLUSION

Is the Long-eared Owl a forest species? These data suggest that the Long-eared Owl may not be a forest species; however, more forest studies are needed. Long-eared Owls obviously depend on trees and shrubs for nesting and roosting. In large

Table 4. Breeding season diet of Long-eared Owls in North America.

Навітат	DOMINANT GROUP	N	LOCATION	Source
Forest	Thomomys	1123	Oregon	Bull et al. (1989)
Edge	Microtus	1935	Michigan	Wilson (1938)
	Microtus	274	Michigan	Armstrong (1958)
	Microtus	153	Oregon	Reynolds (1970)
Open	Microtus	114	Nevada	Johnson (1954)
	Microtus	129	Wyoming	Craighead and Craighead (1956)
	Perognathus	315	Arizona	Stophlet (1959)
	Peromyscus	993	Colorado	Marti (1969)
	Perognathus	171	Washington	Knight and Erickson (1977)
	Peromyscus	346	Idaho	Marks and Yensen (1980)
	Peromyscus/Dipodomys	4208	Idaho	Marks (1984)
	Peromyscus	1000	Idaho	Thurow and White (1984)
	Perognathus/Peromyscus	3977	Idaho	Craig et al. (1985)
	Microtus	3020	Montana	Holt (unpubl. data)

open grasslands or shrubsteppe habitat, Longeared Owls nest and roost in predominately shrublike vegetation. In smaller openings in forests and along forest edges adjacent to open areas, Longeared Owls use trees (often conifers) to nest and roost. Data from this review emphasize that perhaps too much forest may cause Long-eared Owls to leave an area (Bosakowski et al. 1989b), while patches of open areas within or near forest edges may benefit them. Unfortunately, forest age and stand structure requirements are not known for this species. Thus, the impacts of forest management cannot be ascertained at this time. Additionally, forest managers may need to define what a forest owl species is. Perhaps the Long-eared Owl can best be defined as an edge species, when found in or near forest habitats. It may be presumptuous at this point in time to suggest forest-management guidelines regarding the Long-eared Owl, particularly since no conclusive data exist pertaining to effects of present or past forestry practices.

Given the recent interest of metapopulation analysis (Levins 1969), which includes the core-satellite (Boorman and Levitt 1973) and sink and source (Pulliam 1988) models, forest-management considerations must include results of long-term studies from several geographic areas. Within these studies, comparative data of the Long-eared Owl natural history is essential for these models to be useful. Specifically, the following data are needed: Long-eared Owl residency, mating system, reproductive success and home ranges; Long-eared Owl prey species populations, how these effect owl residency, density and home range and how prey species are affected by forest practices; quantitative measures of nest sites; vegetative cover for adult and nestling owl roosting areas; and seasonal use of habitats because different habitats may be important at particular times of the year and avoided at other times.

Therefore, forestry practices may have to be staggered over space and time and perhaps from a few to hundreds of kilometers of habitats must be managed simultaneously or alternately to cover the Long-eared Owls' migratory or nomadic tendencies. The use of artificial nest sites as a management tool must be carefully considered before implementation—what is the biological justification for their use? Consideration of how forestry practices affect the interspecific relationships between Long-eared Owls and invader species must also be taken into account.

To adequately address the questions concerning impacts of forestry, research needs to cover longer periods of time and must also research the species year-round. Although many short-term studies provide useful information, they simply cannot provide enough data to answer questions such as those addressed herein. Given that Long-eared Owls are migratory and nomadic, and often dependent on small mammal cycles three to four yr long (e.g., voles), studies should at the least cover this duration, and preferably several cycles.

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LITERATURE CITED

Andrews, J.W. 1982. A winter roost of Long-eared Owls. Bird Observ. East. Mass. 10:13–22.

ARMSTRONG, W.H. 1958. Nesting and food habits of the Long-eared Owl in Michigan. *Mich. State Univ. Mus. Biol. Ser.* 1:63–96.

BIRKENHOLZ, D. 1958. Notes on a wintering flock of Long-eared Owls. *Ill. Acad. Sci. Trans.* 51:83–86.

BLOOM, P.H. 1994. The biology and current status of the Long-eared Owl in coastal southern California. *Bull. South. Calif. Acad. Sci.* 93:1–12.

BOORMAN, S.A. AND P.R. LEVITT. 1973. Group selection on the boundary of a stable population. *Theor. Popul. Biol.* 4:85–128.

BOSAKOWSKI, T. 1984. Roost selection and behavior of the Long-eared Owl (Asio otus) wintering in New Jersey. Raptor Res. 18:137–142.

——, R. KANE AND D.G. SMITH. 1989a. Decline of the Long-eared Owl in New Jersey. Wilson Bull. 101:481– 485.

——, R. KANE AND D.G. SMITH. 1989b. Status and management of Long-eared Owls in New Jersey. Rec. New Jersey Birds 15:42–46.

BULL, E.L., A.L. WRIGHT AND M.G. HENJUM. 1989. Nesting and diet of Long-eared Owls in conifer forests, Oregon. *Condor* 91:908–912.

Cahn, A.R. and J.T. Kemp. 1930. On the food of certain owls in east-central Illinois. *Auk* 47:323–328.

CRAIG, T.H. AND C.H. TROST. 1979. The biology and nesting density of breeding American Kestrels and Longeared Owls on Big Lost River, southeastern Idaho. Wilson Bull. 91:50–61.

Craig, E.H., T.H. Craig and L.R. Powers. 1985. Food habits of Long-eared Owls (*Asio otus*) at a communal roost site during the nesting season. *Auk* 102:193–195.

— 1988. Activity patterns and home range use of nesting Long-eared Owls. Wilson Bull. 100:204–213.

- CRAIGHEAD, J.J. AND F.C. CRAIGHEAD. 1956. Hawks, owls and wildlife. Stackpole Co., Harrisburg, PA U.S.A.
- CRAMP, S. [Ed.]. 1985. The birds of the western Palearctic, Vol. 4. Oxford Univ. Press, Oxford, U.K.
- Denny, M. 1991. Communal roosting of Long-eared Owls. *Birding* 23:310.
- Errington, P.L. 1932. Food habits of southern Wisconsin raptors: Part I. Owls. *Condor* 34:176–186.
- ENRIQUEZ-ROCHA, P., J. LUIS RANGEL-SALAZAR AND D.W. HOLT. 1993. Presence and distribution of Mexican owls: a review. *J. Raptor Res.* 27:154–160.
- Fyfe, R.W. 1976. Status of Canadian raptor populations. *Can. Field-Nat.* 90:370–375.
- GEORGE, E.F. 1954. A report on the analysis of one hundred thirty-two pellets of the Long-eared Owl (Asio wilsonianus). Indiana Acad. Sci. 64:257–258.
- GETZ, L.L. 1961. Hunting areas of the Long-eared Owl. Wilson Bull. 73:79–82.
- HAYWARD, G.D. AND E.O. GARTON. 1988. Resource partitioning among forest owls in the River of No Return Wilderness, Idaho. *Oecologia* 75:253–265.
- HILLIARD, B.L., J.C. SMITH, M.J. SMITH AND L.R. POWERS. 1982. Nocturnal activity of Long-eared Owls in southwest Idaho. J. Idaho Acad. Sci. 18:29–35.
- HOLT, D.W. AND J.M. HILLIS. 1987. Current status and habitat associations of forest owls in western Montana. Pages 281–288 in R.W. Nero, R.J. Clark, R.J. Knapton and R.H. Hamre [Eds.], Biology and conservation of northern forest owls. USDA For. Ser. Gen. Tech. Rep. RM-142, Ft. Collins, CO U.S.A.
- HOLT, D.W. AND N.N. CHILDS. 1991. Non-breeding season diet of Long-eared Owls in Massachusetts. J. Raptor Res. 25:23–24.
- INGLES, L.G. 1967. Mammals of the Pacific states. Stanford Univ. Press, Stanford, CA U.S.A.
- JOHNSGARD, P.A. 1988. North American owls: biology and natural history. Smithsonian Institute Press, Washington, DC U.S.A.
- JOHNSON, N.K. 1954. Food of the Long-eared Owl in southern Washoe County, Nevada. Condor 56:52.
- KIRK, D.A., D. HUSSELL AND E. DUNN. 1994. Raptor population status and trends in Canada. Bird Trends: A report on results of national and regional ornithological surveys in Canada. 4:2–9.
- KNIGHT, R.L. AND A.W. ERICKSON. 1977. Ecological notes on Long-eared and Great Horned owls along the Columbia River. *Murrelet* 58:2–6.
- LATHAM, R.M. 1950. The food of predaceous animals in northeastern United States. Penn. Game Comm. Rep. 1.
- LEVINS, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15:237–240.
- LINDBERG, A.J. 1978. Overwintering and nesting of the

- Long-eared Owl at Muttontown Park and Preserve, East Norwich, Long Island. *Kingbird* 28:77–83.
- MARKS, J.S. AND E. YENSEN. 1980. Nest sites and food habits of Long-eared Owls in southwestern Idaho Murrelet 61:86–91.
- . 1984. Feeding ecology of breeding Long-eared Owls in southwestern Idaho. Can. J. Zool. 62:1528– 1533.
- . 1986. Nest-site characteristics and reproductive success of Long-eared Owls in southwestern Idaho. Wilson Bull. 98:547–560.
- MARKS, J.S., D.L. EVANS AND D.W. HOLT. 1994. Longeared Owl (*Asio otus*). Pages 1–24 in A. Poole and F.B. Gill [EDS.], The birds of North America, Acad. of Nat. Sci., Philadelphia, PA and Am. Ornithol. Union, Washington, DC U.S.A.
- MARTI, C.D. 1969. Some comparisons of the feeding ecology of four species of owls in north-central Colorado. Southwest. Nat. 14:163–170.
- ——. 1976. A review of prey selection by the Longeared Owl. Condor 78:331–336.
- —, J.S. Marks, T.H. Craig and E.H. Craig. 1986 Long-eared Owl diet in northwestern New Mexico. Southwest. Nat. 31:416–419.
- AND J.S. MARKS. 1989. Medium-sized owls. Pages 124–133 *in* B.G. Pendleton [Ed.], Proc. Western Raptor Manage. Symp. Workshop. Natl. Wildl. Fed. Sci Tech. Ser. No. 12, Washington DC U.S.A.
- MELVIN, S.M., D.G. SMITH, D.W. HOLT AND G.R. TATE. 1989. Small owls. Pages 88–96 in B.G. Pendleton [ED.] Proc. Northeast Raptor Manage. Symp. Workshop. Natl. Wildl. Fed. Sci. Tech. Ser. No. 12, Washington, DC U.S.A.
- MIKKOLA, H. 1983. Owls of Europe. Buteo Books, Vermillion, SD U.S.A.
- MUELLER, H.C. 1986. The evolution of reversed sexual dimorphism in owls: an empirical analysis of possible selective factors. Wilson Bull. 98:387–406.
- NORBERG, U.M. AND R.A. NORBERG. 1986. Ecology of flight and tree-trunk climbing in birds. Proc. 19th Inter. Ornith. Congress, Ottawa, Canada 19:2271–2291.
- NORBERG, R.A. 1987. Evolution, structure, and ecology of northern forest owls. Pages 9–43 in R.W. Nero, R.J. Clark, R.J. Knapton and R.H. Hamre [EDs.], Biology and conservation of northern forest owls. USDA For Serv. Gen. Tech. Rep. RM-142, Ft. Collins, CO U.S.A.
- NORBERG, U.M. 1990. Vertebrate flight: mechanics, physiology, morphology, ecology, evolution. Zoophysiology 27:1–291.
- PAULSON, D.D. AND C.H. SIEG. 1984. Long-eared Owls nesting in Badlands National Park. S. D. Birds 36: 72–75.
- PETERSEN, L.R. 1991. Mixed woodland owls. Pages 85–95 in B.G. Pendleton and D.L. Krahe [EDS.], Proc. Midwest Raptor Manage. Symp. Natl. Wildl. Fed. Sci. Tech. Ser. No. 15, Washington, DC U.S.A.

- POOLE, E.L. 1938. Weights and wing areas in North American birds. Auk 55:511-517.
- Pulliam, H.R. 1988. Sources, sinks and population regulation. *Am. Nat.* 132:652–661.
- RAINEY, D.G. AND T.S. ROBINSON. 1954. Food of the Long-eared Owl in Douglas County, Kansas. *Trans. Kans. Acad. Sci.* 57:206–207.
- RANDLE, W. AND D.R. AUSTING. 1952. Ecological notes on Long-eared and Saw-whet Owls in southwestern Ohio. *Ecology* 33:422–426.
- RAYNER, J.M.J. 1988. Form and function in avian flight. Pages 1–66 *in* R.F. Johnston [Ed.], Current ornithology, Vol. 5. Plenum Press, New York, NY U.S.A.
- REYNOLDS, R.T. 1970. Nest observations of the Longeared Owl (*Asio otus*) in Benton County, Oregon, with notes on their food habits. *Murrelet* 51:8–9.
- ROOT, T.L. 1988. Atlas of wintering North American birds: an analysis of Christmas bird count data. Univ. Chicago Press, Chicago, IL U.S.A.
- Scott, T.G. 1948. Long-eared Owls and red foxes. *Auk* 65:447–448.
- SMITH, D.G. 1981. Winter roost site fidelity by Longeared Owls in central Pennsylvania. *Am. Birds.* 35:339.
- ——. 1984. Winter food of the Long-eared Owl in central Pennsylvania. *Cassinia* 61:38–41.
- —— AND A. DEVINE. 1993. Winter ecology of the Long-eared Owl in Connecticut. *Conn. Warbler* 13:44–53
- SPIKER, C.J. 1933. Analysis of two hundred Long-eared Owl pellets. Wilson Bull. 45:198.

- STAPP, W.B. 1956. Food habits of Long-eared Owls. Audubon Mag. 58:218–220.
- STOPHLET, J.J. 1959. Nesting concentration of Longeared Owls in Cochise County, Arizona. Wilson Bull. 71:97–99.
- SULLIVAN, B.D. 1992. Long-eared Owls usurp newly constructed American Crow nests. J. Raptor Res. 26:97–98.
- Thurow, T.L. AND C.M. White. 1984. Nesting success and prey selection of Long-eared Owls along a juniper sagebrush ecotone in southcentral Idaho. *Murrelet* 65: 10–14.
- ULMSCHNEIDER, H. 1990. Post-nesting ecology of the Long-eared Owl (*Asio otus*) in southwestern Idaho. M.S. thesis, Boise State Univ., Boise, ID U.S.A.
- VOIGHT, J. AND D.C. GLENN-LEWIN. 1978. Prey availability and prey taken by Long-eared Owls in Iowa. Am. Mid. Nat. 99:162–170.
- Weller, M.W. and L.H. Fredrickson. 1963. Small mammal prey of some owls wintering in Iowa. *Iowa State J. Sci.* 38:151–160.
- WILSON, K.A. 1938. Owl studies at Ann Arbor, Michigan. Auk 55:187–197.
- White, C.M. 1994. Population trends and current status of selected western raptors. Pages 161–172 in J.R. Jehl and N.K. Johnson [Eds.], A century of avifaunal change in western North America. Studies in Avian Biol. 15.

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