Chapter 4

Review of Technical Knowledge: Flammulated Owls

D. Archibald McCallum, Department of Biology, College of Charleston, Charleston, SC 29424

INTRODUCTION

The flammulated owl (*Otus flammeolus*) is a tiny, common predator on invertebrates that nests in cavities in western North American coniferous forests. It was thought by early workers to be rare (Bendire 1892, Bent 1938), but more recent opinion is that it is common but secretive (Marshall 1967, Winter 1971, 1974, Richmond *et al.* 1980). The combination of its very small size (Earhart and Johnson 1970), ventriloquial but low-pitched voice (Miller 1947), strictly invertebrate diet (Ross 1969, but see below), and probable migratory behavior (Winter 1974, Balda *et al.* 1975, but see Johnson 1963) suggests an unusual adaptive strategy. Understanding all aspects of this strategy will lead to wise management decisions.

The flammulated owl is the next-to-smallest North American owl (15-17 cm long, 45-63 g mass in nonbreeding season) and among the smallest of its large and cosmopolitan genus. Females are slightly larger than males, but there are no sexual, age, or seasonal differences in adult plumage. Body plumage is gray with black shaft streaks and crossbars and varying degrees of rufescent wash. Flight feathers and wing coverts are gray to brown with lighter bands. Reddish birds are rare in North America.

Dark eyes distinguish it from all other owls of similar size in its North American range. Additionally, size and short ear tufts distinguish it from other American *Otus*. In the field, it is much more often heard than seen. Low-pitched, faint, hoarse, and ventriloquial mono- or disyllabic hoots throughout the breeding season rule out all other forest owls except the long-eared owl (*Asio otus*). If seen, the flammulated owl is easily identified by the unique combination of small size and dark eyes.

Despite its seeming abundance, the flammulated owl does not have a high reproductive rate. As it apparently is restricted to forests of commercially valuable tree species, timber management practices may influence its viability. Baseline population data are sparse and insufficient to model its population dynamics. In addition, virtually nothing is known about its range, habitat, or diet in winter.

Knowledge of the flammulated owl is based on a broad but rather shallow literature. Most publications are anecdotal. Four population studies, begun since 1980, form the foundation of our knowledge. By far the most important of these was begun at Manitou Experimental Forest, west of Colorado Springs, Colorado, in 1981 (Linkhart and Reynolds 1987; Reynolds and Linkhart 1987a,b, 1990a,b, 1992). This study, which has continued through the present, has documented all aspects of the population biology of the species, including movements (Linkhart and Reynolds 1987; Reynolds and Linkhart 1987a, 1990a), breeding biology and food habits (Reynolds and Linkhart 1987b), home range use (Linkhart 1984), pair relations (Reynolds and Linkhart 1990a), longevity (Reynolds and Linkhart 1990b), habitat use (Reynolds and Linkhart 1992), and study techniques (Reynolds and Linkhart 1984, Reynolds 1987).

The only other study that has exceeded 2 years was conducted in the Zuni Mountains of western New Mexico from 1981-1986. The emphasis of this study was breeding biology and habitat use (McCallum and Gehlbach 1988, McCallum *et al.* in review). It was the only one of the major studies not to employ radio-tracking. Radio-tracking studies that focused on habitat use but that also produced some information on breeding biology were conducted in the Blue Mountains of northeastern Oregon from 1983 to 1984 (Goggans 1986) and on Mt. Wheeler near Kamloops, British Columbia, from 1989-1991 (van Woudenberg 1992). The Oregon study was conducted in the Starkey Experimental Forest, site of two shorter-term studies (Bull and Anderson 1978, Bull *et al.* 1990).

SYSTEMATICS

Phylogenetic Position

The genus *Otus* is unanimously classified in the Strigidae (typical owls), which, along with the Tytonidae (barn owls), constitute the order Strigiformes. Most authorities consider another group of night birds, the Caprimulgiformes (nightjars and allies), to be the sister taxon of the Strigiformes. (The taxonomic history of these groups is summarized by Sibley and Ahlquist 1990:402-411.) Sibley and Ahlquist's (1990) classification, based on DNA-DNA hybridization, supports the conventional linkage of these two orders. Cracraft's (1981) resurrection of the 19th-century idea that owls and the Falconiformes are closely related has not been widely accepted. Most authorities apparently prefer convergent evolution as an explanation for the similarities in the raptorial lifestyles of "hawks" and owls.

The position of *Otus* within the Strigidae is of interest because of the possibility that *O. flammeolus* is a primitive member of its large and well-defined genus. Sibley and Ahlquist (1990:figure 362), using DNA-DNA hybridization, united *Otus*, *Asio* (including long-eared (*A. otus*) and short-eared (*A. flammeus*) owls), and a large group including *Bubo* and *Strix* in an unresolved trichotomy. Randi *et al.* (1991), using allozymes, consistently found *Otus* to be more closely related to *Bubo* than to *Asio*. The earliest fossil of *Otus* is from the Miocene (Johnsgard 1988).

Species Status

The most recent treatment of *Otus* (Marshall and King 1988) places more emphasis on vocalizations than morphology and none on molecules. Although the emphasis on vocalizations is plausible (Marshall 1967), some vocal similarities, like similarities in plumage, could be the result of convergent evolution. The systematics of the genus *Otus* has not been subjected to biochemically based analysis.

The position of *O. flammeolus* within *Otus* has been the subject of much debate in the systematic literature. The species was first mentioned in 1854 by Lichtenstein (Ridgway 1914) and described in more detail in 1859 by J. J. Kaup, from two specimens obtained in Mexico. It remained rare in collections for decades, but its specific identity was not challenged until Delacour (1941) merged it with the widespread Old World *Otus scops* complex. He based this decision on the sharing of finely patterned plumage, presumed migratory behavior of northern populations, and voice (Voous 1989). This decision has not met with widespread acceptance and might be considered a symptom of the Holarctic overlumping that gripped avian taxonomy at mid-century. Other authors (Marshall 1966, 1967, 1978; van der Weyden 1975, Hekstra 1982) have agreed that *Otus flammeolus* is more closely related to the Old World scops owl subgenus than to the New World screech-owl subgenus. In particular, it is vocally allied to all but one Old World species, which have high-pitched slow songs (< 3 notes per sec) that contain 1-4 notes. Like them, it has no secondary song, and females do not duet with their mates. The other New World species, all of which are considered screech owls, have lower-pitched rapid songs (>3 notes per sec) that contain > 4 (often considerably more) notes; they do have secondary songs and females duet (van der Weyden 1975).

The position of *O. flammeolus* in the subgenus *Otus* (scops owls) has recently been revised. According to Marshall and King (1988), the closest relative of the flammulated owl is the pallid scops owl (*O. brucei*), a migratory species that breeds from the Middle East to Pakistan. They base this position on the similarly low and unaccented hoots of *O. brucei* (Roberts and King 1986). The *Otus scops* superspecies (*O. scops*, *O. senegalensis*, and *O. sunia*) is more similar morphologically than *O. brucei* to *O. flammeolus*, but "the normal song of *Otus scops* is a high-pitched staccato whose chirping quality runs identically through the differently timed songs of its far-flung races.... It is inconceivable that a female of *scops* would recognize the singing male *flammeolus* as a potential mate and vice versa. They cannot be in the same species" (Marshall 1966:240).

The male hoots of the flammulated owl are the second lowest in frequency of 37, mostly larger-bodied, species of *Otus* examined by van der Weyden (1975). Indeed, this note is barely higher than the equivalent vocalization of the much larger long-eared owl (McCallum, pers. obs.). Miller (1947) explained that an unusually large tracheal diameter and thick, loosely attached vibratile membranes make it possible for this small owl to produce such a low frequency sound.

The voice and the structure responsible for it obviously constitute an autapomorphy. The possible function of this distinctive and often-discussed derived character has not been ascertained. The flammulated owl throughout its range lives near one or more species of *Bubo*, *Strix*, and *Asio*, all effective nocturnal predators. Voous (1989:53) "is tempted to suppose that, in order to survive, the flammulated owl simulates greater size and strength by its bravado and ventriloquial voice, at the same time behaving elusively and inconspicuously by night and day." The mechanism by which such vocal mimicry might benefit a prey species has not, however, been proposed.

Subspecies and Geographic Variation

Of the two "Mexican" specimens examined by Kaup in 1859, one type was grayish, the other rufous (Phillips 1942). It was understandable at the time to assume that they represented the usual gray and red phases found in other species of *Otus*, rather than representing regional variation. For the next 80 years museum workers assumed the flammulated owl was a permanent resident throughout its range, presumably by extension from other (mostly larger) owl species. Phillips (1942) corrected this impression by showing that verified dates of occurrence north of Mexico fell between April 11 and October 31. He also surmised that the type was a migrant from the northern part of the range, rather than a resident of southern Mexico, where most of the birds are more rufous in color. With the breeding range of the type unknown, the name *O. f. flammeolus* could not be applied to a known population, which in the opinion of one authority, "precludes the objective use of subspecific names" (Voous 1989:54).

Nevertheless, up to six subspecies have been described, often on the basis of limited samples. *O. f. rarus* Griscom was based on two large reddish birds from Guatemala (Phillips 1942), while *O. f. idahoensis* (Merriam) was based on a short-winged bird from the northern United States. Breeding of the species has not been demonstrated in Guatemala, so *rarus* is thought to be a migrant, perhaps from southern Mexico (Phillips 1942), perhaps from the interior Pacific Northwest, which caused Marshall (1978:9) to consider it synonymous with *idahoensis*. But Hekstra (1982) retained both *rarus* and *idahoensis* and described another Guatemalan subspecies, *meridionalis*, said to be "smaller and glossier than *rarus*" (Hekstra 1982:56), as well as another northern subspecies, *borealis*, said to be duller than *rarus* and *idahoensis*. Finally, Hekstra (1982) described *frontalis* from the Front Range of Colorado as browner than *flammeolus*, with very black shaft streaks. These subspecies were not based on new data but on reinterpretation of old specimens.

Differences in coloration of the kind used by Hekstra to erect subspecies are said by Marshall (1967) to vary in parallel among sympatric species of *Otus* and thus have no taxonomic value. He therefore recognizes no subspecies of *O. flammeolus*. Marshall (1967) speculated that the color and patterning in an area match tree trunks and foliage found there. For example, the redder birds found in Middle America were said to blend with red-barked trees found there. Moreover, variation due to differential fading, dependent upon local climate and the amount of exposure to sunlight on day roosts, plus postmortem fading of skins, has produced taxonomic confusion in all *Otus* (Marshall 1967:5). And, individual plumage variation is continuous rather than dimorphic in the flammulated owl, hence greater than in other *Otus*, which are thought to have two distinct color phases, with "red" caused by a dominant autosomal allele (Marshall 1967:1). The source of Marshall's statement, however, is not given. Hrubant (1955) showed that for the eastern screech-owl three phenotypic phases could be explained by a single-locus, 3-allele model with graded dominance. The apparently continuous phenotypic variation in *O. flammeolus* suggests polygenic control of plumage variation or at least a multi-allele, incomplete dominance hypothesis such as Hrubant's. Neither hypothesized mode of gene action has been the subject of formal genetic analysis for the flammulated owl.

On the basis of 32 fall (i.e., fresh-plumaged) birds thought to be on their breeding grounds, Marshall described a smooth cline of increasing wing-length and mass from southeast to northwest, presumably correlated with the length of the migratory route (Marshall 1967:24). Great Basin-Rocky Mountain birds are blackest, with broadest shaft streaks and least red trimming. Patterning becomes finer and redness increases to the northwest (the extreme for fineness is in the Pacific Northwest) and southeast (the extreme for redness is on the Mexican Plateau, Marshall 1967:24).

Fossil History

Modern *Otus flammeolus* remains have been recovered from the Pleistocene San Josecito Cave, Aramberri, Nuevo León (with *O. asio* (*sensu lato*) and *O. trichopsis*); from the late Pleistocene Samwel Cave, Shasta County, California (no other *Otus*) (Wetmore 1956). The earliest fossil of *Otus* is from the Miocene (Johnsgard 1988)(see Voous 1989).

DISTRIBUTION AND ABUNDANCE

Recognized Distribution

The flammulated owl is known to occur from southern British Columbia south and eastward to Guatemala and probably El Salvador. Its western limit is the western limit of open pine forests between the latitudinal extremes, and it ranges no closer to the Atlantic than the Rocky Mountain escarpment and the Sierra Madre Oriental. Except during the migratory period, it is with very rare exception found only in montane forests, usually open conifer forests containing pines. Its breeding range in North America is well delineated. The non-breeding range of these northern birds is not known. The year-round range in Middle America is sketchily described and open to question.

In conjunction with surveys for other owl species, and in some instances surveys targeted for flammulated owls, the USDA Forest Service has accumulated records for flammulated owls in the western United States. These data are summarized in Chapter 3 and Map 1. They confirm the widespread occurrence of the species in previously documented parts of its U. S. range, particularly California, Arizona, New Mexico, and southern Colorado. These data also show that it is widespread in west central Idaho, just east of the previously known stronghold in the Blue Mountains of Oregon. It was found in a few new locations in Utah and Montana but remains virtually undocumented on the east slope of the Cascades in Oregon and Washington, where it probably occurs. The species remains undocumented from lodgepole pine (*Pinus contorta*) forests of Wyoming, as well as from ponderosa pine forests in eastern Montana, Wyoming, and the Black Hills.

Breeding Range

North America.—Nesting has been confirmed or adults observed during the breeding season in southernmost British Columbia (Okanagan and S. Thompson Valleys, Fraser River north to Riske Creek, Rocky Mountain Trench, [Howie and Ritcey 1987, R. J. Cannings pers. comm.]), the east slope of the Cascades, and interior ranges of Washington, Oregon (e.g., Blue Mtns., Goggans 1986, Bull *et al.* 1990), northeastern California (Johnson and Russell 1962), and western Nevada. It has been found in most forested ranges of Nevada, including some lacking ponderosa pine (Herron *et al.* 1985, S. Garland, pers. comm.), but the range is poorly documented in Utah. In California (Winter 1974) it is found in summer throughout the Cascades, Sierra Nevada, forested parts of the coast ranges from Del Norte County south to Monterey County, the Transverse ranges, and the Peninsular ranges. Previous to this study (Chapter 3) it was poorly known in the northern Rocky Mountains states (Holt *et al.* 1987). There remain no records from the Black Hills, where seemingly suitable habitat occurs. The species is widespread in Colorado (Webb 1982), New Mexico (Hubbard 1978), and Arizona (Reynolds and Linkhart in press). It breeds in the Guadalupe, Davis, and Chisos Mountains of Texas (Oberholser 1974).

Middle America.—The few available records support the presumption that it breeds primarily in the Sierra Madre Occidental, Sierra Madre Oriental, Sierra Madre del Sur, and the Volcanic ranges of central Mexico. Breeding south of Mexico has not been confirmed. This owl is known in northwestern Mexico from the Sierra Madre Occidental (Sonora and Chihuahua [Stager 1954, Marshall 1957] and Sinaloa [Hubbard and Crossin 1974]). In the northeast it occurs near the Big Bend of the Rio Grande in the Sierra del Carmen (Miller 1955), in an isolated range in central Coahuila (van Hoose 1955), in the Sierra Madre Oriental of eastern Coahuila (van Hoose 1955, Ely 1962) and western Nuevo León (Hubbard and Crossin 1974), and on isolated Cerro Potosí (S. N. G. Howell pers. comm.). In central and southern Mexico breeding is thought to occur in the state of Mexico (AOU 1983), Las Vigas, Veracruz (Sutton and Burleigh 1940), and probably on Cerro San Felipe in Oaxaca, where one was heard in April (Binford 1989) and a specimen was found in June (J. C. Arvin *fide* S. N. G. Howell). Early statements that it breeds south to Guatemala were based on the assumption of residency of winter specimens (Phillips 1942).

Nonbreeding Range

In North America, it occurs in lowlands peripheral to breeding habitat in October, sparingly in November, and occasionally in December. Three midwinter specimens (from Arizona, Louisiana, and California) are the only dependable winter records. An unpreserved specimen and two sight records in Montana (Holt *et al.* 1987) are poorly documented and dubious. An aural record in New Mexico in March (Collins *et al.* 1986) by D. A. McCallum was probably a long-eared owl (based on subsequent observations and spectrographic analysis, DAM). The same is perhaps true for a January aural record in lowland riparian habitat in Arizona (Monson and Phillips 1981) and perhaps some March records (see the Migration section below).

The midwinter range in Middle America is very poorly understood. The species has not been observed in the northern tier of Mexican states during this period. There are a few specimens and aural records in breeding habitat localities farther south (Sinaloa [3-4 Dec., Hubbard and Crossin 1974], Jalisco [22 Feb., Schaldach 1969], Michoacán [Friedmann *et al.* 1950], Guerrero [Navarro 1992], Distrito Federal [Friedmann *et al.* 1950, 20 Dec., Wilson and Ceballos in press], Guatemala [AOU 1983], and El Salvador [22 Dec., Marshall 1978:9, specimen lost]). If, as suggested above, the flammulated owl breeds in Oaxaca, then these winter localities may also be breeding localities. On the other hand, Navarro (1992) found the species during winter but not during the breeding season in the Sierra de Atoyac of Guerrero. Two large, long-winged birds taken in Guatemala (see *O. f. rarus* above) are thought by Marshall (1978:9) to have been migrants from the population breeding in the Pacific Northwest.

Estimates of Local Abundance and Population Trends

Flammulated owls were considered rare until the 1960's, and quantitative baseline data on abundance are not available. Many field guides and compendia now refer to this owl as "locally common." Most authorities (e.g., Marshall 1967, Richmond *et al.* 1980, Marcot and Hill 1980) believe that because of its "secretive" habits the flammulated owl simply went undetected in much of its range until ornithologists and birders, following Marshall (1939, 1967), began imitating calls to incite vocal responses by territorial males. This procedure enabled collectors to begin an assessment of the U. S. and Middle American range in the 1950's and 1960's (Marshall 1967) but contributed little to understanding of densities [although up to 10 birds were sometimes called into one location (e.g., Johnson and Russell 1962)]. Subsequently birders contributed materially to filling in details of the distribution (e.g., Winter 1974, Collins *et al.* 1986), but less attention was paid to numbers. In the 1980's, the four population studies in Colorado, New Mexico, Oregon, and British Columbia began to produce local density estimates (see the Local Density Estimates section). Numerous surveys, many incidental to surveys for the spotted owl (*Strix occidentalis*), have been conducted in recent years (Chapter 3). These recent data suggest that flammulated owls are among the most abundant birds of prey in some areas.

Recent surveys, plus old collecting localities, can be used as a baseline for assessing subpopulation persistence on the basis of presence/absence data. Marshall (1988) revisited the site of his earlier study (1939) and found flammulated owls absent from the portion of the study area that had been logged. Marshall also failed to find the species at Sutton and Burleigh's (1940) site in Veracruz. These observations, plus Franzreb and Ohmart's (1978) finding that the owls were present in mixed conifer forest but absent from nearby logged sites, suggest that elimination and replacement of yellow pine (e.g., ponderosa or Jeffrey pine) and mixed conifer forests by Europeans have reduced the overall abundance of the flammulated owl.

Although suitable habitat probably has declined somewhat, human-caused habitat modification (vs. outright elimination) in the past century (e.g., selective logging, fire-suppression) may have caused undetected increases or decreases in numbers of flammulated owls. Which, if either, has occurred is a matter of speculation, as no historic data exist for drawing a firm conclusion. (See Response to Forest Change section for a discussion of these issues.)

Recent developments in molecular biology, however, make it possible to assess population changes within the twentieth century indirectly by comparing past and present population genetic structure. Small populations lose genetic variation as a result of genetic drift. Current populations, therefore, should be genetically less variable than those at the turn of the previous century if a population bottleneck occurred during the interim. Amplification of microsatellite DNA with the polymerase chain reaction (PCR) is now a fairly routine procedure, and it has been applied successfully to museum skins of birds (D. B. McDonald, pers. comm.). Although few nineteenth century skins of flammulated owls exist in museum collections, there are sufficiently large series from the early part of the present century (McCallum pers. obs.) to allow such a comparison to be made.

MOVEMENTS

Migration

The flammulated owl, at least its North American populations, is now considered a neotropical migrant (e.g., Winter 1974, American Ornithologists' Union 1983, Johnsgard 1988, Voous 1989). This conclusion is based on plausibility rather than hard data, as no banded flammulated owl has ever been recovered outside the immediate vicinity of its original capture site.

The species was originally assumed nonmigratory, presumably by extension from other owls, most of which are permanent residents (Phillips 1942). The assumption was plausible because this insectivore was also assumed to be facultatively carnivorous like other *Otus*, which it is not (Ross 1969, but see Food Habits). Phillips (1942) compiled the earliest and latest dates of verified occurrence for each U. S. state and Canadian province and concluded that flammulated owls breeding north of Mexico are trans-latitudinal migrants. Johnson (1963), while agreeing that the owls are absent from North American breeding grounds during winter, noted the lack of low elevation records (i.e., transients) in Middle America and hypothesized altitudinal migration supplemented with facultative torpor in northern populations. Numerous submontane records in North America are consistent with either long distance or altitudinal migration.

Winter (1974) reviewed the evidence for and against torpor and altitudinal migration and concluded that the species is a trans-latitudinal migrant. There is only a handful of documented lowland records in midwinter in the United States (Collins *et al.* 1986). The flammulated owl appears incapable of entering torpor (Banks 1964, Ligon 1968, J. D. Ligon in Winter 1974, Webb 1982), as do other small owls (Ligon 1969). When experimentally subjected to low temperatures without access to food, they maintain normal body temperatures with high metabolic rates and lose up to 25% of body mass. Moreover, vagrants found in Florida, Alabama, Louisiana, Texas, and on an oil rig in the Gulf of Mexico (Collins *et al.* 1986) reveal the ability of individual flammulated owls to cover long distances. Vagrancy of this magnitude is not often associated with sedentary species (Winter 1974). Finally, the low level of geographic variation in plumage, compared to that of the sedentary screech owls, suggests that gene flow is high (Winter 1974).

Three winter records in Montana, although second-hand and undocumented with specimens or photographs, have been published (Holt *et al.* 1987). There is also an unsubstantiated Christmas Bird Count record from Washington. While each of these records is individually unlikely, collectively their geographic concentration carries some weight. Facultative carnivory would allow the flammulated owl to spend the northern winter on or near the breeding grounds, but experience with captive birds suggests that successful carnivory on adult vertebrates is extremely unlikely. A recent observation by Cannings (pers. comm.) suggests that flammulated owls may take prey from leaf litter, which might allow overwinter survival in some areas (see Food Habits).

The Middle American distribution of the species is so incompletely understood that it is impossible to state with any confidence the migratory status of populations breeding in Mexico. Most winter records are south of 20° N. Lat., so northern Mexican populations may be migratory. Those breeding in southern Mexico are more likely to be resident because winter records are in breeding habitat. Age and sex differences in migration and other movements are unknown.

Nomadic behavior is unlikely to be found in this species. Very high site fidelity has been recorded in the best-studied population in Colorado (Reynolds and Linkhart 1987a, 1992). Also, the flammulated owl preys on insects and other invertebrates and appears to take whichever of several alternate prey taxa are most abundant at the time and location (Goggans 1986, Reynolds and Linkhart 1987b). Neither characteristic is typical of nomadic species, such as the snowy owl (*Nyctaea scandiaca*, Parmelee 1992) and boreal owl (*Aegolius funereus*, Hayward and Hayward 1993). On the other hand, recent population fluctuations of flammulated owls in the Kamloops and Okanagan areas of British Columbia have been interpreted as a numerical response to spruce budworm outbreaks (St. John 1991, A. van Woudenberg, pers. comm.).

Timing and Routes of Migration

Flammulated owls evidently remain in their breeding areas well into October (e.g., October 12, Linkhart and Reynolds 1987), when they become vocal after completing their annual molt (Marshall 1967). North American birds apparently migrate southward primarily in October, peaking in northern Arizona when large noctuid moths are most abundant (Balda *et al.* 1975).

Autumn records in the lowlands are from October and November. Several November records along the U. S. Gulf Coast, one in central Texas, and repeated records (mist-netted) in the southeastern plains of New Mexico (mostly in spring) suggest that a portion of the population may migrate east of the breeding range, perhaps wintering in the Sierra Madre Oriental (where so far the species has not been recorded in winter) or even the U.S. Gulf Coast.

The earliest lowland aural record (Bill Williams River, Arizona, 9 March-18 April 1979, Monson and Phillips (1981)) could be of a migrant, an overwinterer, or misidentified. Some March singers identified as flammulated owls may be long-eared owls, but a sight record near Boulder, Colorado 5-28 March 1966 suggests earlier arrival in breeding habitat is possible. They return north below breeding habitat, primarily in April (Balda *et al.* 1975). Spring arrivals (first dates for singing birds) are mostly in late April-early May in North America (see Phenology of Courtship and Breeding). Some females arrive on breeding grounds as early as males, but others appear later (Reynolds and Linkhart 1987b).

HABITAT OCCUPANCY

Concepts summarized earlier in this book, under Methods and Terminology Used With Studies of Habitat Associations, make it possible to evaluate the information content of published accounts of the habitat of the flammulated owl, most of which are anecdotal or qualitative assessments of habitat occupancy. I have synthesized the observed occupancy patterns into the following composite hypothesis about the habitat requirements of the flammulated owl. A detailed summary of the information used in formulating this hypothesis follows.

Composite Requirements

The common features of reported flammulated owl habitat are a cold temperate and semiarid climate, high abundance or diversity of nocturnal arthropod (mostly insect) prey, open physiognomy, and some dense foliage (used for roosting). Nesting habitat also includes cavities or nest boxes. Occupied forest types (ponderosa pine and Douglas-fir) have the highest insect diversities in the climatic zone occupied by the species (Reynolds and Linkhart 1987b). Open physiognomy seems a requirement in light of the use of thinned Douglas-fir forest in drier parts of British Columbia (Howie and Ritcey 1987). Semiaridity may be a correlate of open forests or it may be a physiological requirement of the species. Warmer microclimates are occupied within the generally temperate elevations occupied by these birds (Reynolds and Linkhart 1987b), but they are uncommon in lower elevation woodlands, perhaps because of structural deficiencies there. Prey availability appears responsible for the migratory behavior of this species, in light of the fact that small carnivorous owls do not migrate, while small insectivorous owls apparently do, but only from locations with seasonal subfreezing temperatures. Cavities are clearly required unless acceptable nest boxes are provided.

A Hierarchical Scheme for Summarizing Information on Habitat

Several authors (e.g., Hildén 1965, Johnson 1980, Hutto 1985) view habitat selection as hierarchically organized with more specific levels nested within more general ones. This seems particularly apt for migratory birds. Brewer and Harrison (1975) suggest, however, that most birds probably choose habitat and even home range before leaving on their first fall migration. Migrants may use hierarchical ordering for navigating to a location they chose previously, but choices of large-scale factors such as range and forest-type may simply involve staying in their natal habitat. In cases where individuals disperse prior to fall migration, hierarchical choice may occur directly.

Reynolds and Linkhart (1990a) have shown that adult owls examine other territories during the breeding season and that territory occupancy in the subsequent year may be influenced by these forays. This phenomenon and territory fidelity (Reynolds and Linkhart 1987a) remind us that adults base current-year site selection on knowledge obtained in the previous year(s). Nothing is known about the timing of habitat selection by juveniles, for they disperse in late summer, and only one has been recaptured in subsequent years (Reynolds and Linkhart 1990b).

Nonetheless, the hierarchical approach is useful for organizing data on habitat use. Moreover, the hierarchical levels are good first approximations of independent axes for the fitness and preference functions of the birds. What is inferred from the habitat requirements of flammulated owls will be described at the following scales for breeding, fall migration, winter, and spring migration.

1. Geographic range
    - history
    - climate
    - elevation
2. Landscape
    - vegetation type
    - home range vegetation
3. Home range/territory
    - foraging habitat
    - roosting habitat
4. Microhabitat
    - singing sites
    - foraging sites
    - nest sites and cavities

Geographic Range

The geographic range of the flammulated owl, when compared to the ranges of other species, reveals significant aspects of its physiological, behavioral, and ecological tolerances.

Biogeography of Related Species

The genus *Otus* occupies temperate and tropical latitudes of all continents but Australia and Antarctica. At the least, then, the potential range of *O. flammeolus* is that of its genus. This species, however, is restricted to the temperate zone and part of the tropics of one continent, North America. Moreover, except for migration, it is further restricted to montane elevations with seasonally temperate climates. Tropical lowlands appear inhospitable.

Like most species whose migration does not carry them across the equator, the flammulated owl does not have disjunct populations in the South Temperate Zone of the Western Hemisphere. It is more common for birds to have populations in the North Temperate Zones of both North America and Eurasia, but this phenomenon is restricted to boreal species whose ranges extend into Beringia (e.g., black-billed magpie (*Pica pica*) and northern hawk owl (*Surnia ulula*)). No species of *Otus* is boreal in distribution.

Otus scops has been considered the ecological equivalent of *O. flammeolus* in Eurasia. The two species have been suggested to be sister taxa, with vicariant historical biogeography, which would explain the absence of *O. flammeolus* from the Old World. But as it turns out (see below), the flammulated owl is a montane pine forest specialist, which is not the case with the scops owl. Ecologically, if not phylogenetically, the scops owl is more similar to the low-elevation generalists *O. asio* and *O. kennicottii* than to the flammulated owl (Voous 1989).

Distinctive Features of the Owl's Range

When compared to unoccupied areas in North America, the range of the flammulated owl is very revealing. First, it is strictly western, like the ranges of many species, but unlike most of these does not extend to the Pacific coast. (Based on available data, National Geographic Society (1987) and Johnsgard (1988) are erroneous in this regard.) Second, it is strictly montane, but unlike the ranges of many western montane species it does not extend farther north than southern British Columbia. Finally, it extends south to Guatemala and El Salvador, but only in interior mountain ranges. The only other species range with a similar pattern is that of the pygmy nuthatch (*Sitta pygmaea*), which is identical in British Columbia and in Mexico, and differs mainly in including coastal pine forests of central California. The combined ranges of the western population of the Nashville warbler (*Vermivora ruficapilla*), the Virginia's warbler (*V. virginiae*), and the Colima warbler (*V. crisallis*), which constitute a superspecies (AOU 1983), are very similar to that of the flammulated owl.

The range of the flammulated owl is essentially coextensive with that of mid-elevation montane pine forests. Pines (see below) may be important or even necessary, but they are not sufficient to guarantee the presence of the flammulated owl. The pygmy nuthatch is thought of as a yellow pine specialist, but it has a sister taxon in lowland southeastern pine forests, where the flammulated owl is absent, and it occurs abundantly in coastal pines of the central California fog belt. These two areas differ from the range of the flammulated owl in being humid and/or hot. If the flammulated owl summers from British Columbia south to southern Mexico and winters from southern Mexico to El Salvador, migrating southward in the uplands mainly in October and northward in the lowlands mainly in April, as is now believed, then the species occurs year-round in a semiarid cool temperate climate and nowhere else. It leaves the northern part of its range during winter, when the adult lepidopterans, coleopterans, and orthopterans it eats are unavailable. The exceptions to this pattern are the few fall and winter records from the southern United States.

Climate and Thermoregulation

The thermoregulatory abilities of the flammulated owl have not been studied (except for attempts to induce torpor), but some tentative inferences may be drawn from studies of its congeners. Specimens of *Otus trichopsis* and *O. kennicottii* from Arizona were very effective at regulating body temperature when subjected to high ambient temperatures, as long as humidity was low (Ligon 1969). A similar thermoregulatory strategy may be the reason *Otus flammeolus* is absent from humid areas.

On the other hand, the screech owls Ligon (1969) studied, especially the smaller *Otus trichopsis*, had rather high lower critical temperatures. This might suggest a heavy energetic cost of thermoregulation for the even smaller flammulated owl in low ambient temperatures. Whatever the cost, flammulated owls meet it. Males do not use cavities for day-roosting or resting at night during the early nesting season, when temperatures often fall below -6° C (R. T. Reynolds, pers. comm.). The fact that spring snowstorms lead to mass loss and death (Ligon 1968, Webb 1982) suggests that food availability is the key to thermoregulation. Starving owls lose up to 25% of their body mass before dying (Winter 1974).

It should be remembered, moreover, that Ligon's measurements were necessarily taken on inactive birds. For nocturnal owls, the period of greatest activity is also the period of coldest temperatures. Heat produced by foraging activity at night may be used to maintain body temperature. Male flammulated owls are very active while provisioning their mates early in the breeding season. The females spend most of this time in their nest cavities. Possibly neither experiences serious cold stress, as long as noctuid moths (the main food at this season, Reynolds and Linkhart 1987b) are plentiful.

Elevational Range

The flammulated owl occurs mostly in mid-level conifer forests that have a significant yellow pine (i.e., *Pinus*, subgenus Pinus, section Pinus, subsection Ponderosa (Critchfield and Little 1966)) component. In addition to floristic differences, higher elevation forests are generally cooler and more humid; lower elevation woodlands are hotter and more arid. The elevational specificity of the owl may stem from thermoregulatory limitations and hence results from climatic factors. On the other hand, the elevational limits of the species may be determined by the availability of prey species, which in turn is determined ultimately by the tree species present and proximally by temperature (R. T. Reynolds pers. comm.). Climate therefore may influence the distribution of the species indirectly through the prey base rather than directly through its thermoregulatory abilities. Finally, the flammulated owl may be physiologically and ecologically capable of occupying a much broader range of the elevational gradient than is occupied but be competitively excluded from the portions of the gradient it does not occupy. Limitation through avian competitors seems unlikely, as the pool of potential avian competitors changes considerably over the latitudinal range of the species. Mammalian nest-site competitors (sciurids) and food competitors (bats) are more plausible causes of competitive limitation (see Community Ecology).

The migratory routes of this species remain essentially unknown. Balda *et al.* (1975) captured 20 birds during spring in pinyon-juniper woodland (elevation 2040 m) in New Mexico, but none during spring in ponderosa pine forest in Arizona (elevation 2510 m). Just the reverse occurred in fall, 25 being captured or observed in the ponderosa site in Arizona, while none were captured in the lower site in New Mexico. These results suggest that breeding habitat, or habitat just below it, is used during north-south movements, but a series of sight records published in *American Birds* (McCallum unpubl.) shows that even lower elevations are used in both spring and fall.

Landscape (Vegetation Type)

Both floristics (the purely taxonomic component of habitat) and structure are merged in the concept of vegetation type, so this category and the next (structure of home range habitat) overlap. I will limit this section to discussions of gross vegetation types and summarize quantitative studies of habitat structure in the following section. This discussion is limited to breeding habitat, as only anecdotal information exists for habitat used outside the breeding season.

General Floristics

Reynolds and Linkhart (1992) reported that all published North American records of nesting, save one, came from forests in which western yellow pine (essentially *Pinus ponderosa* and *P. jeffreyi*) was at least present, if not dominant. There are several other forest types that also contain cavities suitable for nesting by this species, including low elevation riparian zones, pinyon-juniper woodland, Douglas-fir forest, and spruce-fir forest. Because these are virtually unoccupied, while yellow pine forest types are densely occupied, preference for yellow pine is suggested. Exceptions include several occupied mountain ranges in Nevada that lack yellow pines but support breeding owls in old aspen stands (S. Garland pers. comm). One nesting record from the Argus Mountains of California was in an old pinyon forest (Huey 1932), and the species occurs in pinyon-juniper stands containing no ponderosa pine on the Colorado plateau (R. T. Reynolds, pers. comm). McCallum and Gehlbach's (1988) study site was an old pinyon woodland, but all home ranges did contain some ponderosa pines. The range of the species extends far to the south of the ranges of *P. ponderosa* and *P. jeffreyi*, but numerous other species of subsection Ponderosae are present in the highlands of southern Mexico and southeastward (Critchfield and Little 1966). As all of these pine occur at mid-elevations on rather xeric mountain slopes, the influence of floristics and various correlates of the elevational range at which these species occur cannot be disentangled (see above).

Howie and Ritcey (1987) noted the flammulated owl's strong association with the very dry submontane interior Douglas-fir zone and absence from the ponderosa pine zone. These Douglas-fir forests, however, had been selectively logged in the past and approximated the structure of ponderosa pine forests to the south (see next two sections).

Characteristics of Entire Home Range

In Colorado, male foraging, territorial defense, resting, and day-roosting were restricted to home ranges averaging 14.1 ha during the prefledging period (minimum polygon method, range = 8.5-24.0, sd = 5.0; Jennrich-Turner [1969] model: mean = 20.0, range = 13.5-34.0, sd = 7.0). Range size appeared determined by canopy volume and range shape by topography (Linkhart 1984). Ranges of females are not known but were probably much smaller, as females were fed by males during incubation and the early nestling period.

Reynolds and Linkhart (1992) compared percentage representation of four vegetation types in the territories (103 ha) and in the entire study area (452 ha). A chi-square test of their data (Reynolds and Linkhart 1992) was highly significant (chi-square = 22.672, df = 3, $P < 0.001$). Inspection of cell chi-squares suggest that old ponderosa pine/Douglas-fir is favored and young Douglas-fir/blue spruce (a more closed, colder, and humid forest type) is disfavored. Preference for old forest was further supported by observations of foraging owls. Trees in which arthropods were captured had a mean age of 199 years, compared to 111 years for a random sample from the study area (Reynolds and Linkhart 1992).

Additional support for the hypothesized preference for old forest comes from the frequency of occupation of individual territories during the 12-year study. Those territories that were in continuous old ponderosa pine/Douglas-fir forest were occupied with few interruptions by a succession of males. Those with < 75% of this forest type were occupied only as long as the original male returned (1-3 years). Moreover, during the 12-year study only one male changed territories from one year to the next, and he moved to a traditional territory with a much greater complement of old-growth forest (Reynolds and Linkhart 1990a).

In Oregon five home ranges mapped via radio-tracking averaged 10.3 ha (minimum convex polygon method, range = 5.5-19.3, sd = 6.3)(Goggans 1986). Goggans speculated that they were smaller than home ranges in Colorado because the broken canopy in Oregon allowed more grass and shrubs to grow, which may in turn harbor more arthropods than the closed-canopy forest in Colorado. It should be noted, however, that three of her five home range estimates included no data for the incubation period, when home ranges are largest (see below), while Linkhart's (1984) estimate of 14.1 ha included no data from the postfledging period, when home ranges are smallest. The Oregon and Colorado data, then, are not comparable.

Marcot and Hill (1980) analyzed the vegetation composition of seven so-called territories in northwestern California and found that California black oak (*Quercus kelloggii*) was as ubiquitous (67%) as yellow pine (50% presence). These "territories," however, were actually singing sites. Both Goggans (1986) and Reynolds and Linkhart (1987a,b) have documented singing by unmated territorial males. The habitat Marcot and Hill (1980) described is therefore not necessarily suitable for nesting. Moreover, some of these birds were called in with tape recordings, and hence may not have been singing from within their defended areas.

Oak (*Quercus* spp.) has been mentioned in numerous accounts, particularly those of Marshall (1957) and Marcot and Hill (1980). Marcot and Hill (1980) noted that the California black oak provides many cavities, which may be important for nesting. They did not compare occupied habitat to that available, but they did note that occupied areas had certain characteristics generally associated with the species. These include association with ridge tops and xeric mid-slopes, two-layered canopies, tree density of 1270 trees/ha, and basal area of 58 m^2/ha.

In British Columbia, "most owls were found in mature-old growth stands of Douglas-fir that had been selectively harvested 20-30 years prior to our surveys" (Howie and Ritcey 1987:251). Occupied habitat on Wheeler Mountain, which had the highest densities of flammulated owls, featured canopy closure of only 35-65% and many old Douglas-firs and ponderosa pines, with thickets of regenerating Douglas-firs. This site is especially instructive, because it implies that the structure, rather than the floristics, of a site is most important to these owls. In common with sites farther south, Wheeler Mountain habitat was mature to old forest, the canopy was multi-layered and open, and the area was punctuated with thickets. No owls were found in clearcuts or stands < 80 years old. Another factor possibly related to occupancy of these sites was a spruce budworm outbreak. After the budworms defoliated the small Douglas-firs they crashed, and the owls disappeared (A. van Woudenberg, pers. comm.).

Goggans (1986) remarked that home ranges were on upper slopes and plateaus, where ponderosa pines and Douglas-firs grew, and did not overlap dense mixed conifers in draws. Confinement of owl territories to south slopes, ridgetops, and plateaus is a characteristic of a variety of other sites as well (e.g., Marcot and Hill 1980, Reynolds and Linkhart 1987a, McCallum and Gehlbach 1988, Bull and Anderson 1978). These aspects experience more solar radiation and hence more evapotranspiration than more shaded microhabitats. The resulting deficit in soil moisture affects both the floristics (favoring drought tolerant species) and structure (leading to wide spacing among plants) of the vegetation.

Home Range

Foraging Areas

The flammulated owl's preference for yellow pine and/or Douglas-fir has been linked to prey availability. Reynolds and Linkhart (1992:168) noted that "there are up to four times as many lepidopteran species associated with Douglas-fir and ponderosa pine than other common western conifers" (Furniss and Carolin 1977). High prey diversity and the structure of these forests may both favor successful foraging by flammulated owls. Foraging, then, may be one reason yellow pine forest types seem favored over higher elevation spruce-fir and lower elevation pinyon-juniper.

In Colorado, foraging (80% of radio-telemetry locations) was concentrated in 1-4 intensive foraging areas (IFAs) averaging 1 ha per range. One of these usually overlapped the nest (Linkhart 1984). The IFA nearest the nest was used during peak feeding times at dawn and dusk. More distant IFAs were used late at night when nest visits were less frequent. "Twelve of 15 (80%) IFAs were associated with mature, mostly open patches of ponderosa pine mixed with Douglas-fir on mid-slopes and ridgetops, and had exposures between 90-270 degrees" (Linkhart 1984). A multiple comparison of use and availability of forest types within territories showed significant selection of patches of old ponderosa pine/Douglas-fir and avoidance of patches of both young conifer and mature aspen vegetation (Reynolds and Linkhart 1992).

Goggans (1986) found that flammulated owls foraged more than expected by chance in stands with low to medium stem density. They also favored ponderosa pine and Douglas-fir over mixed conifers and grassland. But forest/grassland edge was most preferred of all, when compared to all forests and grassland.

These studies of actual use of home ranges for foraging are supplemented by studies of the structure of habitat immediately surrounding the nest, where foraging is concentrated during the nestling period (Linkhart 1984). The most quantitative study is that of McCallum and Gehlbach (1988). They evaluated vegetation structure around 17 independently chosen nest cavities. Some cavities were used more than once during the 6-year study, but a use was not considered independent if either bird had used the cavity before. Vegetation around occupied sites was compared to the vegetation around a matched set of the nearest available cavities (of appropriate size) that were not occupied. The study was designed to reveal nest-site selection, not territory selection.

Nest-site characteristics are summarized in table 1. Both a variance and a means test showed the owls in New Mexico were selective with respect to vegetation. Principal components analysis and stepwise discriminant function analysis were used in post hoc analyses to hypothesize the criteria of choice. The first principal component was interpreted as a successional gradient, and occupied sites had significantly lower variance on this gradient than did unoccupied sites. This result indicates high selectivity on the successional gradient. The discriminant analysis showed that the mean values of occupied and unoccupied sites differed on this gradient. The two results lead to the hypothesis that flammulated owls prefer open, mature vegetation around the nest. A further post hoc analysis, suggested by the data, showed that shrub densities were lower in front of cavity entrances than they were behind them. In only 2 of 17 cases did an owl choose a site less desirable than the nearest alternative, according to the discriminant function. In one of these, both the used and unused sites were comparatively undesirable, and neither site was used again. The other case involved a nest that was 10 m from its previous alternative site in a year following much human disturbance in front of the previous year's nest.

McCallum and Gehlbach (1988) felt that the owls may have chosen sites with low shrub cover in front of the nest in order to have a clear flight path to the nest. They observed that owls approaching and leaving some nests did so within 2 m of the ground, below the cavity. In fact, it may be that they fly low because of the open vegetation, rather than preferring sites that allow them to fly low. Reynolds and Linkhart (1987b) have shown that flammulated owls forage intensively near the nest, and that open vegetation is preferred for foraging. This could explain the apparent preference of the New Mexico owls for open vegetation as well.

Bull *et al.* (1990) assessed both habitat structure and nest-tree characteristics on the Starkey Experimental Forest in the Blue Mountains of northeastern Oregon. (Starkey was also the site of Goggans's (1986) population study.) Availability was assessed by measuring a subset of these variables around unoccupied but minimally suitable cavity trees. Means of continuous variables they measured are summarized in table 1. Univariate tests comparing used and available sites suggested nonrandom occupancy. The analysis covered 10 variables, each with $\alpha = 0.05$, which lowers confidence in the inferences reached about habitat selection. Apparently, selection is indicated at some lower level of confidence. Ridges, upper slopes, south slopes, and east slopes apparently were selected, as in Colorado (Linkhart 1984) and perhaps in British Columbia (Howie and Ritcey 1987, slope position only). Stands with trees > 50 cm dbh (diameter at breast height) appeared to be preferred, and although 58% of nests were in ponderosa pine/Douglas-fir forest types, this percentage did not differ from availability.

Table 1.—Habitat characteristics of nest-sites of flammulated owls in two regions. The two Oregon studies were both in the Starkey Experimental Forest. Cavity entrance and cavity floor are maximal linear measures of each. Species diversity was calculated as $H' = \sum (p_i)(\log_2 p_i)$ where p_i = proportion of individuals in species "i". Species importance values (IVs) were relative density + relative basal area + relative frequency. Pinyon IV - ponderosa IV was calculated because pinyons outnumbered ponderosas in the general vegetation, but more nests were in ponderosas. Sample sizes are in parentheses.

Feature	New Mexico McCallum and Gehlbach 1988	Oregon Goggans 1986	Oregon Bull *et al.* 1990 (n = 33)
Cavity/nest tree			
Tree height (m)		26.6±12.0 (20)	24 ± 9.1
Tree dbh (cm)	46.2±10.7 (17)	56.3±11.9 (20)	72 ± 14.4
Cavity height (m)	4.89±1.60 (17)	10.0 ±5.9 (20)	12 ± 4.7
Cavity depth (cm)	21.2±5.2 (15)	20.4 ± 15.9 (9)	
Cavity entrance (cm)	5.9±0.9 (16)	7.2±1.4 (9)	
Cavity floor (cm)	13.5±2.8 (15)	16.5±1.5 (9)	
Surrounding woody vegetation			
Tree density/ha	504±416 (17)	589±451 (20)	330±146
Shrub density/ha	442±619 (17)		480±296
Basal area (m^2/ha)	2.1±1.26 (17)[1]	23.7±19.4 (20)	
Distance to opening (m)		< 30 (20)	50±51.3
Pinyon IV - ponderosa IV	102±196 (17)		
Canopy height (m)	10.1±1.80 (17)		
Canopy closure (%)			55±20.1
Number of canopy layers		> 1 (20)	2.5±0.5
Slope gradient (%)		16-25 (20)	18±11.8
Plant species diversity (H')	1.45±.337 (17)		

[1] *Recalculated from original data.*

Roost Sites

In contrast to foraging habitat, preferred roosting habitat appears to be dense vegetation. Goggans (1986) located 35 roost sites and found that none was in pure ponderosa pine forest, although the owls roosted disproportionately in mixed-conifer forest with a ponderosa pine component. Multilayered stands were favored, and mean stem density and basal area in 0.008-ha plots around roost trees were 2016 trees/ha and 129 m^2/ha (vs. 589 trees/ha and 23.7 m^2/ha for territories, cf. table 1). Although these Oregon owls avoided pure stands of ponderosa pine for roosting, they strongly selected ponderosa pines for roost trees within mixed-conifer stands. Colorado owls did not roost preferentially in ponderosa pine but usually used large Douglas-firs or ponderosa pines with sprawling form, which may have the dense foliage found in thickets elsewhere. Mistletoe may augment the usefulness of such trees for roosting (R. T. Reynolds, pers. comm.). Thickets of regeneration are said to be used for roosting in British Columbia (Howie and Ritcey 1987) and are available on all territories studied in New Mexico (McCallum and Gehlbach 1988).

Linkhart (1984) found that mean distances from roost sites to the nest decreased from < 100 m to < 20 m just before fledging. In Oregon, mean distances from roosts to the nest were 24.9 m (n = 5) during the nestling stage, but greater before and after (Goggans 1986).

Microhabitat

Roost Sites

In second-growth forests, roosting flammulated owls typically perch at the base of a horizontal limb, next to the trunk. Their generally gray plumage, highlighted with rufous, blends well with the bark of younger, "blackjack" stage, ponderosa pines, which is generally gray, the reddish color of more mature bark appearing between the plates. This same effect occurs on younger, higher limbs of old ponderosa pines. The remarkable crypsis of owl plumage against pine bark may be responsible for the nonrandom use of ponderosa pine as roosting sites in Oregon (Goggans 1986).

Singing Sites

Marshall (1939) noted that singing sites were well up in tall trees. Reynolds and Linkhart (1992) used radio-tracking to locate the exact tree singing birds occupied in 22 cases. Only ponderosa pines and Douglas-firs were used, and these averaged 289 years of age, compared to 111 for the random sample of trees. Owls "sang from hidden positions next to tree trunks or in dense clumps of foliage" (Reynolds and Linkhart 1992:167).

Foraging Sites and Maneuvers

In Colorado, three of four foraging tactics (hawk-gleaning, hover-gleaning, and hawking) occurred in the more open lower two-thirds of tree crowns, either within the crown of a single tree or in the space between two trees (Reynolds and Linkhart in press). In late summer both adults and fledglings drop-pounced to the ground, grasses, or shrubs (Reynolds and Linkhart 1987b). In northeastern Oregon the most commonly taken prey were Orthopterans, most of which were probably taken from the ground, grass, and shrubs (Goggans 1986). All of these foraging sites are more likely to occur in open mature forests than in dense even-aged stands of young trees. Indeed, trees in which arthropods were captured had a mean age of 199 years, compared to 111 years for a random sample from the study area (Reynolds and Linkhart 1992).

The wings of flammulated owls are relatively long (Earhart and Johnson 1970), perhaps a constraint of migratory behavior. Long wings increase speed, but at the cost of higher wing-loading, which reduces maneuverability (R. Å. Norberg 1987). Limited maneuverability may contribute to preference for hunting in open forest and the near absence of flammulated owls from dense forest types. Indeed, Reynolds and Linkhart (in press) remark that foraging flights of flammulated owls are surprisingly high in speed. Bats, many of which are moth specialists, are known for very slow speed and great maneuverability. And hovering, a common foraging maneuver (Reynolds and Linkhart 1987b), is more efficient with slow wing-beat frequency, which requires low wing-loading and/or low aspect ratio (U. M. Norberg 1979). Perhaps flammulated owls hover inefficiently. Another correlate of low wing-loading and slow flight, low aerodynamic noise, is apparently superfluous for an insect-eater. Low wing-loading also reduces power demands when carrying prey but may not be important for this species because prey mass is low (prey are always single-loaded, Reynolds and Linkhart 1987b). It is at least possible, therefore, that the restriction of this owl to open forests is forced upon it by aerodynamic constraints resulting from its (presumed) migratory behavior.

Characteristics of Nest Trees and Nest Cavities

Because flammulated owls are secondary cavity-nesters, the presence of suitable cavities is an absolute prerequisite of successful nesting. It does not follow, however, that all defended territories necessarily contain suitable cavities. It is known that not all territorial males have mates (Goggans 1986, Reynolds and Linkhart 1987a). Less experienced or subordinate males may defend territories with no adequate nesting sites rather than emigrating. It may fall to females to decide the adequacy of territories for nesting. This logical possibility is mentioned to underscore the danger of assuming that male presence is an indicator of habitat sufficiency. Successful nesting is the only criterion of habitat sufficiency.

Moreover, as almost all cavities used for nesting have been excavated by woodpeckers, site quality is constrained by the species of woodpeckers present and the tree species they have to work with. In the northernmost part of its range the flammulated owl uses cavities excavated by the pileated woodpecker (*Dryocopus pileatus*). In one Oregon sample the occupancy rate of pileated woodpecker cavities was significantly higher than the availability rate (Bull *et al.* 1990). Goggans (1986) found no difference between availability and occupancy of pileated woodpecker cavities in the same area of Oregon. The southern part of the range overlaps the former range of the now (nearly?) extinct imperial woodpecker (*Campephilus imperialis*), and their cavities may have been favored in the past as well. The central part of the range, however, has neither of these large woodpeckers, and northern flicker (*Colaptes auratus*) cavities, which are underutilized in Oregon (Bull *et al.* 1990), and sapsucker (*Sphyrapicus* spp.) cavities appear to be the main cavity resource (see Complex Interactions).

Characteristics of nest-trees and nest-cavities are straightforward to assess once nests are found, and several such studies have been done. McCallum and Gehlbach (1988) measured a suite of characteristics (table 1) and used multivariate statistics to test the hypothesis that flammulated owls were selecting cavities nonrandomly from the source pool of minimally acceptable cavities. Means tests were not significant, but variance tests showed nonrandom occupancy had occurred. Evidently the owls had a strong preference for the cavity values that happened to be modal in the pool of woodpecker cavities. It should be emphasized that this analysis addressed nest-site selection within territories, not selection of the territories themselves.

Goggans (1986) measured similar variables and likewise found no differences among the means of occupied and minimally acceptable but unoccupied cavities. She did not employ a variance test. Except for cavity depth, her results (table 1) appear no more variable than McCallum and Gehlbach's (1988), and it appears that the owls used a narrow range of available sites in her Oregon study area as well as in their New Mexico area. Bull *et al.* (1990), working in the same area, found no difference between used and available cavity sites with regard to tree species, or dbh, but nest-trees were significantly taller than unused trees.

Scale Effects

Because seemingly basic requirements are disparate, habitat selection necessarily occurs on several potentially independent dimensions. Sites acceptable for some functions may not be occupied because requirements for other functions are not found nearby. McCallum and Gehlbach (1988) reasoned that flammulated owls in their New Mexico study area were more limited by foraging habitat around the nest than by nest-cavity characteristics per se. They based their conclusion on the finding that the owls selected cavities that were modal in the source pool while preferring vegetation that was rather extreme (i.e., in the tail of the source-pool distribution).

A certain amount of irony attends nest-site selection in this species. Males clearly select territories without female influence, as shown by the existence of unmated but territorial males in both Colorado (Reynolds and Linkhart 1987a) and Oregon (Goggans 1986). Males "show" nest-sites to females, which then choose the nest cavity from those offered by the male (Reynolds and Linkhart 1987a). Because males tend to roost and forage close to the nest-tree (Linkhart 1984, Goggans 1986), their mates essentially choose for them the areas in which they will carry out these important and time-consuming activities. Reynolds (pers. comm.) suspects that females choose mates on the basis of provisioning rates. If this is the case, then females sample habitat quality indirectly through the foraging efficiency of the males.

Seasonal Difference in Habitat

Although it is highly likely that the flammulated owl is a trans-latitudinal migrant (Winter 1974), all data supporting this conclusion are circumstantial. If northern birds do not leave their breeding latitude, they must either hibernate, prey on vertebrates, or, in the southern United States, migrate downslope to habitats in which arthropods are available in winter. Each of these options, discussed in detail under Migration above, would involve habitat or prey shifts. Hibernation is unknown for strigiformes, and caves are not present in much of the flammulated owl's range. Flammulated owls appear unable to process the bones of mature vertebrates in captivity (M. Altenbach pers. comm., Johnson and Russell 1962), so this option remains unlikely. Downslope migration seems plausible (Johnson 1963), but this would flood lowland riparian areas with birds, a phenomenon that would seem to be readily apparent in this restricted and well-studied habitat.

FOOD HABITS

Feeding

Food Capture and Consumption

The flammulated owl eats mainly nocturnal arthropods and hunts exclusively at night. A hunting bird locates prey from a perch visually, then flies to capture it aerially, to glean from needles (while hovering) or branches, or to pick it up from the ground. Marshall (1939) described hawkers as returning to the same perch while Reynolds and Linkhart (1987b) described hawkers as landing on a new perch. Captive fledglings used their feet to capture prey, including moths taken in an upside-down position from a ceiling. These captives swallowed soft-bodied prey whole, but large grasshoppers were held in the feet and torn apart with the bill (Richmond *et al.* 1980).

Foraging has been observed only during the nesting season. The distribution of feeding visits to the nest (Hayward 1986, Reynolds and Linkhart 1987b, McCallum *et al.* in review) suggests peak activity about 1 hour after sunset and 1 hour before sunrise, but this pattern has not been tested for non-nesting birds.

Most foraging in Arizona was aerial or in foliage (Marshall 1957). In Colorado, hawk-gleaning and hover-gleaning from needles were the most frequently used foraging tactics through the time of fledging (Linkhart 1984, Reynolds and Linkhart 1987b). In late summer both adults and fledglings drop-pounced to the ground, grasses, or shrubs (Reynolds and Linkhart 1987b). In northeastern Oregon, Orthopterans, the most available and most commonly taken prey (table 2), were 2.2 times more abundant in contiguous grassland than in pine forest where nests were located (Goggans 1986).

Acuity of the senses has not been investigated, but hearing may not be as important as for carnivorous owls, in that flight is not silent and the combs on the leading edges of the wings are not well developed. Karalus and Eckert (1974) reported a direct attack by an owl sitting a quarter mile away after the squeak of a mouse was simulated, but their description suggests another owl species was under observation.

Diet

Major Food Items

The flammulated owl preys almost exclusively on invertebrates. No vertebrates were delivered in > 200 hr of observation at 37 nests (>2000 prey items observed) by Reynolds (pers. comm.). Similarly, McCallum *et al.* (in review) observed no deliveries of vertebrates in 141 hr of observation at four nests.

Several authors have reported stomach contents of breeding owls (table 2), Ross's (1969) study of 46 stomachs being the largest and most extensive geographically. Reynolds and Linkhart (1987b) sampled flying insects with a black-light trap from 20 May through 18 September (1981 and 1982) in central Colorado. They identified food items by observing males provisioning females and nestlings. Goggans (1986) sampled available arthropods from May through August 1984 in northeastern Oregon with 6 ground-level and 6 aerial (2.1 m above ground) window traps. She used remote photography to identify 311 prey items brought to nestlings (6 July-14 August, 1983 and 1984) but did not evaluate diet before or after this stage. Anecdotal reports of invertebrate food do not enlarge the taxonomic list given in table 2.

In North America during summer, Orthoptera, Lepidoptera or Coleoptera predominate in the diet, depending upon availability (table 2). "Noctuids appeared to be the only food available to the owls during the cold spring nights, ... and were frequently seen in May flying about the forest canopy when temperatures were below freezing" (Reynolds and Linkhart 1987b). Noctuid moths constituted over 70% of the insects (Lepidoptera) captured in light traps by these authors in May and increased to over 90% in September. This increase agrees with Balda's qualitative assessment that noctuids are most abundant in northern Arizona in September and October (Balda *et al.* 1975). Noctuids may be the only prey taxon that is a potential limiting factor for flammulated owls, and they are probably limiting only in May and early June. Goggans (1986) captured no adult Lepidoptera in her traps in May and June, but this may be an artifact of her trap placement and limited number of sample sites. In July and early August she found no significant difference between frequencies of taxa brought to nestlings and those in her insect traps. Numerous other arthropod taxa are also taken (table 2).

Table 2.—Percent composition of diet (and available insects in one case) during summer.

Prey taxon	Oregon[1]	Oregon[2]	Various[3]	Arizona/ northern Mexico[4]	Western Great Basin[5]
Myriapoda					
Chilopoda	4.8	<1	1.4	4.9	
Diplopoda	<1	<1	0.2		
Arachnida					
Scorpionida			3.2	0.8	
Solpugida			0.9	0.4	
Phalangida				0.4	
Araneida	5.9	3.3	4.1	0.8	
Insecta					
Orthoptera	61.9	60.5	19.3	11.4	42.9
Hemiptera			1.6		
Lepidoptera adults	6.3	7.9	36.5	24.4	33.3
Lepidoptera larvae	6.5	<1	9.6	15.4	9.5
Hymenoptera			0.2		
Ephemeroptera	<1				
Diptera				1.2	
Homoptera	<1		1.8		
Coleoptera	<1	14.6	21.4	34.1	14.3
Unidentified/ Other	11.6	10.3		6.1	

[1] *Goggans (1986), photographed at nest (n = 352).*
[2] *Goggans (1986), traps.*
[3] *Ross (1969), stomach contents (n=46).*
[4] *Marshall (1957), stomach contents (n=27).*
[5] *Johnson and Russell (1962), stomach contents (n=10).*

The assertion that small vertebrates are taken has been repeated for a century without convincing documentation. Smith (1891) took a female whose stomach "contained the remains of some small rodents." Presumably on the basis of this report and the assumption of similarity to other *Otus*, Bendire (1892:375) concluded that "smaller mammals" were a major part of their diet. Bent (1938) concluded the species was "largely, if not wholly, insectivorous, though it may occasionally capture a small mammal or bird." Bent's statement has been repeated in several uncritical compendia. Karalus and Eckert (1974:160) have gone further in asserting that "this owl will eat mice of many varieties, shrews, moles, and, during the nesting season only, a few small birds." It appears that the food habits, as well as the weights, they report are those of the *Otus asio* complex.

In Oregon Bull and Anderson (1978) found a pellet containing the remains of a red-backed vole (*Clethrionomys gapperi*) below a nest tree, and junco feathers in another nest, but the previous occupants, e.g., northern saw-whet owl (*Aegolius acadicus*), may have taken these prey (E. Bull, fide, Cannings pers. comm.). Legs (with bands) of a juvenile mountain chickadee (*Parus gambeli*) were found in a nest in New Mexico; the chickadee had been banded as a nestling 30 m away (McCallum *et al.* in review). Linkhart and Reynolds (in press) found a *Peromyscus* carcass in a nest in Colorado but concluded another species was responsible for killing it. These findings do not demonstrate that the vertebrates were killed or even consumed by flammulated owls, but Cannings (pers. comm.) removed a dusky shrew (*Sorex monticolus*) from the stomach of an apparently healthy (mass = 60 g) owl that struck a window 15 November 1988 in Kelowna, British Columbia. Two unsubstantiated sightings in Montana in 1981, one of an owl perched in a tree with a vole in its talons on 21 November and another of an owl chasing passerines at a bird feeder on 20 December (Holt *et al.* 1987) are likely misidentifications. Nonetheless, the possibility that some flammulated owls overwinter in northern areas by subsisting on vertebrates cannot be completely discounted.

A pair captured by Johnson (1965:101) "died in an emaciated condition after several days in captivity despite nightly consumption of bird carcasses placed in their cage." Captives can be maintained indefinitely on a diet of meal worms and neonatal mice ("pinkies"), but apparently cannot process the bone of mature vertebrates (M. Altenbach, pers. comm.). Captives eat juvenile mice (< 9 g, K. McKaever, fide, Cannings pers. comm.), as well as grasshoppers (Richmond *et al.* 1980).

Role of Diet in Species Behavior

As shown by the observations reported by Ligon (1968) and Webb (1982), prey availability is essential to thermoregulation and survival during cold spring nights. This role of diet may in fact determine at least the upper limit of the elevational range occupied by the species (see above). The presumed migratory behavior of the species also appears determined by the seasonal availability of arthropods. The early availability of noctuid moths may therefore advance by up to one month the suitability of North American territories, although this conjecture is untested. Failure to begin nesting in May and early June would require adults to molt while still feeding their young in late summer. They may be able to tolerate such overlap, but it would require more vigorous foraging.

The available data suggest that flammulated owls will forage as readily in grassland/forest edges (Goggans 1986) as in tree crowns (Reynolds and Linkhart 1987b), which results in different primary prey taxa. Unfortunately the relative fitness consequences of these options are not known, and both food studies were of short duration.

Overall, flammulated owls appear to be opportunistic insectivores. As such they are not tied to the population cycles of a particular group of prey taxa. On the other hand their clutch size is quite invariant (see below), and they are unable to increase productivity in response to increased prey abundance in the manner of the boreal owl (Korpimaki 1989), the snowy owl (Parmelee 1992), and the barn owl (*Tyto alba*, Marti 1992). On the other hand, immigration into areas with high prey abundance (e.g. spruce budworm outbreak) is suggested by findings in British Columbia (St. John 1991, van Woudenberg pers. comm.). The response of this species to crashes of prey populations is unknown, and the population dynamics of typical prey species is not well known.

BREEDING BIOLOGY

Phenology of Courtship and Breeding

In North America males arrive on their breeding grounds in late April to early May in southern California (Garrett and Dunn 1981), New Mexico (McCallum *et al.* in review), and Colorado (Reynolds and Linkhart 1987b) and in early May in northeastern Oregon (Bull *et al.* 1990) and British Columbia (Cannings and Cannings 1982). Females, which are inconspicuous before pairing, are thought to arrive later, but pairs have been found at reoccupied nests as early as 3 May (Reynolds and Linkhart 1987b).

Pair Formation

In Colorado pairs remate in the previous year's territory if both return (Reynolds and Linkhart 1987a). Extra-range movements during the previous breeding season serve to acquaint males and females with potential mates if the previous mate does not return. In such cases the male tends to stay on his previous territory and the female to shift territories (Reynolds and Linkhart 1990a). Both these practices tend to shorten and simplify the pair formation process, which allows nesting to begin shortly after the arrival of females. Pairing can take place as late as 8 June (Reynolds and Linkhart 1987a). Mated pairs move through the home range with the male entering and calling from cavities. The female follows the male into cavities (Reynolds and Linkhart 1987b), presumably selecting a nest site in the process. Association of pairs during the winter has not been investigated.

Clutch Initiation and Laying

The southernmost nest recorded in the literature, in Veracruz (328 m), had incubated eggs on 4 April 1939 (Sutton and Burleigh 1940). A female weighing 63.0 g with a 2 mm ovum (indicative of the early pre-laying period) and 6 males in breeding condition were collected in early April in the Sierra del Carmen (Miller 1955). Breeding males were collected south of Ocampo and east of San Antonio de las Alazanas, Coahuila, in April (van Hoose 1955). A nest in adjacent Nuevo León had three incubated eggs on 4 May 1972 (Hubbard and Crossin 1974). An incubating female was taken from a nest in extreme southwestern Chihuahua 15 May 1950 (Stager 1954). Apparently laying is in mid-April, with hatching in May in northern Mexico.

Eggs were laid between 16 May and 4 June in western New Mexico (n = 11 eggs from 6 clutches, mean ± sd = 28 May ± 5.15) (McCallum *et al.* in review). In Colorado, clutches were completed between 29 May and 14 June (n = 14 females, mean = 7 June ± 4.6). Mid-July fledglings in British Columbia (Cannings *et al.* 1978) require early June laying there. Initiation of nest occupancy (which precedes laying) was on 12 June in Oregon (Goggans 1986).

Repeat nesting and second clutches remain unverified, but fledging dates of 15 and 19 August at one Oregon nest (Goggans 1986) and 16 August in British Columbia (Cannings and Cannings 1982) indicate laying between 1 and 5 July, which is suggestive of renesting. The latter nest was in a box erected on 12 June, > 1 month after arrival of the males, suggesting release from nest-site competition (Cannings and Cannings 1982).

The incubation period is 22 nights in Colorado (n = 3 clutches, range = 21-22) (Reynolds and Linkhart 1987b), 23 ± 2 nights (n = 2) in Oregon (Goggans 1986), and 24 nights (n = 1) in New Mexico (McCallum *et al.* in review).

Eggs hatched between 6 June and 28 June (n = 13, mean = 19 June ± 8.55) in New Mexico (McCallum *et al.* in review), while farther north in Colorado the last egg in 14 clutches hatched between 20 June and 6 July (mean = 29 June ± 4.6) (Reynolds and Linkhart 1987b). Hatching in a single nest in Idaho was on 30 June (Hayward 1986).

The nestling period averaged 22.9 nights (sd = 2.07, range = 20-26) for 11 New Mexican nestlings from 6 broods, 23.0 for 5 Colorado broods (sd = 1.1, range = 22-24) (Reynolds and Linkhart 1987b), and 22 ± 2 nights (n = 3) in Oregon (Goggans 1986). One British Columbia fledgling flew from the nest box 23 nights after its estimated hatching date (Cannings and Cannings 1982).

Fledging occurred between 27 June and 24 July (n = 14 birds from 8 broods, mean = 9 July ± 10.36) in New Mexico (McCallum *et al.* in review), from 13-29 July in Colorado (n = 14 broods, mean = 22 July ± 4.5) (Reynolds and Linkhart 1987b), and from 19 July through 1 August (annual means 26 July (n = 5, sd = 7.2) and 28 July (n = 4, sd = 4.6)) in Oregon (Goggans 1986). In British Columbia fledglings were on the wing 15-17 July 1977 (Cannings *et al.* 1978) but another fledged on 16 August 1980 (Cannings and Cannings 1982, and see above).

Home Range Size

Home ranges diminished in size during the breeding season in Oregon, from a mean of 15.9 ha (n = 2, telemetry points = 81, range = 12.5-19.3) during incubation to 7.9 ha (n = 5, points = 320, range = 2.2-12.5) during the nestling period, to 3.6 ha (n = 4, points = 126, range = 0.4-7.2) during the fledgling period (Goggans 1986). Linkhart (1984) also noted that home ranges became smaller after fledging, when males spent proportionately more time foraging, but did not quantify this difference. Small home ranges during the nestling period indicate that males are busy foraging and that they reduce the distance traveled to minimize the time between feedings (Goggans 1986). This suggests that foraging habitat around the nest, as well as cavity characteristics, may influence nest-site selection.

Courtship Characteristics

Pair Formation

Unmated males sing throughout the summer at the prehatching rate of mated males (Reynolds and

Linkhart 1987b) and, as in many species of birds, are apparently advertising their single status to unmated females. Returning females presumably reestablish a pair bond with their previous mates shortly after arriving. Unmated females move through territories of males giving food solicitation calls (Reynolds and Linkhart 1987a), but these are not loud and hence not useful for surveys. After pairing they move through the territory, with the male entering and calling from cavities. The female follows the male into the cavities (Reynolds and Linkhart 1987b) and presumably selects the nest site.

Courtship, Feeding, and Copulation

Away from the nest, the male approaches the female silently (McCallum pers. obs.) or while giving faint 2-note hoots (Reynolds and Linkhart 1987b); the female repeats mewing hoots believed to be food solicitation calls. The male perches beside the female and delivers food bill-to-bill. Copulation, when it occurs, follows food transfer. In one case, after a male gave a "location call" (2-note hoot), the female leaned forward in a horizontal position and rocked from side to side before copulation. An intruder male copulated with the same female on the same night without vocalizing (Reynolds and Linkhart 1990a). Mates may preen each other after copulation (Reynolds and Linkhart 1987b). Reynolds and Linkhart (1990a) observed 14 copulations in 17.5 hr of observation during the copulatory period, the first occurring 11 nights before the laying of the first egg.

The rate of allo-feeding of females by males increases to a peak four nights before laying, when female mass is maximal. Both feeding rate and female mass then decrease through incubation. Feeding rates then increase as the male provisions nestlings, but the female continues to lose mass (Reynolds and Linkhart 1987b). McCallum *et al.* (in review) estimated that females lost approximately .5 g per night during this period. Females resume feeding themselves about 12 nights after the young hatch (Reynolds and Linkhart 1987b).

Clutch

Flammulated owls lay clutches of 2-4 eggs, with little annual or regional variation. Mean clutch size ± standard deviation, sample size, and range for three United States populations are as follows: New Mexico, 2.28±0.49, n = 7, range = 2-3 (McCallum *et al.* in review); Colorado, 2.7±0.47, n = 11, range = 2-3 (Reynolds and Linkhart 1987b); Oregon, 2.7±0.76, n = 6, range = 2-3 (Goggans 1986). Anecdotal records in the literature all indicate clutches of 2-3, except 2 clutches of 4 in Colorado (Smith 1891) and Oregon (Bull and Anderson 1978). Johnsgard (1988) reported a mean of 3.12 (n = 26, range = 2-4, 14 clutches of 3) for a geographically scattered sample, mostly from the collection of the Western Foundation of Vertebrate Zoology (WFVZ), but some of the latter, including 3 of 4 clutches of 4, were misidentified as to species by the original collectors (L. F. Kiff, pers. comm.). Statistics for authentic clutches at WFVZ are mean = 2.83 ± 0.753, n=6, range = 2-4. Only 5 clutches of 4 can be verified, 1 each in Utah (WFVZ), Oregon (Bull and Anderson 1978), and British Columbia (R. J. Cannings, pers. comm.) and 2 in Colorado (Smith 1891 and U. S. National Museum).

In Colorado, females lay 2 eggs with inexperienced males, 3 eggs when the males have prior experience. This may be the result of males unfamiliar with their territories providing less food for egg-production by the female, who does not forage during the laying period (R. T. Reynolds, pers. comm.). High male turnover, therefore, may be deleterious to the persistence of a population, even though there appears to be a surplus of males (Goggans 1986, Reynolds and Linkhart 1987a).

Parental Care

Only the female incubates and broods the young. The male brings food to the incubating and brooding female up through about the 12th night of nestling life. Whether he feeds the nestlings directly or the female relays food to them is not known. Both male and female deliver food to the nestlings from the 12th night onward through fledging. The fledgling period lasts 25-32 nights (Reynolds and Linkhart 1987b).

Nest visitation rates are highest just after dusk and before dawn, and variable throughout the rest of the night. Visitation rates differed among four nests studied in New Mexico (McCallum *et al.* in review). Feeding visits are pulsed, and Hayward's (1986) extensive data on one nest suggest that pulses are averaged out such that the nightly total increases monotonically through the nestling stage; thus nests should be monitored all night for accurate representation of nightly rates.

In Colorado, nightly visitation rates peaked midway through the nestling period, which would be about the time the growth rates of the nestlings were maximal (Reynolds and Linkhart 1987b).

DEMOGRAPHY

Demographic modeling allows not only projection (i.e., a prediction of future population increase or decline), but also an assessment of the current status of a population. The Lotka-Euler equation for seasonally breeding species

$$\sum \lambda^{-x} l_x b_x = 1 \qquad [1]$$

specifies the effects of age-specific survival probabilities (l_x) and fertilities (b_x, often symbolized m_x) on the (geometric) intrinsic rate of natural increase (λ). If $\lambda = 1$ the population is stationary, neither decreasing nor increasing. (For continuously breeding populations λ^{-x} is replaced by e^{rx}, and the $l_x b_x$ are integrated instead of summed. The discrete equation also appears in different but mathematically equivalent forms; see Caswell 1989, McDonald and Caswell 1993.)

It would be desirable to estimate λ in these populations in order to assess current trends. Vital rates are, unfortunately, very poorly known for this species. Breeding behavior is fairly well understood, and annual fertility has been estimated in several locations. Otherwise, virtually nothing is known. Below I review the state of knowledge of various demographic parameters, and then use these data in a preliminary demographic model.

Life History Characteristics

Age at First Reproduction (α)

Age at first reproduction is not known. The only bird banded as a nestling ever found breeding had not been recaptured as a yearling, although the territory in which he was eventually recaptured (2.4 km from natal nest) had been occupied continuously since his first year (Reynolds and Linkhart 1990b). It is reasonable to assume $\alpha = 1$ year for females, because females of the much larger eastern screech-owl breed at that age (F. R. Gehlbach pers. comm.). The common existence of unmated territorial males and putative mate-assessment (Reynolds and Linkhart 1990a) suggest that unavailability of mates may force some territorial males to delay onset of breeding for 1 or more years. Both sexes breed annually (Reynolds and Linkhart 1987a).

Annual Fertility and Reproductive Success

One clutch is laid per year. (The two possible cases of late nesting or renesting are discussed above (under Clutch Initiation and Laying). Annual fertility is, therefore, identical to clutch size, which varies between 2 and 4 eggs. Means are 2.28 in New Mexico, 2.7 in Colorado, 2.7 in Oregon, and 2.8 for a sample from throughout North America (details above under Clutch Initiation and Laying).

Gross fertility is the number of eggs laid. Net fertility can be thought of as the number of fledglings produced. Three independent survival probabilities link these two parameters. The first is the *success rate* of all nesting attempts, that is, the probability that at least one fledgling is produced. Total nest failure can occur at any time between the onset of nesting and fledging because the entire reproductive output is in one vulnerable location. (The likelihood of renesting appears so low for this species that it can be ignored for these estimates.) Nest predators usually destroy the entire contents of a nest, so the effect of nest predation is included in this parameter. Death of either parent before about night 12 (see Phenology) of the nestling period will likely result in starvation of the young, leading to nest failure. The second probability is the *hatching rate* of all eggs in nests that last long enough for hatching to occur. This can be estimated from nests that succeed as well as those that fail completely after the completion of hatching. The final probability is the *fledging rate* of nests that succeed in fledging at least one young. Estimating this probability requires knowing brood size but not clutch size. The product of these three probabilities is the probability that an egg will produce a fledgling. It is permissible statistically to estimate these probabilities from different nests (Lande 1988). Estimating each separately makes it possible to use nests for which data are incomplete. Nest success probabilities from four North American samples are presented in table 3.

The probability of surviving to fledging can be multiplied by clutch size to predict the number of fledglings per nest (table 4). The estimate agrees very well with the average number of fledglings for all nests in the New Mexico data, but not as well for the other three data sets. The study sites represented in these data are reasonably well-distributed geographically, and these data are more extensive than data for other life history parameters.

The number of fledglings produced per nest is often used as an estimate of net annual fertility. When halved (assuming a 1:1 sex ratio) this number becomes *b*, the age-independent number of female offspring produced per female of breeding age (Leslie 1966, Mertz 1971). Age-specific fertilities are not yet available, but they should be gathered. Age-specific data may show that fertility is age-independent, which would reduce the complexity of demographic sampling in the future.

In Colorado the number of young produced by two inexperienced parents was less than the production of two experienced parents ($0.05 < P < 0.10$), while pairs with one experienced adult of either sex produced an intermediate number of fledglings (Reynolds and Linkhart 1987a). This difference would be partially reflected if age-specific fertility were available, but it shows that stage-specific (in this case stages would be inexperienced and experienced) modeling may be more useful.

First-Year Survival (l_1)

Although the survival of fledglings to independence is still mainly a parental responsibility, it typically is not included in fertility. It therefore must be included as one of the multiplicative factors in first-year survival. Linkhart's (1984) radio-tracking data yield an estimate of 0.79 for this crucial period, but the predation of several radio-fitted fledglings (Linkhart and Reynolds 1987) by *Accipiter* spp. may have been exacerbated by the extra burden of carrying the radios. The correct figure may be closer to 1.0 (R. T. Reynolds, pers. comm.) for this short but crucial interval.

The probability of surviving the first year is the product of two independent probabilities: survival from fledging to independence (above) and survival from independence to the age of 1 year (at which time breeding presumably commences, see above). The latter probability is unknown for the flammulated owl. None of the > 100 nestlings banded by Reynolds and Linkhart (in press) and the 13 banded by McCallum *et al.* (in review) have returned to their respective study areas in the first or subsequent years after banding. This is typical of young birds (Greenwood 1980) and does not mean they all died. Some fraction must have survived to the age of 1 year in another location, but the size of this fraction is unknown.

It is useful to partition survival from independence to age 1 into two phenologically distinct periods. The first is post-fledging dispersal. It is known that fledglings leave their natal areas earlier in fall than do adults (Linkhart and Reynolds 1987a), but it is not known how far they go or whether they make the entire trip to their subsequent summer home ranges before or after winter. Radio-tracking a large number of fledglings would make it possible to learn not only survival rates but dispersal distances during the immediate post-fledging period. This will require a study area of 10's of km rather than the more typical 100s of m in perimeter (see Chapter 7).

The second "installment" of post-independence survival is the probability of surviving the winter (including migration) independent of the costs of dispersal. This factor is also unknown for the flammulated owl. It could be obtained by banding juveniles in late summer and early autumn, under the assumptions that natal dispersal is completed before migration and that first-year owls return to the location they left in the previous autumn (Brewer and Harrison 1975). Adults return in exactly this way, so it would be no surprise for yearlings to have the same ability.

Adult Annual Survival

Adult survival has not been estimated with a statistical procedure (e.g., Jolly-Seber, SURGE). A minimum estimate of survival is given by return rates. An estimate of 0.59 was obtained from return rates in the first 4 years of the Colorado study (Linkhart 1984:6). As of 1986 the annual return rate of breeding adults was 8/17 for males and 10/19 for females (Reynolds and Linkhart 1987a)(rates not significantly different: $\chi^2 = 0.111$, df = 1, $P = 0.738$). The probability of returning the first year after banding was only 0.38 but increased for subsequent years. Because the first year of banding probably was not the first year of breeding for all these birds, especially at the beginning of the study, survivorship cannot be estimated from these data. An accurate survivorship schedule is gravely needed to assess the viability of this species. It will be difficult to obtain because flammulated owls cannot be aged after

Table 3.—Components of survival from egg to fledging for flammulated owls. Sample sizes are in parentheses.

Source	Nest success	Hatching rate	Fledging rate	Survival to fledging
Colorado[1]	0.88 (58)	0.88 (11)	0.95 (23)	0.74
New Mexico[2]	0.82 (12)	0.95 (7)	0.83 (10)	0.66
Oregon[3]	1.00 (9)	-	-	0.88 (6)
Various[4]	0.70 (10)	1.00 (5)	0.91 (4)	0.64

[1] *Reynolds and Linkhart (1987b).*
[2] *McCallum et al. (in review).*
[3] *Goggans (1986).*
[4] *Hasenyager et al. (1979), Richmond et al. (1980), Cannings and Cannings (1982), Bloom (1983).*

Table 4.—Predicted (from clutch size and nest success probabilities) and observed fledgling production by flammulated owls. Sample sizes (N) are in parentheses.

Source	Survival to fledging	Clutch size (N)	Predicted fledglings per nest	Actual fledglings per nest (N)
Colorado[1]	0.74	2.7 (11)	2.00	2.3 (26)
New Mexico[2]	0.67	2.27 (11)	1.50	1.50
Oregon[3]	0.88	2.7 (6)	2.38	2.66 (9)
Various[4]	0.64	2.80	1.79	1.43

[1] *Reynolds and Linkhart (1987b).*
[2] *McCallum et al. (in review).*
[3] *Goggans (1986).*
[4] *Hasenyager et al. (1979), Richmond et al. (1980), Cannings and Cannings (1982), Bloom (1983).*

the first molt of flight feathers, which occurs in late summer after the first birthday as in all *Otus* (Marshall 1967). Aging is most accurate in the first summer, because juveniles retain some of their barred juvenile plumage at least into August, but unfortunately independent juveniles are difficult to find. It may be possible to discern yearlings on the basis of flight feather wear, but this has not been documented. Possible delayed breeding by males makes obtaining a male life table very difficult. Fortunately, male data are not needed for assessing the viability of the population with standard demographic methods.

Lifespan

The maximum lifespan so far detected in the wild is 7 years and 1 month for females, and 8 years and 1 month for males (Reynolds and Linkhart 1990b). True maxima are probably much longer, as these results are based on a small sample. Estimation of average lifespan based on currently available data is not possible because the age at the time of initial capture is not known.

Nonbreeders

Reynolds and Linkhart (1987a) found some territories in which territorial males were present, but no attempt at nesting was evident. These males were believed to be unpaired because they continued to sing through the summer. These males are apparently a surplus and do not contribute to population growth, although their existence would buffer population decline if breeding males but not females were decimated. Nonbreeding females may exist but are unknown.

Geometric Rate of Natural Increase

Because first-year survival (l_1) is unknown, and adult survival is poorly known (although its mean appears ≥ 0.50), it is not possible to calculate λ for any population. The intensive field work required to estimate l_1 in several locations would be well worth the expense because it would make it possible for the first time to assess viability of populations of this species with some measure of objectivity. In the interim various indirect analyses are available. McDonald (pers comm) has investigated several stage-specific models that generally agree with what follows. What follows is simpler, but involves fewer assumptions. Both analyses are useful.

Assuming that adult survival and fertility do not vary with age, equation [1] may be simplified to

$$\lambda(1-s/\lambda)=lb \qquad [2]$$

(Lande 1988), where s = adult annual survival, l = first-year (juvenile) survival (from fledging to age 1), and b = annual fertility. Taking this route, rather than using a projection matrix, eliminates inaccuracies owing to truncation of the life table (Lande 1988) but omits important details, such as the effect of experience on breeding success.

Setting $\lambda = 1$, one may solve for combinations of s, l, and b that ensure a stationary population. Using the 4 net fertilities of table 4 to estimate b, one may ask if values of s and l necessary to guarantee population survival are realistic. The values from table 4 are halved because demographic modeling conventionally treats the number of females in a population. Because b is modeled as the number of fledglings, l is necessarily the survival rate from fledging to age 1. This is the product of 3 probabilities: (1) survival from fledging to independence, which was at least 0.79 in Colorado (see Annual Fertility and Reproductive Success above), (2) successful dispersal, and (3) surviving the winter.

Using the pooled return rate of 18/36 = 0.50 from data reported by Reynolds and Linkhart (1987a) as a first approximation of s, solving equation [2] for l shows that about 40% of fledglings in the Blue Mountains of Oregon and about 45% in the Colorado population must survive to the age of 1 year in order for the populations to persist indefinitely. Over 60% must survive in the New Mexico population.

These are high numbers; the comparable value for the northern spotted owl is 0.11 (Lande 1988). Return rates are a minimum estimate of adult annual survival, but even if survival is 50% higher than this minimum, yearling survival must be quite high.

Sensitivity analyses (Lande 1988, Caswell 1989, McDonald and Caswell 1993) of these data performed by D. B. McDonald (results to be presented elsewhere) show that λ is generally far more sensitive to changes in adult survival than to changes in other demographic parameters, including first-year survival. In evolutionary terms this means that a species with such low fertility must have very high adult survival in order to persist. In practical terms it means that conserving adults is more important than protecting nests (D. B. McDonald, pers. comm.).

The high sensitivity of λ to adult survival does not mean that fertility is unimportant. Indeed, the survival rates required for $\lambda = 1$ in the New Mexico population appear so high that the plausible explanation is that in fact $\lambda << 1$. This deficit could be partially made up if clutch size were increased to the value seen elsewhere in the range of the species (see Clutch Initiation and Laying above). Perhaps the frequent occurrence of 2-egg clutches in this population indicates that most of the birds are inexperienced (cf. Reynolds pers. comm.), a plausible conclusion if pinyon-juniper woodland is suboptimal habitat inhabited mainly by young and/or inefficient birds unable to obtain territories or mates in ponderosa pine forest upslope.

But increases in fertility appear limited in their potential for this species. When compared to the large clutches produced in times of food abundance by snowy owls (Parmalee 1992), barn owls (Marti 1992), and even the smaller boreal owls, at least in Europe (Hayward and Hayward 1993), the small and almost invariant clutches of the flammulated owl do suggest a firm commitment to a conservative, survival-oriented life history strategy. This works well enough for large raptors, but the flammulated owl is small, nonresident, and insectivorous. For this reason, its designation as a sensitive species indeed seems prudent.

Ecological Influences on Survival and Reproduction

The ecology of survival and reproduction have not been studied explicitly. For example, diet has not been correlated with growth of nestlings, although this is a straightforward undertaking, or with overall reproductive success. Home range use has been assessed in two localities (Linkhart 1984, Goggans 1986) but was not correlated with nest success or adult return rate in either case. In part this is because variation in nesting success is low. McCallum and Gehlbach (1988) compared reproductive parameters with habitat measures and found no correlation, perhaps because of low variance in the former. Reynolds and Linkhart (1992) did show that territories in old-growth forest were more likely to be settled than other sites. This implies that reproduction and/or survival is enhanced in old forest, but the hypothesis has not yet been tested. The higher occupancy of the old growth territories still shows the importance of old growth to the viability of the population.

Causes of Death

Egg mortality is minimal. Siblicide and cannibalism are not substantiated, but younger nestlings have been found dead in the nest after fledging of their siblings (McCallum pers. obs., n = 2), and one nestling disappeared (McCallum pers. obs.). Starvation apparently occurs during spring snowstorms (Ligon 1968, Webb 1982). One owl apparently died when a large insect became lodged in its throat (Kenyon 1947). Predation is poorly documented but likely given the owl's small size. Nest predation has been documented for the northern flying squirrel (*Glaucomys sabrinus*, Cannings and Cannings 1982) and either a felid or bear (Richmond *et al.* 1980); otherwise, nest predation is unknown. Remains of flammulated owls have been recovered from the stomach of a great horned owl (Johnson and Russell 1962), and Borell (1937) observed predation by a Cooper's hawk. Several fledglings have been killed by accipiters in Colorado (Linkhart and Reynolds 1990a), but maneuverability of fledglings may have been influenced by radio-mounts. Feathers were found on an accipiter "plucking post" near a nest that failed in New Mexico (McCallum pers. obs.). Diseases such as avian pox have not been reported, and feather parasites are very rare.

Social Pattern for Spacing

Estimates of home ranges vary from 5.5-24.0 ha, based on radio-tracking in Colorado (Linkhart 1984) and Oregon (Goggans 1986). Males sing throughout their home ranges, most frequently before hatching. Following hatching most singing occurs late at night. Intense singing bouts occur along the common boundaries of home ranges (before hatching) and sometimes escalate to physical combat (Linkhart 1984), demonstrating the degree of territoriality. Attempted nest-site takeovers have not been observed.

Evidently defense of an all-purpose territory is sufficient to ensure access to nest sites. Silent males occasionally intrude and approach a nest in another territory. The local male vocalizes and sometimes chases the intruder, albeit ineffectively (Marshall 1939, Linkhart 1984, Reynolds and Linkhart 1990a). Territory defense apparently ceases after fledging, for family subgroups disperse without interference at this time (Linkhart 1984).

In Colorado, some territories are contiguous and have long common boundaries (where many interactions occur), but the landscape is not saturated with territories and much space is unoccupied (Reynolds and Linkhart 1987a). Such sites appear suboptimal (Reynolds and Linkhart 1992), but whether they would be occupied if the population were denser is not known.

Territories generally occupy the same space from year to year regardless of occupancy of contiguous territories. Because males do not expand their defended areas when neighbors are absent (with one exception, Reynolds and Linkhart 1990a), it seems unlikely that territoriality depresses viable population size. Rather, territoriality may optimize population size by ensuring that high-quality pairs have the resources they need for maximizing reproduction (£omnicki 1988).

Local Density Estimates

Population density estimates are of three kinds: (1) nest and occupied-territory counts from intensively studied sites, (2) spot-mapping estimates from intensively studied sites, and (3) call surveys of a more extensive but less intensive nature. The former, of course, provides more dependable data than the latter two methods. Spot-mapping and call surveys are a potentially useful source of information on flammulated owl abundance, but care must be taken in interpreting the data (Reynolds 1987). For example, the owls were said to be "more common than robins" (Kingery 1980) in the Manitou study area in Colorado, on the basis of clusters of singing birds. Subsequent radio-tracking of this population showed that singing owls move widely in their home ranges and that several clusters of song registrations were due to single birds (Reynolds 1987). Call surveys conducted to date have not been calibrated with estimates based on intensive study of a single area. All survey data, then, may suffer from at least three sources of error:

1. The methods used to estimate the area surveyed (the sound or aural envelope) are subject to considerable error owing to wind, topography, etc.
2. Males have been known to travel up to 1 km to answer a tape recorded song (see Goggans 1986), so surveys using recorded calls to stimulate males may overestimate numbers in the assumed study area. On the other hand, not all males sing at all times, so underestimates are also possible.
3. Some males are unmated (Reynolds and Linkhart 1987a), so call counts do not accurately reflect the number of breeding units, which is far more important for demographic analysis than is the number of males.

Population Studies

Table 5 summarizes data from population studies of flammulated owls. Density estimates are calculated by dividing the count of owls (either nests or males) by the size of the study area. Estimates based on the data of Bull *et al.* 1990 are minimal. These authors surveyed a large area incompletely while conducting a habitat study. Nonetheless, their data fall into the population study category.

Spot-Mapping and Equivalent Studies

Marshall (1939) counted 24 males in an area of about 2 square miles, which yields a density of about 1.9 males/40 ha. The area of his study area was not measured, and he called birds actively, so this is a crude estimate. Nonetheless the species was clearly common in this area, as in other locations in the Sierra Nevada of California where 1-night surveys have been conducted (Winter 1974).

Franzreb and Ohmart (1978) conducted a 2-year spot-mapping study of breeding birds of a mixed-conifer site in the White Mountains of Arizona. Their estimates of 10.6 and 10.2 birds/40 ha actually reflect half that many estimated territories. But their study plots were only 15.5 ha, close to the average size of a territory in Colorado (Linkhart 1984). It appears likely that several territories partially overlapped their study site, or that they misinterpreted clusters of song registrations as several males when only one was responsible. Nevertheless, their comparison between logged and unlogged sites is valuable (see below).

Call Surveys

Marcot and Hill (1980) conducted nocturnal surveys for owls in potential timber sale areas in northwestern California. They did not report how they estimated the aural envelope surveyed but reported admittedly crude density estimates of 0.03-1.09 males/40 ha.

Howie and Ritcey (1987) conducted surveys along roads in the Kamloops region of British Columbia in 1983-1985. They assumed that the detection limit for singing owls was 0.5 km, and they stopped each 0.5 km along routes varying from 3 - 10 km. Density estimates ranged from 0.03 - 0.5 males/40 ha. Clusters of males along one route were estimated at 0.4-0.7 males/40 ha.

In general, densities are not > 1 territory per 40 ha. Exceptions are several sites in the Sierra Nevada of California (Marshall 1939, Winter 1974), where nests were not located and the study area was not measured, and one site in New Mexico (McCallum *et al.* in review), where the estimates were based solely on nests, but home ranges were not mapped. Territories are known to be clumped, so it is possible that the rather small New Mexico study area happened to overlap a local concentration of owls.

Limiting Factors

Limiting factors have not been addressed explicitly in published studies. Nest-site availability is a potential limiting factor, as it is for any obligate secondary cavity nester. Cavities excavated by pileated woodpeckers and northern flickers are used in the northern part of the range. Farther south, where the pileated woodpecker does not occur, cavity limitation might become serious. Flammulated owls in New Mexico will, however, squeeze into hairy woodpecker cavities (McCallum and Gehlbach 1988) and they typically use sapsucker (*Sphyrapicus*) cavities in Colorado (R. T. Reynolds, pers. comm.). Habitat, especially foraging habitat, may limit population growth more than is currently appreciated (see Metapopulation Structure below).

Patterns of Dispersal

Natal Dispersal

In Colorado, each of five broods averaging 2.8 young fledged over a 2-night period. Young who fledged on the same night associated in subgroups, and the two subgroups separated by the third night after fledging began. One parent attended each subgroup, and they dispersed in opposite directions. As the flight and foraging capabilities of fledglings improved they foraged more for themselves and became independent of parental provisioning by mid-

Table 5.—Breeding densities of flammulated owls based on counts of territories or nests in measured population study areas.

Source	Count	Area (ha)	Number/40 ha
New Mexico[1]			
1982	5	95	2.11
1983	5	159	1.26
1984	2	159	0.50
1985	5	159	1.26
1986	2	95	0.84
Colorado[2]			
Minimum estimates from 5-year period			
nests	4	452	0.35
males	6	452	0.53
Maximim estimates from 5-year period			
nests	6	452	0.53
males	9	452	0.80
Oregon			
1984[3]			
pairs	19	1657	0.46
territorial males	27	1657	0.65
1987[4]			
nests	13	5270	0.10
callings sites	24	5270	0.18
1988[4]			
nests	21	5270	0.16
calling sites	62	5270	0.47

[1] *McCallum et al. (in review).*
[2] *Reynolds and Linkhart (1987b).*
[3] *Goggans (1986).*
[4] *Bull et al. (1990).*

August. Siblings being attended by the same parent roosted close together until mid-August, at which time their roost sites began drifting apart (n = 1). They apparently left the study area in late August. Brood division may spread the risk of total brood destruction by predators in that the loud begging of fledglings renders them conspicuous to nocturnal predators and the habit of roosting close together may lead to multiple predation by diurnal predators (Linkhart 1984, Linkhart and Reynolds 1987). Brood division was also recorded by Goggans (1986) in Oregon.

As with most other birds, locally banded nestlings do not return to the study area where they were banded (Reynolds and Linkhart 1990b, McCallum *et al.* in review). This does not necessarily imply that dispersing young travel great distances. Rather, they may travel 5-10 territory diameters like other birds (Shields 1982), which is usually too far to be detected in the study area. One male found 2.4 km (< 6 territory diameters) from its natal nest by Reynolds and Linkhart (1990b) fits this pattern. An exhaustive survey of potential nest sites in a 100 km^2 area would likely reveal significant information about dispersal of nestlings banded in a typical study area located at the center of the area.

Breeding Dispersal

In Colorado, males reoccupied their previous territories every year they returned, with a single exception. Females were also site-faithful but moved to the adjacent territory to join an unmated male if their mates did not return. In the one case in which a mated male moved, he and his mate occupied an adjacent territory after the resident male disappeared. The abandoned territory had only a few hectares of old forest, while the new one consisted entirely of old growth. Another male expanded his territory to include an adjacent territory that had not been reoccupied (Reynolds and Linkhart 1990a).

In New Mexico, one female used the same nest cavity 3 years, while two females and one male were found in different territories in subsequent years. Otherwise, 18 banded birds neither returned to previously used sites nor were found elsewhere (McCallum *et al.* in review). In Oregon, 5 of 10 territories were reoccupied in the second year of the study, but no cavity was reoccupied (Goggans 1986).

Metapopulation Structure

Winter (1974) reviewed the idea that flammulated owls are "semi-colonial." Several subsequent authors have remarked on finding clusters of calling owls with large unoccupied (i.e., silent) spaces in between. Caution must be used in discussing this phenomenon, because it is based solely on patterns of calling males and not on locations of nests. Several workers who have sought nests systematically have found them in abundance and not in an obviously clustered pattern (e.g., Goggans 1986, Reynolds and Linkhart 1987a, McCallum and Gehlbach 1988, Bull *et al.* 1990). There are, of course, unoccupied areas in these locales, but the aggregations of territories do not comprise colonies in any sense. Singing males are known to move extensively in response to other singers or to tape recordings (Marshall 1939, Reynolds and Linkhart 1984, Goggans 1986). These clusters, which typically have not been revisited by those reporting them, may be ephemeral aggregations of males engaging in song duels, especially early in the breeding season before females have arrived.

If the phenomenon of clumped distribution of territories is real, and the possibility should not be dismissed peremptorily, it has important conservation implications. Either large areas of suitable habitat are unoccupied, as Winter (1974) concluded or large areas of seemingly suitable habitat are not in fact suitable or are at least are suboptimal (Howie and Ritcey 1987, Reynolds and Linkhart 1992).

Unsaturated Habitat Hypothesis

If suitable habitat is unoccupied the cause is most likely to be found in the demography of the species and/or the landscape mosaic of the region. A long-lived, low-fecundity species will be slow to reoccupy its range after a population decline because its intrinsic rate of natural increase is low. The flammulated owl is such a species (it has a small, invariant clutch and is not known to respond to regional variation in food abundance with nomadism). Current information implies that the flammulated owl is intrinsically incapable of rapid population growth. It is, therefore, a plausible, but perhaps untestable, hypothesis that the flammulated owl suffered a continental population decline in connection with widespread habitat change in the past century. The location of these local clusters of birds, the "semi-colonies" of the literature, may be an artifact of such environmental alteration. Such clusters are especially likely if natal dispersal distances are short, a subject on which little is known (Reynolds and Linkhart 1990b). These clusters may spread and the species may reoccupy all mid-elevation conifer forest in the future. Even if the clusters are not artifacts of habitat alteration but are, instead, evidence of social attraction of nesting pairs (or just territorial males), the assumption that unoccupied habitat is suitable implies future population growth as colonies spread in extent. This "unsaturated habitat" interpretation of the cluster phenomenon implies that current forest management schemes are compatible with viability and even growth of flammulated owl populations.

Suboptimal Habitat Hypothesis

An alternative interpretation of these putative clusters of flammulated owls is that not all the habitat that appears to humans to be suitable (i.e., similar to occupied habitat) is in fact suitable by the owl's standards. If this is the case then suitable habitat may be saturated, populations are not likely to increase, and current forest management practices may be responsible for forcing remaining owls into enclaves of suitable habitat.

Metapopulation structure has not been investigated intentionally. The phenomenon described above indicates that it should be. Assuming that the owl currently occupies all ponderosa pine forest, or even all old-forest stands may lead to serious overestimation of its total population size.

COMMUNITY ECOLOGY

Habitat Change and Vulnerability to Predation

Logging has been said to increase contact between great horned and Mexican spotted owls, to the possible detriment of the latter (Ganey *et al.* 1986). If opening the structure of the already open pine forests increases the number of great horned owls there, the flammulated owl might also suffer greater predation. Heavy logging may also reduce the attractiveness of a site to accipiters, thereby benefiting the small owls. Fire suppression has resulted in denser forests, often with an emergent overstory (Chapter 5). These conditions may have deterred predators on terrestrial mammals, such as great horned owls. But, they may also offer superior hunting for northern goshawks that prey on Abert's squirrels, and bird-eating hawks. The effect of habitat change on predation pressure is a complex question that has not been addressed in existing research.

Competitors

Other owls are the major potential avian competitors for food, and of them, only the two screech-owls, *O. kennicottii* and *O. trichopsis*, and the elf owl (*Micrathene whitneyi*) take significant numbers of insects. Marshall (1957, 1967) felt that competition was minimal among the species of *Otus*. Range overlap with the elf owl is not great. Some prey species (e.g., grasshoppers, cicadas) are taken by diurnal predators, which might seriously depress prey availability for the owls. Bats, many species of which co-occur with the flammulated owl, are the most likely vertebrate competitors for food, especially in April and May when the diet of owls is dominated by moths. Insect predators and parasitoids may also take a toll on the food supply. None of these possibilities has been studied, but the opportunistic diet selection of the flammulated owl suggests that it is not seriously threatened by food competition, except perhaps in the early breeding season. Nevertheless, population changes in bats may seriously influence population dynamics of this species.

Nest-site competition is a more obvious threat to this obligate secondary cavity nester. Smaller birds (wrens, parids, nuthatches) tend not to nest in the large cavities required by flammulated owls. Birds from the size of bluebirds upward are potential competitors. Owl nests containing bluebird eggs (McCallum pers. obs.) and flicker eggs (Smith 1891) suggest that flammulated owls may evict some potential nest competitors. (An active flicker nest was in the same tree in which Smith found the owl nest containing flicker eggs.) Even if these owls are capable of evicting all passerines and woodpeckers during the early stages of nesting, larger raptors and some mammals are potential nest competitors.

Habitat preferences tend to separate the flammulated owl from other species of *Otus* that are usually found downslope in drier sites. Northern pygmy owls and saw-whet owls are more likely nest-site competitors. Boreal owls are usually found in more mesic forests; nonetheless, four flammulated owl territories in Idaho overlapped boreal owl territories (Hayward and Garton 1988).

As with competition for food, the most serious nest-site competitors may be mammals. Sciurids, such as *Sciurus aberti* in the southwest, *Glaucomys sabrinus* in the northwest (Cannings and Cannings 1982), and *Tamiasciurus* spp. may out-compete owls for nest-sites and also prey on them. Delayed nest initiation, followed by immediate occupancy of a newly erected nest box, in British Columbia suggests serious nest-site competition (Cannings and Cannings 1982). Reynolds and Linkhart (in press) reported seeing a flammulated owl chasing a northern saw-whet owl, which also supports the conjecture that nest-site competition may be serious.

Particular harvest prescriptions may increase overlap of flammulated owls and potential nest-site competitors. Franzreb and Ohmart (1978) found increases in American kestrels, northern pygmy owls, and northern saw-whet owls, as well as great horned owls, in logged sites in Arizona. Whether these changes are responsible for the absence of flammulated owls from the logged sites is of course unknown, but increased nest-site competition or predation pressure is a possible explanation.

Complex Interactions

Because flammulated owls depend upon woodpeckers for nest cavities and alternate sources of cavity production are rare, the well-being of woodpecker populations is essential to the survival of this owl (and many other species as well). The imperial woodpecker, whose cavities may have been used preferentially in the past, is now absent from most, if not all, of its former range, which broadly overlapped that of the flammulated owl in Middle America. The pileated woodpecker is the preferred source of cavities in Oregon (Bull *et al.* 1990). This species is considered an old-forest species in western North America (although it has expanded into suburban areas in the east). Loss of old forest in the northern part of the owl's range could, therefore, have both an indirect effect (via loss of pileated woodpecker cavities) as well as a direct effect (via loss of preferred foraging and roosting habitat) on the owl's viability. The northern flicker appears to be one of the main excavators of cavities used by the owl south of the range of the pileated woodpecker. This is a common species, but the impact of European starlings (*Sturnus vulgaris*) on flicker populations cannot yet be assessed, as the starling is still in the process of colonizing western mountain ranges. Flickers are indifferent excavators and often reuse old cavities. Starling expulsion of flickers from old cavities (which is rumored to happen) could actually lead to an increase in the number of flicker cavities, if it did not lead to the extinction of local flicker populations.

RESPONSE TO FOREST CHANGE

Stand Scale Response

Logging

Franzreb and Ohmart (1978) studied the effect of timber harvesting on a mixed-conifer forest bird community by comparing densities in harvested and unharvested sites in Arizona. Their spot-mapped densities of flammulated owls (5.3 and 5.2 territories/40 ha) appear unrealistically high, but the effect of timber harvesting is unmistakable. The unlogged plot had 626.2 trees/ha, 61.1 snags/ha, and 113,984 m^2/ha of foliage volume. Comparable figures on the logged plot were 167.7, 21.0, and 15,269.8. Flammulated owls were obviously dense on the unlogged plot, where ponderosa and southwestern white pines provided nearly 80% of foliage volume; they were absent from the logged plot in both years of the study. Loss of nest sites may be the main reason for the difference, but changed vegetation structure cannot be ruled out.

In Oregon, Bull *et al.* (1990) did not find a significant difference between nest sites and unused cavity-bearing trees with regard to logging activity. Nesting or singing owls have also been found in other selectively logged (Hasenyager *et al.* 1979, Bloom 1983, Howie and Ritcey 1987, Reynolds and Linkhart 1987b) or second-growth (Johnson and Russell 1962, Winter 1974, McCallum and Gehlbach 1988) stands. It appears that in British Columbia selective logging is responsible for producing the open-stand structure that characterizes this owl's habitat everywhere it has been studied. Some logging, therefore, may not be detrimental per se, as long as large old trees, open physiognomy, and some dense vegetation for roosting persist.

Clear-cutting, however, apparently renders an area useless for flammulated owls for many decades. Reynolds and Linkhart (1992) have noted that regardless of forest type, all known nests accompanied by habitat descriptions were in or adjacent to mature or old-forest stands. In addition to the obvious connection that old trees are more likely to contain cavities, they may also provide a richer prey base and denser foliage for roosting. Many older second-growth stands may be acceptable to the owls because they were logged without the aid of chainsaws, and hollow trees typically were left standing. Recent practice, however, has been to remove such trees, probably rendering an area uninhabitable for at least 50 years.

Fire

The effects of fire on the species have not been assessed directly. It is known, however, that 20th century fire suppression and the resulting replacement of frequent cool fires with infrequent conflagrations has led to stand structure that did not characterize ponderosa pine forests before European settlement (Chapter 5). The resulting "doghair" stands of stagnant regeneration may provide suitable roosting habitat for flammulated owls, but they probably seriously reduce foraging potential. Grass and small shrubs, which harbor numerous prey species, are completely shaded out by the dense thickets of stunted pines. The typical foraging maneuvers of the owls may be difficult to perform in close quarters (Reynolds and Linkhart in press). A comparative study of foraging performance and reproductive success in doghair and artificially thinned stands of second growth would help clarify the contribution of fire history to the current status of the owl. Monument Canyon RNA in the Santa Fe National Forest, New Mexico, would be an ideal site for such a study.

Population Response

Although longitudinal studies of the response of flammulated owl populations to forest change have not been conducted, some retrospective analysis may be useful. In the past century ponderosa pine forests in the western United States were subjected first to heavy logging and then to nearly total fire suppression (Chapter 5). How might these activities have affected the owl? Ironically, their ill effects may have canceled each other out. It appears that these owls favor open forest structure for foraging but dense foliage for roosting. Most early logging did not destroy all the trees. The few that remained may have been sufficient in number and size to provide some nesting cavities, but they were not sufficiently dense to allow for safe roosting. As fire suppression led to the establishment of doghair stands under them, adequate roosting sites may have become abundant. This would leave foraging quality as the major determinant of population persistence. This artificial mix of acceptable habitat characteristics is, however, inferior to presettlement forests in at least one respect. Fire suppression eventually leads to conflagrations, which kill all the trees, making large areas as unsuitable for these owls as a clearcut. Nonetheless, management practices that completely eliminate snags and/or doghair in the name of reducing fuel loads may also make an area unsuitable.

Effects of Fragmentation

In general, fragmentation (here I refer to the isolation of quality habitat in small patches) is thought to negatively influence forest interior species by (1) increasing nest failure owing to increased access by edge-associated predators and brood parasites, (2) increasing competition, especially for nest-sites, with edge-associated species, and (3) decreasing dispersal success owing to the dangers of crossing large open spaces. The effects of fragmentation on the flammulated owl have not been studied.

Past research suggests that the flammulated owl is an old-growth species (Reynolds and Linkhart 1992). Old pine forest, however, has an open structure with numerous interior edges. Edges are favored for foraging in both Colorado (Linkhart 1984) and Oregon (Goggans 1986). Moreover, cavity nesters are less susceptible to the increased predation and parasitism associated with fragmentation than are open nesters. Finally, although the risk of crossing openings may be increased by fragmentation, especially for inexperienced juveniles, it should be remembered that the species faces this risk during migration and presumably has evolved a means of minimizing it.

In summary, many flammulated owls live in habitat that is naturally fragmented to begin with. While forest fragmentation should not be ignored as a potential threat to the survival of the species, current information suggests that alteration of *stand* structure within the forest landscape is more deleterious than fragmentation.

Response to Human or Mechanical Disturbance

These owls are very tolerant of humans, nesting close to occupied areas and tolerating observation by flashlight all night while feeding young. Nest abandonment is rare. One female that was dropped 5 m in a weighing bag abandoned its nest but returned to the same cavity the following year (McCallum pers. obs.). The effects of mechanical disturbance have not been assessed, but moderate disturbance may not have an adverse impact on the species. Whether a nesting pair would tolerate selective harvesting during the breeding season is not known.

A sensitivity analysis of life-history parameters by D. B. McDonald (pers. comm.), however, points out that adult survival is probably much more critical to the maintenance of flammulated owl populations than is annual nesting success. McDonald suggests that mechanical disturbance, e.g., thinning or controlled burn, that flushes roosting birds may be a more serious threat to adult survival in October when migrating *Accipiters* may be common than in June, even though the possibility of lost reproduction is obviously greater in the summer.

REFERENCES

Altenbach, M. former Director, Animal Care, University of New Mexico, Albuquerque, NM. [Personal communication]. October 1992.

American Ornithologists' Union. 1983. Check-list of North American birds. Sixth edition. Washington, DC, USA.

Balda, R. P., B. C. McKnight, and C. D. Johnson. 1975. Flammulated Owl migration in the southwestern United States. Wilson Bulletin 87:520-533.

Banks, R. C. 1964. An experiment on a Flammulated Owl. Condor 66:79.

Bendire, C. E. 1892. *Megascop flammeolus* (Kaup). Flammulated Screech Owl. Pages 374-376 *in* Life histories of North American birds. U. S. Nat. Mus. Spec. Bull. 1:1-466.

Bent, A. C. 1938. Flammulated Screech Owl. Pages 291-295 *in* Life histories of North American birds of prey. Part 2. United States National Museum Bulletin Number 170.

Binford, L. C. 1989. *Otus flammeolus* (Kaup). Flammulated Owl. Page 278 *in* A distributional survey of the birds of the Mexican state of Oaxaca. Ornithological Monographs Number 43.

Bloom, P. H. 1983. Notes on the distribution and biology of the Flammulated Owl in California. Western Birds 14:49-52.

Borell, A. E. 1937. Cooper's Hawk eats a Flammulated Screech Owl. Condor 39:44.

Brewer, R., and K. G. Harrison. 1975. The time of habitat selection by birds. Ibis 117:521-522.

Bull, E. L., and R. G. Anderson. 1978. Notes on Flammulated Owls in northeastern Oregon. Murrelet 59:26-28.

Bull, E. L., A. L. Wright, and M. G. Henjum. 1990. Nesting habitat of Flammulated Owls in Oregon. Journal of Raptor Research 24:52-55.

Cannings, R. J. Assistant Curator. Cowan Vertebrate Museum, Department of Zoology, University of British Columbia, Vancouver, BC. [Personal communication].

Cannings, R. J., and S. R. Cannings. 1982. A Flammulated Owl nests in a box. Murrelet 63:66-68.

Cannings, R. J., S. R. Cannings, J. M. Cannings, and G. P. Sirk. 1978. Successful breeding of the Flammulated Owl in British Columbia. Murrelet 59:74-75.

Caswell, H. 1989. Matrix population methods. Sinauer Associates, Inc., Sunderland, Massachusetts, USA.

Collins, P. W., C. Drost, and G. M. Fellers. 1986. Migratory status of Flammulated Owls in California, with recent records from the California Channel Islands. Western Birds 17:21-31.

Cracraft, J. 1981. Toward a phylogenetic classification of the recent birds of the world (class Aves). Auk 98:681-714.

Critchfield, W. B., and E. L. Little. 1966. Geographic distribution of the pines of the world. United States Department of Agriculture Forest Service Miscellaneous Publication 991.

Delacour, J. 1941. On the species of *Otus scops*. Zoologica 26:133-142.

Earhart, C. M., and N. K. Johnson. 1970. Size dimorphism and food habits of North American owls. Condor 72:251-264.

Ely, C. A. 1962. The birds of southeastern Coahuila, Mexico. Condor 62:34-39.

Franzreb, K. E., and R. D. Ohmart. 1978. The effects of timber harvesting on breeding birds in a mixed coniferous forest. Condor 80:431-441.

Friedmann, H., L. Griscom, and R. T. Moore. 1950. Distributional check-list of the birds of Mexico. Part 1. Pacific Coast Avifauna 20.

Furniss, R. L., and V. M. Carolin. 1977. Western forest insects. United States Department of Agriculture Forest Service Pacific Northwest Range and Experiment Station Miscellaneous Publication 1339.

Ganey, J. L., J. A. Johnson, R. P. Balda, and R. W. Skaggs. 1986. The Mexican Spotted Owl. Pages 145-150 *in* Proceedings of the Southwestern Raptor Management Symposium and Workshop, National Wildlife Federation, Washington, DC, USA.

Garland, S. Masters student. University of Nevada, Reno, NV. [Personal communication]. January 1993.

Garrett, K., and J. Dunn. 1981. Flammulated Owl. Los Angeles Audubon Society, Los Angeles, California, USA.

Gehlbach, F. R. Professor. Department of Biology, Baylor University, Waco, TX. [Personal communication]. Autumn 1993.

Goggans, R. 1986. Habitat use by Flammulated Owls in northeastern Oregon. Thesis. Oregon State University, Corvallis, Oregon, USA.

Goodman, L. A. 1971. On the sensitivity of the intrinsic growth rate to changes in the age-specific birth and death rates. Theoretical Population Biology 2:339-354.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28:1140-1162.

Hasenyager, R. N., J. C. Pederson, and A. W. Heggen. 1979. Flammulated Owl nesting in a squirrel box. Western Birds 10: 224.

Hayward, G. D. 1986. Activity pattern of a pair of

Nesting Flammulated Owls (*Otus flammeolus*) in Idaho. Northwest Science 60:141-144.

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.

Hayward, G. D., and P. Hayward. 1993. Boreal Owl. *in* A. Poole, P. Stettenheim, F. Gill, editors. The birds of North America. Academy of Natural Science, Philadelphia; American Ornithologists' Union, Washington, DC, USA.

Hekstra, G. P. 1982. Description of twenty-four new subspecies of American *Otus*. Bulletin Zoologisch Museum Universiteit van Amsterdam 9:49-63.

Herron, G. B., C. A. Mortimer, and M. S. Rawlings. 1985. Nevada raptors, their biology and management. Nevada Department of Wildlife, Biological Bulletin No. 8.

Hildén, O. 1965. Habitat selection in birds: a review. Annales Zoologici Fennici 2:53-75.

Holt, D. W., J. A. Hoy, and P. L. Wright. 1987. Occurrence and first nest record of Flammulated Owls in Montana. Journal of Raptor Research 21:120-121.

Howell, S. N. G. Scientist, Point Reyes Bird Observatory, Point Reyes, CA. [Personal communication]. May 1993.

Howell, S. N. G., and S. Webb. 1994. Flammulated Owl. *in* A guide to the birds of Mexico and northern Central America. Oxford University Press, New York, New York, USA.

Howie, R. R., and R. Ritcey. 1987. Distribution, habitat selection, and densities of Flammulated Owls in British Columbia. Pages 249-254 *in* R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre, editors. Biology and conservation of northern forest owls. Proceedings of a symposium. United States Department of Agriculture Forest Service General Technical Report RM-142.

Hrubant, H. E. 1955. An analysis of the color phases of the Eastern Screech Owl, *Otus asio*, by the gene frequency method. American Naturalist 89:223-230.

Hubbard, J. P. 1978. Revised check-list of the birds of New Mexico. New Mexico Ornithological Society Publication Number 6.

Hubbard, J. P., and R. S. Crossin. 1974. *Otus flammeolus* (Kaup). Flammulated Owl. Pages 9-10 *in* Notes on northern Mexican birds: an expedition report. Nemouria 14.

Huey, L. M. 1932. Two noteworthy records for California. Auk 49:107.

Hutto, R. L. 1985. Habitat selection by nonbreeding, migratory land birds. Pages 455-476 *in* M. L. Cody editor. Habitat selection in birds. Academic Press, Orlando, Florida, USA.

Jennrich, R. I., and F. B. Turner. 1969. Measurement of a non-circular home range. Journal of Theoretical Biology 22:227-237.

Johnsgard, P. A. 1988. North American owls: biology and natural history. Smithsonian Institution Press, Washington, DC, USA.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

Johnson, N. K. 1963. The supposed migratory status of the Flammulated Owl. Wilson Bulletin 75:174-178.

Johnson, N. K. 1965. The breeding avifaunas of the Sheep and Spring ranges in southern Nevada. Condor 67:93-124.

Johnson, N. K., and W. C. Russell. 1962. Distributional data on certain owls in the western Great Basin. Condor 64:513-514.

Karalus, K. E., and A. W. Eckert. 1974. Flammulated Owl. Pages 156-162 *in* The owls of North America (north of Mexico). Doubleday and Company, Garden City, New York, USA.

Kenyon, K. W. 1947. Cause of death of a Flammulated Owl. Condor 49:88.

Kiff, L. F. Director, Western Foundation of Vertebrate Zoology, Los Angeles, CA. [Personal communication]. Autumn 1993.

Kingery, H. E. 1980. Mountain west region. American Birds 34:205-208.

Korpimaki, E. 1989. Breeding performance of Tengmalm's Owl Aegolius funereus: effects of supplementary feeding in a peak vole year. Ibis 131:51-56.

Lande, R. 1988. Demographic models of the Northern Spotted Owl (*Strix occidentalis caurina*). Oecologia 75:601-607.

Leslie, P. H. 1966. The intrinsic rate of increase and the overlap of successive generations in a population of guillemots (*Uria aalge* Pont.). Journal of Animal Ecology 25:291-301.

Ligon, J. D. 1968. Starvation of spring migrants in the Chiricahua Mountains, Arizona. Condor 70:387-388.

Ligon, J. D. 1969. Some aspects of temperature relations in small owls. Auk 86:458-472.

Linkhart, B. D. 1984. Range, activity, and habitat use by nesting Flammulated Owls in a Colorado ponderosa pine forest. Thesis. Colorado

State University, Fort Collins, Colorado, USA.

Linkhart, B. D., and R. T. Reynolds. 1987. Brood division and postnesting behavior of Flammulated Owls. Wilson Bulletin 99:240-243.

Linkhart, B. D., and R. T. Reynolds. *In press* . *Peromyscus* carcass in the nest of a Flammulated Owl. Journal of Raptor Research.

£omnicki, A. 1988. Population ecology of individuals. Monographs in Population Biology Number 25. Princeton University Press, Princeton, New Jersey, USA.

Marcot, B. G., and R. Hill. 1980. Flammulated Owls in northwestern California. Western Birds 11:141-149.

Marshall, J. T. 1939. Territorial behavior of the Flammulated Screech Owl. Condor 41:71-78.

Marshall, J. T. 1957. Flammulated Screech Owl. Page 652 *in* Birds of pine-oak woodland in southern Arizona and adjacent Mexico. Pacific Coast Avifauna 32:1-125.

Marshall, J. T. 1966. Relationships of certain owls around the Pacific. Natural History Bulletin of the Siam Society 21:235-242.

Marshall, J. T. 1967. Parallel variation in North and Middle American Screech-Owls. Monographs of the Western Foundation of Vertebrate Zoology 1:1-72.

Marshall, J. T. 1978. Systematics of smaller Asian night birds based on voice. Ornithological Monographs 25:1-58.

Marshall, J. T. 1988. Birds lost from a giant sequoia forest during fifty years. Condor 90:359-372

Marshall, J. T., and B. F. King. 1988. Genus *Otus*. Pages 331-336 *in* D. Amadon and J. Bull, editors. Hawks and owls of the world: a distributional and taxonomic list. Proceedings of the Western Foundation of Vertebrate Zoology 3:294-357.

Marti, C. 1992. Barn Owl. *in* A. Poole, P. Stettenheim, F. Gill, editors. The birds of North America. Academy of Natural Sciences, Philadelphia; American Ornithologists' Union, Washington, DC, USA.

McCallum, D. A., and F. R. Gehlbach. 1988. Nest-site preferences of Flammulated Owls in western New Mexico. Condor 90:653-661.

McCallum, D. A., F. R. Gehlbach, and S. W. Webb. (in review). Natural history of the flammulated owl (*Otus flammeolus*) in western New Mexico. Wilson Bulletin.

McDonald, D. B. Research Scientist, Dept. of Zoology, Univ. of Florida, Gainesville, FL. [Personal communication]. November 1993.

McDonald, D. B., and H. Caswell. 1993. Matrix methods for avian demography. Pages 139-185 *in* D. Power, ed. Current Ornithology, Volume 10. Plenum Press, New York.

Mertz, D. B. 1971. The mathematical demography of the California Condor population. American Naturalist 105:437-453.

Miller, A. H. 1947. The structural basis of the voice of the Flammulated Owl. Auk 64:133-135.

Miller, A. H. 1955. The avifauna of the Sierra del Carmen of Coahuila, Mexico. Condor 57:154-178

Monson, G., and A. R. Phillips. 1981. *Otus flammeolus* (Kaup). Pages 70-71 *in* Annotated checklist of the birds of Arizona. University of Arizona Press, Tucson, Arizona, USA.

National Geographic Society. 1987. Birds of North America. Second edition. National Geographic Society, Washington, DC, USA.

Navarro S., A. G. Curator of Birds, Universidad, Nacional, Autonoma de Mexico. [Personal communication]. June 1993.

Navarro S., A. G. 1992. Altitudinal distribution of birds in the Sierra Madre del Sur, Guerrero, Mexico. Condor 94:29-39.

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, editors. Biology and conservation of northern forest owls. United States Department of Agriculture Forest Service General Technical Report M-142.

Norberg, U. M. 1979. Morphology of the wings, legs and tail of three coniferous forest Tits, the Goldcrest, and the Treecreeper in relation to locomotor pattern and feeding. Philosophical Transactions of the Royal Society of London Biological Sciences 287:131-165.

Oberholser, H. C. 1974. Flammulated Scops Owl. Pages 446-447 *in* E. B. Kincaid, Jr., ed. The birdlife of Texas. Univ. Texas Press, Austin, Texas, USA.

Parmelee, D. F. 1992. Snowy Owl. *in* A. Poole, P. Stettenheim, F. Gill, editors. The birds of North America. Academy of Natural Sciences, Philadelphia; American Ornithologists' Union, Washington, DC, USA.

Phillips, A. R. 1942. Notes on the migrations of the Elf and Flammulated Screech Owls. Wilson Bulletin 54:132-137.

Randi, E., G. Fusco, R. Lorenzini, and F. Spina. 1991. Allozyme divergence and phylogenetic relationships within the Strigiformes. Condor 93:295-301.

Reynolds, R. T. Research Scientist. U.S. Forest

Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO [Personal communication]. November 1993.

Reynolds, R. T. 1987. Census of Flammulated Owls. Pages 308-309 *in* R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre, editors. Biology and conservation of northern forest owls. U.S.D.A. For. Svc. Gen. Tech. Rep. RM-142.

Reynolds, R. T., and B. D. Linkhart. 1984. Methods and materials for capturing and monitoring Flammulated Owls. Great Basin Naturalist 44:49-51.

Reynolds, R. T., and B. D. Linkhart. 1987a. Fidelity to territory and mate in Flammulated Owls. Pages 234-238 *in* R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre, editors. Biology and conservation of northern forest owls. Proceedings of a symposium. United States Department of Agriculture Forest Service General Technical Report RM-142.

Reynolds, R. T., and B. D. Linkhart. 1987b. The nesting biology of Flammulated Owls in Colorado. Pages 239-248 *in* R. W. Nero, R. J. Clark, R. J. Knapton, and R. H. Hamre, editors. Biology and conservation of northern forest owls. Proceedings of a symposium. United States Department of Agriculture Forest Service General Technical Report RM-142.

Reynolds, R. T., and B. D. Linkhart. 1990a. Extra-pair copulation and extra-range movements in Flammulated Owls. Ornis Scandinavica 21:74-77.

Reynolds, R. T., and B. D. Linkhart. 1990b. Longevity records for male and female Flammulated Owls. Journal of Field Ornithology 61:243-244.

Reynolds, R. T., and B. D. Linkhart. 1992. Flammulated Owls in ponderosa pine: evidence of preference for old growth. Pages 166-169 *in* Old-growth forests in the Southwest and Rocky Mountain regions: proceedings of a workshop. United States Department of Agriculture Forest Service General Technical Report RM-213.

Reynolds, R. T., and B. D. Linkhart. *In press* . Flammulated Owl. *in* R. Glinski, editor. Raptors of Arizona.

Richmond, M. L., L. R. DeWeese, and R. E. Pillmore. 1980. Brief observations on the breeding biology of the Flammulated Owl in Colorado. Western Birds 11:35-46.

Ricklefs, R. E. 1990. Ecology. Third edition. W. H. Freeman, New York, New York, USA.

Ridgway, R. 1914. *Otus flammeolus* (Kaup). Pages 728-732 *in* The birds of North and Middle America. Part 6. Bulletin of the United States National Museum.

Roberts, T. J., and B. King. 1986. Vocalizations of the owls of the genus *Otus* in Pakistan. Ornis Scandinavica 17:299-305.

Ross, A. 1969. Ecological aspects of the food habits of insectivorous Screech Owls. Proceedings of the Western Foundation of Vertebrate Zoology 1:301-344.

St. John, D. 1991. The distribution of the flammulated owl (*Otus flammeolus*) in the south Okanagan. Unpublished report prepared for B.C. Environment and Okanagan Wildlife Heritage Fund Society.

Schaldach, W. J., Jr. 1969. Further notes on the avifauna of Colima and adjacent Jalisco, Mexico. Anales del Instituto de Biologica Universidad Nacional Autonoma de Mexico Seri Zoologica 40:299-316.

Shields, W. M. 1982. Philopatry, inbreeding, and the evolution of sex. State University of New York Press, New York, USA.

Sibley, C. G., and J. E. Ahlquist. 1990. Phylogeny and classification of birds. Yale University Press, New Haven, Connecticut, USA.

Smith, W. G. 1891. Nesting of the Flammulated Screech Owl. Ornithologist and Oologist 16:27-28.

Stager, K. E. 1954. Birds of the Barranca de Cobre region of southwestern Chihuahua, Mexico. Condor 56:21-32.

Sutton, G. M., and T. D. Burleigh. 1940. Birds of Las Vigas, Veracruz. Auk 57:234-243.

Svardson, G. 1949. Competition and habitat selection in birds. Oikos 1:157-174.

van der Weyden, W. J. 1975. Scops and Screech Owls: vocal evidence for a basic subdivision in the genus *Otus* (Strigidae). Ardea 63:65-77.

van Hoose, S. G. 1955. Distributional and breeding records of some birds from Coahuila. Wilson Bulletin 67:302-303.

van Woudenberg, A. M. Student. Univeristy of British Columbia, Vancouver, BC. [Personal communication]. March 1993.

van Woudenberg, A. M. 1992. Integrated management of Flammulated Owl breeding habitat and timber harvest in British Columbia. Thesis. University of British Columbia, Vancouver, British Columbia, Canada.

Voous, K. H. 1989. Flammulated Owl. Pages 53-58 *in* Owls of the Northern Hemisphere. MIT Press, Cambridge, Massachusetts, USA.

Webb, B. 1982. Distribution and nesting requirements of montane forest owls in Colorado. Part III. Flammulated Owl (*Otus flammeolus*). Journal of Colorado Field Ornithologists 16:76-81.

Wetmore, A. 1956. A check-list of the fossil and prehistoric birds of North America and the West Indies. Smithsonian Miscellaneous Collections 131:1-105.

Wilson, R. G., and H. Ceballos L. *In press* . The birds of Mexico City. Second edition.

Winter, J. 1971. Some critical notes on finding and seeing the Flammulated Owl. Birding 3:204-209.

Winter, J. 1974. The distribution of the Flammulated Owl in California. Western Birds 5:25-44.