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BARRED OWL HABITAT AND PREY: A REVIEW AND SYNTHESIS OF THE LITERATURE

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ABSTRACT.—Barred Owls (*Strix varia*) historically inhabited the forests of eastern North America. During the last century, they expanded their range to include forests throughout the southern provinces of Canada, southeastern Alaska, British Columbia, Washington, Oregon, and northern California. To date, there has been no synthesis of the varied habitats or prey used by Barred Owls in their expanded range. Here I review and synthesize studies concerning habitat ($N = 114$) and prey ($N = 43$) of Barred Owls throughout North America north of Mexico. Barred Owls nested in wilderness areas and national parks as well as small suburban woodlots. They typically preferred old or mature, mixed deciduous/coniferous forests with fairly high canopy closure. Barred Owl nests in natural locations ($N = 341$) were in cavities (74.8%), hawk nests (12.9%), tops of hollow trees (8.2%), squirrel nests (2.1%) and other locations (2.1%). Trees used by Barred Owls for nesting ($N = 169$) included 22 genera, although one-fourth of all reported nest trees were *Populus.* Barred Owls used significantly more coniferous nest trees than deciduous nest trees in their expanded range vs. their historic range. They also nested in nest-boxes ($N = 103$), in buildings ($N = 6$), on nesting platforms ($N = 2$), on the ground ($N = 2$), in a creek bank ($N = 1$), and under a bridge ($N = 1$). Prey individuals ($N = 7077$) obtained from pellets ($N = 5504$) were mammals (74.7%), birds (8.3%), amphibians (6.4%), insects and spiders (5.6%), crayfish (3.0%), fish (1.5%), reptiles, snails and slugs, and earthworms (<1.0% each). The distribution of prey types documented by other means (e.g., observations, prey remains; $N = 1573$) was significantly different, due especially to more earthworms in non-pellet samples: mammals (62.0%), birds (13.5%), insects and spiders (9.5%), amphibians (4.8%), earthworms (4.5%), fish (3.3%), reptiles (1.1%), snails, and crayfish (<1.0% each). The distributions of prey types in all samples that could be placed into winter or non-winter months ($N = 4631$) differed seasonally, with more mammals in the winter diet (98.4%, vs. 58.9% in non-winter months) and more birds (11.9%), insects or spiders (11.4%), amphibians (10.7%), earthworms (2.3%), fish (2.0%), and crayfish (2.0%) in non-winter months.

KEY WORDS: *Barred Owl*; Strix varia; *habitat*; *prey*.

HÁBITAT Y PRESAS DE *STRIX VARIA*: UNA REVISIÓN Y SÍNTESIS DE LA LITERATURA

RESUMEN.—Históricamente el búho *Strix varia* habitaba los bosques del este de Norte América. Sin embargo, durante el último siglo estas aves expandieron su distribución incluyendo los bosques de todas las provincias del sur de Canadá, sudeste de Alaska, Columbia Británica, Washington, Oregón y norte de California. Hasta el momento, no se ha hecho ninguna síntesis de la variedad de presas y hábitats usados por *S. varia* en su área de distribución expandida. Aquí, reviso y sintetizo los estudios sobre el hábitat ($N = 114$) y las presas ($N = 43$) de *S. varia* en América del Norte, excluyendo México. Este búho nidificó en áreas naturales protegidas y parques nacionales, como también en pequeños fragmentos de bosque suburbanos. Típicamente prefirieron bosques mixtos deciduos y de coníferas en estado maduro o primario con un dosel bastante cerrado. Los nidos de *S. varia* en los ambientes naturales ($N = 341$) se encontraron en cavidades

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(74.8%), en nidos de halcones (12.9%), encima de árboles huecos (8.2%), en nidos de ardillas (2.1%) y en otros sitios (2.1%). Los árboles usados para nidificar ($N = 169$) incluyeron 22 géneros, aunque un cuarto de todos los árboles con nido fueron del género *Populus.* Estos búhos utilizaron significativamente más coníferas que árboles deciduos para nidificar en las áreas de expansión que en sus áreas de distribución histórica. También construyeron nidos en cajas de nidificación ($N = 103$), en edificios ($N = 6$), sobre plataformas de nidificación ($N = 2$), sobre el suelo ($N = 2$), en paredes de acantilados ($N = 1$) y bajo un puente ($N = 1$). Los individuos presa ($N = 7077$) obtenidos a partir de egagrópilas ($N = 5504$) fueron mamíferos (74.7%), aves (8.3%), anfibios (6.4%), insectos y arañas (5.6%), cangrejos (3.0%), peces (1.5%), reptiles, caracoles y babosas, y lombrices ($<$1.0% cada uno). La distribución de los tipos de presa reportada a partir de otros medios (e.g., observaciones, restos de presas; $N = 1573$) fue significativamente diferente debido especialmente a la presencia de más lombrices en las muestras que no provinieron de egagrópilas: mamíferos (62.0%), aves (13.5%), insectos y arañas (9.5%), anfibios (4.8%), lombrices (4.5%), peces (3.3%), reptiles (1.1%), caracoles y cangrejos ($<$1.0% cada uno). La distribución de presas considerando todas las muestras que pudieron ser asignadas a los meses de invierno y a los de verano ($N = 4631$) difirieron estacionalmente, con más mamíferos en la dieta de invierno (98.4%, vs. 58.9% en los meses de verano) y más aves (11.9%), insectos o arañas (11.4%), anfibios (10.7%), lombrices (2.3%), peces (2.0%) y cangrejos (2.0%) en los meses que no correspondieron a los de invierno.

[Traducción del equipo editorial]

During the past century, Barred Owls (*Strix varia*) expanded their range from eastern North America to much of central and western North America (Mazur and James 2000), from Saskatchewan (Mazur et al. 1998, Takats 1998), British Columbia (Rand 1944, Hobbs 2005), and southeastern Alaska (D. Gibson pers. comm.) through Washington (Herter and Hicks 2000, Gremel 2005), Oregon (Kelly et al. 2003) and central California (Jensen et al. 2004, Steger et al. 2006). To date, there has been no synthesis of the varied habitats or prey used by Barred Owls in their expanded range. Here I review and synthesize publications, unpublished reports, and personal communications concerning habitat use and prey of Barred Owls throughout North America north of Mexico (1) in total; (2) by ecoregion (Bailey 1998) to present the varied forests used by Barred Owls and to compare use of habitats and prey across ecoregion domains; and (3) by their historic range vs. expanded range to see whether Barred Owls used different habitats or prey in their expanded range. In addition, I compare prey taken by Barred Owls in winter vs. non-winter months to determine seasonal variations in diet.

METHODS

I compiled publications, theses, dissertations, reports, and personal communications (''studies'') that provided original field data concerning habitat use and food habits of Barred Owls. Other than two studies with regional locations (Fisher 1893, Apfelbaum and Seelbach 1983) and a portion of one study with a state-only location (Bent 1938), I mapped the location(s) of each study relative to the distribution of ecoregions developed by Bailey (1998; R. Bailey pers. comm.). This hierarchical system is composed of ecoregion domains, divisions, and provinces based primarily on climatic conditions and on the prevailing plant formations determined by those conditions. North America north of Mexico has four ecoregion domains: (1) ''Polar'' with tundras and boreal forests; (2) ''Humid Temperate'' with broadleaf deciduous and needleleaf evergreen forests; (3) ''Dry'' with arid deserts, semiarid steppes, montane coniferous forests, and alpine meadows; and (4) ''Humid Tropical'' with savannahs (Bailey 1998). Each domain is divided into divisions which are further subdivided into provinces. Mountains exhibiting altitudinal zonation and having the climatic regime of the adjacent lowlands are distinguished according to the character of the zonation (R. Bailey pers. comm.). I analyzed habitat use and food habits of Barred Owls across ecoregion domains and between their historic range (i.e., prior to about 1900; Manitoba and North Dakota eastward), and their expanded range (Saskatchewan and Montana westward; Mazur and James 2000).

''Sites'' were single or multiple detections or observations of Barred Owls where neither nests nor fledglings were found, whereas ''nest sites'' included nests or fledglings; both sites and nest sites excluded nests in human-made structures. I differentiated among: (1) ''preference'' results that were statistical analyses of variables of Barred Owl nest sites or sites relative to the surrounding area or to random plots; (2) ''description'' results that described variables without statistical analysis; and (3) ''comparison'' results that compared, via statistics or descriptions, Barred Owl nest sites or sites to those of other sympatric owl species. Many studies had two or three types of results for different variables. Herein, I used ''preference'' and ''avoidance'' only when reporting preference results that showed use of habitats significantly more or less than expected. I focused primarily on the five habitat variables that were most frequently reported: elevation, slope, proximity to water (streams, rivers, wetlands, lakes), forest composition, and forest age. Because of the relative nature of these variables throughout North America, I used the categories and definitions of these five variables as provided by the studies and did not attempt to standardize them. Because forest age was reported in different classifications in various studies, I simply used two categories for that

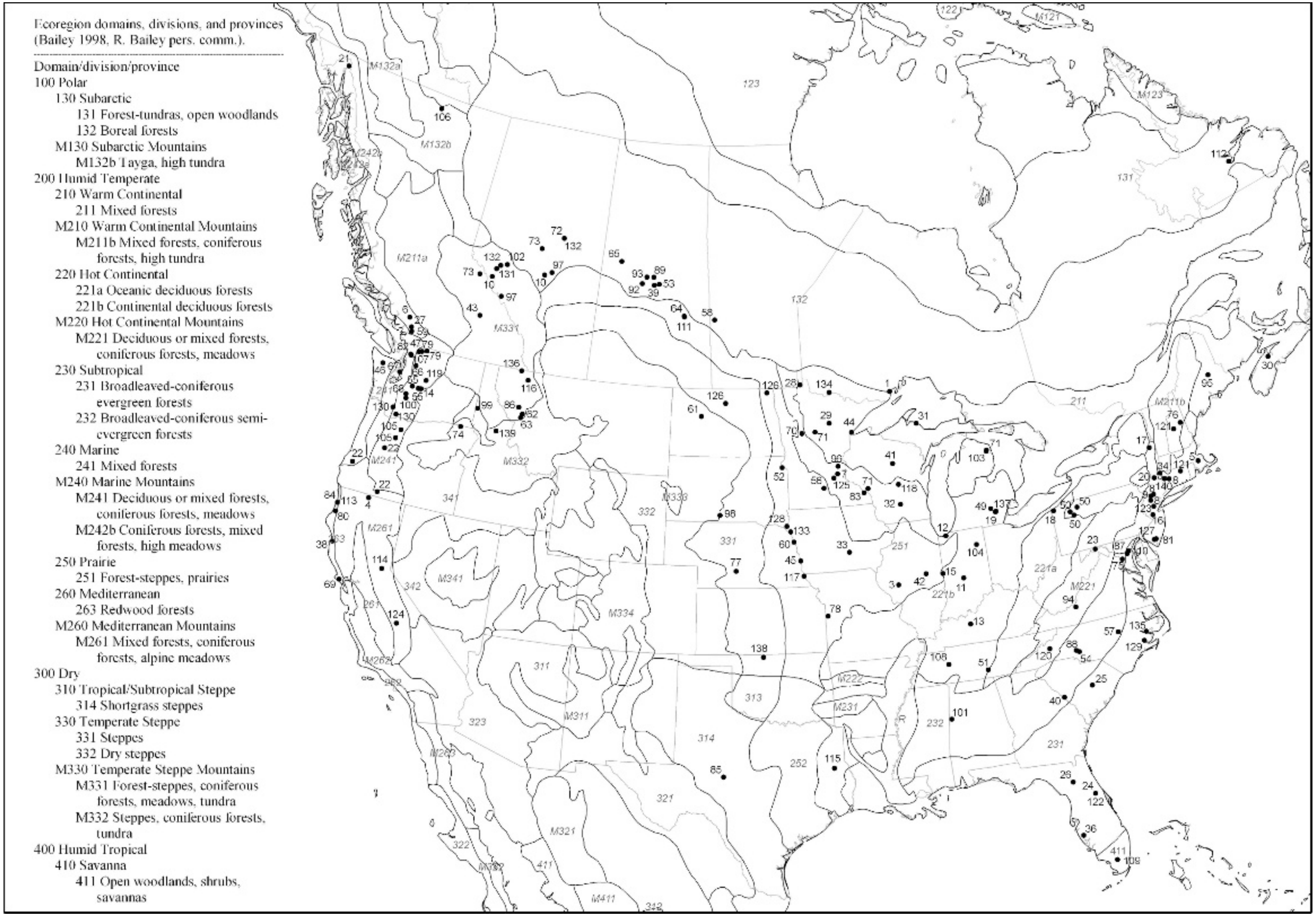

Figure 1. Location of Barred Owl studies (numbers in regular font) listed in Appendix and ecoregion provinces (light italics; see legend).

variable: ''old or mature'' and ''intermediate or young.'' I pooled studies that reported results within the same study area by the same author(s) during either the same year or sequential years (e.g., Devereux 1982 with Devereux and Mosher 1984); I reported all studies in the Appendix but only the earliest of pooled studies in the text. I recorded ''3'' for studies that reported sample sizes of ''few'' (Apfelbaum and Seelbach 1983) or ''several'' (Dingle 1926). I included habitat information concerning sites of hybrids between Barred and Northern Spotted Owls (*S. occidentalis caurina*; Fullerton and Meekins 2004, $N = 2$; Seamans et al. 2004, $N = 2$).

For studies that provided occurrence of taxonomic prey rather than the number of individual prey items per stomach (Mendall 1944) or pellet (Coon 1917, Korschgen and Stuart 1972, Leder and Walters 1980), I attributed one prey item per stomach or pellet, which probably underestimated numbers of some prey. I included probable prey captures of a Northern Spotted Owl (Leskiw and Gutiérrez 1998) and of a Great Gray Owl (*S. nebulosa*; Graves and Niemi 2006). I divided prey studies into two seasonal categories: ''winter'' (November to February or specifically called ''winter'' data by investigators) and ''non-winter'' (March to October), excluding studies which combined data for all seasons. In one study which combined 54 winter pellets with 14 pellets of undisclosed season (Cahn and Kemp 1930), I assumed all were winter pellets.

When comparing variables, I followed accepted statistical protocols (Conover 1980, Zar 1984, Fowler et al. 1998), avoiding the use of chi-square tests if any expected value for a given category <1 or if >20% of the expected categorical values <5. In some cases, in order to decrease the number of low expected values, I grouped similar variables and excluded small-sample categories. Because of low sample sizes, I excluded some studies from some statistical comparisons: studies in the humid tropical domain ($N = 1$) from ecoregion domain tests; comparison studies that addressed the five variables relative to nesting season habitat ($N = 4$) from historic vs. expanded range tests; and snail and slug (Gastropoda) prey ($N = 16$) from seasonal diet analyses.

RESULTS

Habitat. A total of 114 studies reported habitat use by Barred Owls (Appendix), of which 35 (30.7%) were single-sample description studies. The studies were located in 4 ecoregion domains, 16 divisions, and 22 provinces, ranging from the mixed forests of Nova Scotia to the redwood (*Sequoia sempervirens*) forests of California, and from the open woodlands, shrubs, and savannahs of southern Florida to the mixed forests of southeast Alaska (Fig. 1, Appendix).

Nesting habitat. Studies documented 466 nest sites and 1411 sites during the nesting season (Appendix). Barred Owls showed preference for areas of low elevation and flatter slope in the deciduous forests of Connecticut (Yannielli 1988) and coniferous forests of Alberta (Piorecky 2003) and Washington (Pearson and Livezey 2003, Singleton et. al 2005; Table 1). However, elevation and slope were nonsignificant variables in the eastern deciduous forests of Maryland (Devereux 1982) and Connecticut (Falk 1990) and the boreal forests of Manitoba (Hinam 2001; Table 1). Two studies (Nicholls and Warner 1972, Fuller 1979) that showed preference for upland oak (*Quercus*) forests were conducted in the same study area in Minnesota. Some Barred Owls in one of these studies frequently used alder (*Alnus* spp.) lowland (Fuller 1979; recorded as 0.5 low and 0.5 high elevation in Table 1); the author of this study suggested that these somewhat contradictory results may have been due to differences in sampling intervals and lack of alder lowlands in the home ranges of the Barred Owls in the other Minnesota study.

Of the studies that simply described elevation or slope, 11 of 13 described Barred Owl use of low-elevation areas, and seven of eight studies reported use of forests on terrain with low slope (Table 1). Relative to sites of Northern Spotted Owls, Barred Owl sites were significantly lower in elevation in the western Cascade Mountains of Washington (Pearson and Livezey 2003, Hamer pers. comm.) and were significantly lower in elevation and flatter in slope in the Olympic Mountains of Washington (Gremel 2005; Table 1).

Barred Owls during the nesting season preferred sites near water in seven of 15 of the preference studies that tested that variable (Table 1). These seven studies were conducted in deciduous forests of Connecticut (Yannielli 1988), mixed forests of Michigan (Elody and Sloan 1985), oak and palm (*Sabal palmetto*) woodlands of Florida (Franz 1992), boreal forests of Manitoba (Hinam 2001), and coniferous forests of Alberta (Olsen 1999, Piorecky 2003, Takats 1998; Table 1). Two studies (Fuller 1979, Mazur et al. 1997a) provided differing preference results for nesting habitat relative to proximity to water: (1) some radio-tagged Barred Owls in the deciduous forests of Minnesota preferred oak uplands, while others preferred mixed deciduous lowlands (Fuller 1979); (2) in the boreal forests of Saskatchewan, 3.0-km-radius circles centered on Barred Owl locations contained significantly more water than those of random locations, but 1.5-km-circles did not (Mazur et al. 1997a). Two preference studies showed avoidance of wetlands because, suggested the researchers, the forested wetlands of those areas were too dense for owl flight (Nicholls and Warner 1972, Van Ael 1996). Proximity to water was not a significant variable in four other preference studies (Devereux 1982, Falk 1990, Mazur 1997, Hamer pers. comm.).

In contrast, almost all descriptions that reported proximity of sites to water noted that Barred Owl sites were situated close to water (96.9%, Table 1). In comparison studies, Barred Owl sites were significantly closer to water than those of Great Horned Owls (*Bubo virginianus*; Bosakowski et al. 1987) and Northern Spotted Owls (Herter and Hicks 2000; Table 1).

Mixed coniferous/deciduous forests and deciduous forests were used by Barred Owls approximately equally during the nesting season in preference studies, while coniferous forests were used less than one-half as often as these other forests (Table 1). Most description studies were located in mixed forests (Table 1). In a comparison study, Barred Owl sites contained more deciduous forest than did sites typically used by Northern Spotted Owls (Herter and Hicks 2000).

Mature or old forests were used by Barred Owls during the nesting season significantly more than young forests in all 13 preference studies that analyzed that variable (Table 1). In addition, mature or old forests were used by Barred Owls in 27 of 30 (90.0%) descriptions that mentioned forest age (Table 1). Of the three studies in which Barred Owls used younger forests, two described large remnant individual trees or stands of trees present (Duncan and Kearns 1997, J. Buchanan pers. comm.); in the third study, nest boxes in young forests were used (Elderkin 1987). In comparisons, Barred Owl sites in the Washington Cascades contained significantly less old forest within 0.8 km of site-centers than did those of Northern Spotted Owls (Herter and Hicks 2000) and site-centers of Barred Owls were located in forest stands that were significantly younger than those of Northern Spotted Owls (Pearson and Livezey 2003). Also, Barred Owl sites in the mixed forests of New Jersey contained significantly more mature forest than did those of Eastern Screech-Owls (*Otus asio*; Bosakowski et al. 1987). Low expected values prohibited comparisons of elevation, slope, proximity to water, forest composition, and forest age (Table 1) among the three ecoregion domains and between eastern and western studies in preference and description studies.

The amount of habitat fragmentation and proximity to human development were tested in preference studies with equivocal results. Measures of fragmentation were positive in two studies (sites were

Table 1. Studies (N) that reported nesting, roosting, or foraging habitat of Barred Owls relative to elevation, slope, proximity to water, forest composition, or forest age by preferences (Pref), descriptions (Desc), or comparisons to other owl species (Comp).[a]

	ELEVATION			SLOPE			PROXIMITY TO WATER			FOREST COMPOSITION			FOREST AGE		
	LOW	HIGH	NS[b]	FLAT	STEEP	NS	CLOSE	FAR	NS	MIXED CONIF./ DECID.	CONIF.	DECID.	OLD OR MATURE	INTERMED. OR YOUNG	APPROX. EQUAL USE OF BOTH
Nesting															
Pref	4.5[c]	1.5[c]	3	4	0	3	8	2.5[c]	4.5[c]	6	2.5[c]	6.5[c]	13	0	0
Desc	11	2	–	7	1	–	31	1	–	35	9	15	27	2	1
Comp	3	0	0	1	0	0	2	0	0	0	0	1	1	2	0
Roosting															
Desc	0	0	0	0	0	0	0	0	0	1	2	2	2	1	0
Foraging															
Desc	0.5[c]	1.5[c]	0	0	0	0	0.5[c]	1.5[c]	0	1	1	3	1	1	0

[a] Reference study numbers. Nesting, preference: 23, 31, 34, 36, 37, 48, 50, 58, 89, 90, 94, 96, 97, 100, 102, 119, 131, 134, 140. Nesting, description: 1, 2, 4, 5, 6, 10, 12, 13, 14, 16, 19, 21, 22, 25, 27–30, 36, 38, 40, 43, 45, 46, 47, 51–54, 58, 59, 61, 62, 65–70, 73–75, 77, 79–82, 85, 88, 91, 97–100, 103, 105–107, 112–117, 123, 126–130, 133, 135, 137–139. Nesting, comparison: 9, 46, 48, 55, 100. Roosting, description: 3, 9, 89, 93, 131. Foraging, description: 25, 59, 89, 119, 131. No studies used preference analyses in roosting or foraging habitat for any of these five variables.

[b] Not significant.

[c] When a single study presented preference for two results for a variable, I recorded 0.5 study for one result and 0.5 study for the other.

Table 2. Locations (N) of natural nests used by Barred Owls.[a]

	CAVITY	TOP OF HOLLOW OR BROKEN-TOPPED TREE	TREE FORK OR SPLIT LIMB	MISTLETOE CLUMP	HAWK NEST	SQUIRREL NEST	ON GROUND OR IN STREAMBANK HOLE	TOTAL
No. nests	255	28	2	2	44	7	3	341
(%)	74.8	8.2	0.6	0.6	12.9	2.1	0.9	

[a] Reference study numbers: 1, 2, 4, 5, 8, 14, 16, 23, 29, 36, 37, 39, 42, 43, 50, 54, 59, 62, 64, 70, 71, 73, 75, 82, 83, 87, 88, 91, 97, 103, 105, 109, 115, 117, 119, 123, 125, 131, 132, 137.

close to openings, Devereux 1982; more edge, more forest patches, more small forest patches, Olsen 1999), negative in two studies (less edge, Yannielli 1988, Van Ael 1996), and not significant in two studies (amount of fragmentation, Hinam 2001, Hamer pers. comm.). Analyses of proximity to human development were both positive (closer to trails) and negative (fewer close buildings) in one study (Yannielli 1988) and not significant in another (distance to farmland, McGarigal and Fraser 1984). Barred Owls nested in areas ranging from small suburban woodlots (Yannielli 1988, Harrold 2003, Mason 2004) to wilderness areas (Wright and Hayward 1998) and national parks (North Cascades National Park, Kuntz and Christophersen 1996; Olympic National Park, Gremel 2005; Mt. Rainier National Park, J. Schaberl pers. comm.). In a comparison study, Barred Owl sites in New Jersey had significantly fewer clearings and were significantly farther from human habitations than were those of Great Horned Owls and Eastern Screech-Owls (Bosakowski et al. 1987). Similarly, another comparison study indicated that when numbers of large deciduous woodlots with hollow trees decreased in southeastern Michigan, Great Horned Owls replaced Barred Owls (Craighead and Craighead 1969).

Canopy closures of nest sites and sites during the nesting season were significantly higher than expected in three of the five preference studies that tested that variable (67–80% in Takats 1998; ≥70% in Hinam 2001; ≥70% in Singleton et. al 2005); those in the other two preference studies were 68% (Devereux 1982) and 51–70% (Piorecky 2003). In descriptions, canopy closures of sites of the deciduous forests of Manitoba were >71% (Duncan and Kearns 1997), those of the marine-climate mountains of British Columbia and Washington were 50–60% (J. Hobbs pers. comm.), 50–70% (R. Christophersen pers. comm.), 70.6% (Buchanan et al. 2004), >70% (J. Schaberl pers. comm.), and 86.0 ± 1.7% (Gremel 2005), and those of 30 of 34 sites in the redwood forests of California were 85–90% (L. Diller pers. comm.).

Barred Owl nests in natural locations ($N = 341$) were in cavities and other locations (Table 2). Stick nests occupied by Barred Owls were attributed to Red-shouldered Hawks (*Buteo lineatus*) or Cooper's Hawks (*Accipter cooperii*, $N = 18$), Red-shouldered Hawks ($N = 8$), Red-tailed Hawks (*Buteo jamaicensis*, $N = 4$), Northern Goshawks (*Accipiter gentilis*, $N = 3$), Broad-winged Hawk (*Buteo platypterus*, $N = 1$), and Cooper's Hawk ($N = 1$; Bent 1938, Johnson and Follen 1984, Shupe 1985, Postupalsky et al. 1997, Buchanan et al. 2004, J. Hobbs pers. comm.; nine of 44 nests in Table 4 were not attributed to any species). Two pairs of Barred Owls nested on the ground (Robertson 1959, Postupalsky et al. 1997), and one pair nested in a creek bank (Shackelford and Earley 1996). Comparison of seven locations of natural nests (Table 2) across ecoregion domains had prohibitively low expected values; after excluding two small-sample categories (mistletoe clump; on ground or in streambank hole) and combining two sets of similar categories (top of hollow or broken-topped tree with tree fork or split limb; hawk nest with squirrel nest), expected values were still too low. Further exclusion of the domain (Polar) with the smallest number of nests (5.7%) yielded adequate expected values, but no significant difference in the distribution of the three combined groups of natural nest locations in humid temperate vs. dry domains ($\chi^2_2 = 3.17$, $P > 0.10$). Between eastern and western studies, low expected values prohibited testing of the seven locations of natural nests. After excluding and grouping categories as described above, there were no significant differences among the three groups of natural nest locations ($\chi^2_2 = 3.16$, $P > 0.10$).

Barred Owls also nested in human-made locations. They nested in nest boxes ($N = 103$; Appen-

Table 3. Trees used as nest trees by Barred Owls.[a]

TREE SPECIES	NO. NEST TREES	% OF CONIFEROUS NEST TREES	% OF DECIDUOUS NEST TREES	% OF ALL NEST TREES
Palm trees				
Cabbage palmetto (*Sabal palmetto*)	3			1.8
Coniferous trees	33			19.5
Pine (*Pinus* spp.)	2	6.1		1.2
Larch (*Larix* spp.)	6	18.2		3.6
Spruce (*Picea* spp.)	5	15.2		3.0
Hemlock (*Tsuga* spp.)	2	6.1		1.2
Douglas-fir (*Pseudotsuga menziesii*)	12	36.4		7.1
Fir (*Abies* spp.)	2	6.1		1.2
Cedar (*Thuja* spp.)	4	12.1		2.4
Deciduous trees	133			78.7
Willow (*Salix* spp.)	1		0.8	0.6
Poplar, cottonwood, aspen (*Populus* spp.)	40		30.1	23.7
Tulip poplar (*Liriodendron tulipifera*)	2		1.2	1.2
Hickory (*Carya* spp.)	3		2.3	1.8
Walnut (*Juglans* spp.)	1		0.6	0.6
Birch (*Betula* spp.)	5		3.8	3.0
Beech (*Fagus* spp.)	17		12.8	10.1
Oak (*Quercus* spp.)	24		18.0	14.2
Elm (*Ulmus* spp.)	12		9.0	7.1
Sweetgum (*Liquidambar styraciflua*)	3		2.3	1.8
Sycamore (*Platanus occidentalis*)	2		1.5	1.2
Maple (*Acer* spp.)	16		12.0	9.5
Ash (*Fraxinus* spp.)	2		1.2	1.2
Linden (*Tilia* spp.)	5		3.8	3.0
Total	169			

[a] Reference study numbers: 1, 2, 5, 9, 11, 14, 16, 21, 29, 36, 37, 42, 43, 50, 54, 59, 62, 64, 70, 73, 75, 82, 83, 87, 91, 97, 103, 105, 117, 119, 123, 125, 131, 137.

dix), in buildings ($N = 6$; Crosby 1912, Houston 1999, Harrold 2003, Mason 2004), on nesting platforms ($N = 2$; Postupalsky et al. 1997, Takats Priestley 2004), and under a bridge ($N = 1$; Gibbs 1988). Barred Owls sometimes used nest boxes when natural nesting opportunities were available (Elderkin 1987, Johnson and Follen 1984).

Trees used by Barred Owls for nesting ($N = 169$) included 22 genera (Table 3). Barred Owls used deciduous trees (78.7%) four times more often than coniferous trees (19.5%). Approximately one-fourth (23.7%) of all reported nest trees were *Populus* (Table 3). The distributions of nest tree types (coniferous vs. deciduous) did not differ among the three domains ($\chi^2_2 = 0.37$, $P > 0.90$) but did differ significantly between the eastern and western studies ($\chi^2_1 = 33.58$, $P < 0.001$), with greater use of coniferous trees in the west (42.4%, 28 of 66) than the east (1.4%, 1 of 69). Nest trees averaged 18.2 m in height ($N = 77$) and 65.7 cm in diameter at breast height (dbh; $N = 94$), and nest cavities averaged 9.8 m above the ground ($N = 159$; Table 4).

Roosting habitat. Barred Owls roosted in coniferous, deciduous, and mixed forest, and often roosted during the day in forest stands where they had hunted the previous night (Mazur 1997, Mazur et al. 2000). A winter roost in New Jersey was located in a grove of Norway spruce (*Picea abies*) that bordered a large field and marsh (Bosakowski et al. 1987). In Illinois, Barred Owls roosted and foraged in a pine (*Pinus* spp.) plantation composed of trees 3 m tall (Applegate 1975). In boreal forests of Saskatchewan (Mazur et al. 2000) and primarily coniferous forests of Alberta (Takats 1998), however, most roosts were in deciduous trees. In the Saskatchewan study, summer roosts were in quaking aspen (*Populus tremuloides*, $N = 5$), balsam poplar (*P. balsamifera*; $N = 2$), white spruce (*Picea glauca*, $N = 1$), and black spruce (*P. mariana*, $N = 1$), and winter roosts in quaking aspen ($N = 3$), white spruce ($N = 2$), jack

Table 4. Nest tree and nest cavity measurements for Barred Owls (mean ± SD) (range) (*N*) by ecological province (EP) and study (ordered by EP number then study number).

EP No.	Location	Study No.	Nest-Tree Height (m)	Nest-Tree DBH (cm)	Nest-Tree Diameter at Cavity (cm)	Cavity Height Above Ground (m)	Cavity Depth (cm)	Cavity Diameter (Inside) (cm)	Nest-floor Area (cm²)
–	N. Amer.	2				9.0 ± 5.7 (1.5–30.5) (49)[a]			
132	ON	1	9.9 ± 1.1 (9.1–10.7) (2)	68.6 ± 10.7 (61.0–76.2) (2)					
132	SK	39				6.1 (1)			
132	AB	73				8.4 ± 1.1 (7.6–9.1) (2)	46 (1)		
132	SK	91	18.8 ± 6.2 (7.8–29.5) (15)	47.4 ± 12.8 (31.9–74.5) (15)		13.3 ± 4.1 (6.9–22.3) (15)			
211	MI	103		48.4 (27–74) (18)	44.5 (30–64) (14)	6.8 (1.5–12.8) (22)	35.2 (0–112) (18)	25 (18–44) (19)	508 (250–1540) (19)
221a	NJ	16				6.1 (1)			
221a	NJ	123				7.3 (1)	35.6 (1)	40.6 (1)	
221b	MN	83	4.3 (1)			4.3 (1)			
221b	MN	125				3 (1)	60 (1)		
M221	MD	23		61 ± 15 (42–88) (7)	46 ± 8 (36–54) (4)	9.1 ± 2.9 (4–14) (7)[b]	54 ± 44 (3–130) (6)	33 ± 8 (22–41) (6)	
231	FL	36	5.9 ± 1.9 (1.6–7.7) (8)				71.0 ± 41.6 (19.5–164.0) (8)	55.0 ± 21.6 (31.3–89.0) (8)	
231	MD	87		89 (1)		4 (1)	76 (1)	51 (1)	
232	NC	54[c]	20.76 (9–27.9) (11)	78.54 (30–126) (11)	42.82 (38–60) (4)	8.74 (4.8–17.9) (10)	15.45 (0–33) (7)	43.81 (21.6–120) (7)	686.6 (366–1256) (4)
232	NC	54[d]	13.03 (5.9–24.5) (9)	62.53 (45–100) (9)	43.16 (21–57) (7)	6.86 (4.4–8.7) (9)	29.85 (3–100) (7)	28.79 (17–37) (7)	636.3 (227–1075) (6)
241	OR	105	28.0 ± 8.6 (18–41) (5)	98.0 ± 32.3 (66–143) (5)	71.8 ± 16.0 (52–91) (4)	19.4 ± 3.8 (14–23) (5)	45.5 ± 19.9 (13–100) (4)[e]	49.5 ± 9.5 (36–57) (4)	
241	WA	82				10 (1)	1 (1)		
M241	WA	14	25.1 ± 2.6 (10)	106.0 ± 15.4 (10)		16.4 ± 1.2 (10)			

Table 4. Continued.

EP No.	Location	Study No.	Nest-Tree Height (m)	Nest-Tree DBH (cm)	Nest-Tree Diameter at Cavity (cm)	Cavity Height Above Ground (m)	Cavity Depth (cm)	Cavity Diameter (Inside) (cm)	Nest-floor Area (cm²)
251	IL	42					1.2 (1)	30.5 (1)	
251	SK	64				5.5 (1)			
251	NE	117				6.5 (6)			
M331	AB	97	16.0 ± 2.6	51.6 ± 4.3		10.4 ± 2.1			
			(6.5–29.2) (10)	(33.5–77) (10)		(5.8–26.8) (10)			
M331	AB	131	25.3 ± 3.6	74.0 ± 8.7		15.6 ± 2.6			
			(19.0–28.9) (6)	(61.8–85.0) (6)		(10.4–17.3) (6)			
Weighted mean of means (*N* of total)			18.2 (77)	65.7 (94)	47.5 (33)	9.8 (159)	39.4 (55)	35.7 (53)	559.2 (29)

[a] Apfelbaum and Seelbach (1983) did not differentiate between cavity nests and other nests.

[b] The nest-cavity heights were significantly higher than (3 m higher than) random cavities in Devereux (1982) and Devereux and Mosher (1984).

[c] For the suburban nests in Harrold (2003).

[d] For the rural nests in Harrold (2003).

[e] I converted one cavity depth of ">100 cm" reported by R. Gerhardt (pers. comm.) to 100 cm here, so the actual mean and maximum were higher.

pine (*Pinus banksiana, N* = 1), and white birch (*Betula papyrifera, N* = 1; Mazur et al. 2000). In that study, investigators suggested that Barred Owls did not select thick cover for roosting because use of deciduous trees in the summer allowed the owls to be cooled by breezes and use of leafless deciduous stands in the winter permitted the owls to be warmed by the sun (Mazur et al. 2000). In Alberta (Takats 1998), 25 roost-trees were quaking aspen (*N* = 11), balsam poplar (*N* = 8), and white spruce (*N* = 6). These roost trees averaged 35.7 cm in dbh (range 17.0–69.7 cm), and stand characteristics of roosting sites were similar to those of nesting stands (Takats 1998). Twenty stands had canopy closures of 71–100%, four had 51–70%, and one had 31–50%; 10 stands were in stand-height class 21.1–24 m, eight were in 24.1–27 m, five were >27 m, and two were ≤21 m (Takats 1998).

Foraging habitat. Foraging sites of Barred Owls in two studies conducted in the same study area in Minnesota were higher-elevation oak forests due, apparently, to the openness of these stands that permitted flight between trees, the many available hunting perches, and the concealing cover (Nicholls and Warner 1972, Fuller 1979; Table 1). Barred Owls in the earlier study did not routinely hunt in lower-elevation forested swamps and ponds in deciduous forests, concluded the researchers, because the dense understory and herbaceous plants on the forest floor there limited their ability to fly between trees and hunt prey in swamps (Nicholls and Warner 1972). Some Barred Owls in the later study frequently hunted in alder lowlands and along field-forest edges (Fuller 1979). In Alberta, foraging stands had lower mean canopy closure than that in nesting or roosting stands, slightly lower mean dbh than surrounding stands, and significantly less shrub/herb cover than surrounding stands (Takats 1998). Nine of 11 foraging perches were in *Populus*, one was in white spruce snag, and one was a human-made post (Takats 1998).

Home-range sizes and site densities. Nine studies reported home-range data (Table 5). Four studies estimated home-range sizes using the same metric and recorded data throughout a full breeding season, nonbreeding season, or year. Mean home-range sizes in these studies, all of which were in the west, were 256.7 ha for breeding-season males (*N* = 24), 297.8 ha for breeding-season females (*N* = 25), 900.4 ha for nonbreeding-season males (*N* = 12), and 536.2 ha for nonbreeding-season females (*N* = 17; Table 5). Densities of Barred Owl sites varied

Table 5. Home-range sizes of Barred Owls determined by radiotelemetry by ecological province (EP) and study (ordered by EP number then study number).[a]

EP No.	Location	Study No.	Home-range Size (ha; mean ± SD, range when provided)			Method[b]
			Breeding Season	Nonbreeding Season	Annual	
132	SK	89	3m,9f: 148.6 ± 111.6	4m,9f: 1234.0 ± 630.7	4m,11f: 970.6 ± 406.7	95% MCP
211	MI	31	7np: 118		7np: 282	np
221b	MN	37[c]	3j: 36.9 ± 17.2 (9.3–22.5), 80.1 ± 8.4 (1.2–19.8), 62.1 ± 24.9 (5.5–53.6)		Breeding m: 655.2 ± 196.3 (59.0–398.7); breeding f: 550.4 ± 199.6 (141.4–364.3), 465.2 ± 81.0 (1.5–285.5); nonbreeding f: 251.4 ± 154.7 (103.8–228.9), 293.6 ± 57.6 (16.2–132.7), 1219.3 ± 174.5 (9.5–519.7)	100% MCP
221b	MN	96[d]			2m,2f,5np: 289 (86–369)	100% MCP
232	NC	54[e]	5m: 118.2 ± 71.4 (76.2–243.6); 4f: 86.3 ± 85.9 (35.1–214.1)			95% MCP
M241	WA	47[f]	9m: 266 ± 46; 14f: 340 ± 64; 9m,14f: 310 ± 42	9m: 1084 ± 360; 14f: 613 ± 87; 9m,14f: 805 ± 158	9m: 1179 ± 345; 14f: 673 ± 103; 9m,14f: 869 ± 151	100% MCP
M241	WA	119[g]	8m: 193.1 ± 62.6; 5f: 226.8 ± 54.8	3m: 349.7 ± 149.8; 2f: 181.5 ± 96.9	7m: 271.6 ± 182.8; 6f: 225.2 ± 76.9	100% MCP
M331	AB	97	5m: 365.26 ± 153.68; 4f: 303.78 ± 167.57; 5m, 4f: 337.94 ± 152.93			100% MCP
M331	AB	131	1m: 240 and 155 (diff yrs); 1f: 150 and 185	1f: 170		100% MCP
Weighted mean of means (*N* of total)[h]			m: 256.7 (24); f: 297.8 (25)	m: 900.4 (12); f: 536.2 (17)	m: 782.0 (16); f: 538.7 (20)	100% MCP

[a] np = information was not provided; m = male(s), f = female(s), j = juvenile(s).

[b] MCP = minimum convex polygon.

[c] Data in Fuller (1979) were weekly (weekly mean, weekly range).

[d] The nine Barred Owls in Nicholls and Warner (1972) and Nicholls (1973) were tracked for a mean of only 99 d (range 51–197 d).

[e] Harrold (2003) also reported home-range data as 95% kernel and 50% probability polygons.

[f] Hamer (pers. comm.) also reported home-range data as 75% and 95% isopleths of the adaptive kernel.

[g] Calculated from Singleton et al. (2005:Table 4).

[h] For studies with 100% MCP and data throughout a season or year (Takats 1998, Olsen 1999, Singleton et al. 2005, Hamer pers. comm.).

Table 6. Density of Barred Owl sites by ecological province (EP) and study (ordered by EP number then study number).

EP No.	Location	Study No.	No. Sites	Density
M211b	NH	120	11	0.21 sites/km^2
221a	NJ	9	62	0.07 pairs/km^2
241	WA	66	18	0.25 sites/km^2
M241	WA	55	53	0.063 sites/km^2 in areas with >150 cm annual precipitation; 0.019 sites/km^2 in areas with <150 cm annual precipitation
M241	WA	99	149	0.068 sites/km^2
M331	AB	130	13, 17	0.05 sites/km^2

among the few studies that reported them (Table 6), ranging from 0.02–0.25 sites/km^2. In a study area that spanned from the wetter west side to the drier east side of the Cascade Mountains of Washington, density of sites in wetter areas was >3 times greater than that in the drier areas (Herter and Hicks 2000).

Diet. Diet of the Barred Owl was reported in 43 studies (Appendix), of which 17 (39.5%) were single-sample description studies. The diet studies

Table 7. Barred Owl prey items, quantified by six methodologies.[a]

Taxonomic Group of Prey	Observations of Prey Captures or Deliveries		Camera-documented Food Deliveries		Intact Prey at Nest		Prey Remains at Nest		Prey in Stomachs[b]		Prey in Pellets[c]		All Samples	
	N	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%	*N*	%
Mammals (Mammalia)	12	34.3	69	38.8	62	59.0	640	67.7	193	62.3	4109	74.7	5085	71.9
Birds (Aves)	5	14.3	34	19.1	27	25.7	121	12.8	25	8.1	457.8	8.3	669.8	9.5
Reptiles (Reptilia)	2	5.7	1	0.6	1	1.0	11	1.2	3	1.0	23.1	0.4	41.1	0.6
Amphibians (Amphibia)	3	8.6	0	0.0	13	12.4	48	5.1	11	3.5	353	6.4	428	6.0
Fish (Osteichthyes)	4	11.4	8	4.5	1	1.0	36	3.8	3	1.0	81.7	1.5	133.7	1.9
Earthworms (Annelida)	7	20.0	64	36.0	0	0.0	0	0.0	0	0.0	2	0.0	73	1.0
Snails, slugs (Gastropoda)	0	0.0	0	0.0	0	0.0	1	0.1	10	3.2	5	0.1	16	0.2
Insects (Insecta) and spiders (Arachnida)	2	5.7	2	1.1	1	1.0	88	9.3	56	18.1	308.2	5.6	457.2	6.5
Crayfish (*Cambarus* spp.)	0	0.0	0	0.0	0	0.0	0	0.0	9	2.9	164.2	3.0	173.2	2.4
Total	35	100.0	178	100.0	105	100.0	945	100.0	310	100.0	5504	100.0	7077	100.0
% of all samples		0.5		2.5		1.5		13.4		4.4		77.8		100.0

[a] References used are listed in Appendix.

[b] Blakemore (1940) also reported prey in 81 stomachs by volume (not by individual prey): rodents (44.0%), insects (35.4%), passerines (9.8%), arthropods (7.2%), amphibians and reptiles (2.4%), and poultry (1.2%).

[c] Errington and McDonald (1937) also described by season, but did not quantify, the types of prey found in pellets ($N = 305$).

Table 8. Barred Owl prey items documented by pellet analyses and by all other methodologies.[a]

	Prey in all Samples Except Pellets[b]		Prey in Pellets		All Samples	
Taxonomic Group of Prey	*N*	%	*N*	%	*N*	%
Mammals (Mammalia)	976	62.0	4109	74.7	5085	71.9
Arboreal				0.0		0.0
Squirrels (Sciuridae)	81	5.1	171	3.1	252	3.6
Terrestrial				0.0		0.0
Opossum (*Didelphis marsupialis*)	0	0.0	3	0.1	3	0.0
Moles (Talpidae), shrews (Soricidae)	437	27.8	471	8.5	908	12.8
Bats (*Myotis* spp.)	8	0.5	2	0.0	10	0.1
Mustelids (Mustelidae)	2	0.1	3	0.1	5	0.1
Rabbits, hares (Leporidae)	41	2.6	189	3.4	230	3.2
Rodents (Rodentia)	377	24.0	3270	59.4	3647	51.5
Unidentifed	30	1.9	0	0.0	30	0.4
Birds (Aves)	212	13.5	458	8.3	670	9.5
Ducks (Anatidae)	1	0.1	0	0.0	1	0.0
Hawks (Accipitridae)	1	0.1	1	0.0	2	0.0
Owls (Strigidae)	9	0.6	4	0.1	13	0.2
Grouse, quail, pheasant, chicken (Galliformes)	13	0.8	30	0.5	43	0.6
Pigeons, doves (Columbidae)	1	0.1	2	0.0	3	0.0
Kingfishers (Alcedinidae)	1	0.1	0	0.0	1	0.0
Woodpeckers (Picidae)	14	0.9	18	0.3	32	0.5
Songbirds (Passeriformes)	102	6.5	258	4.7	360	5.1
Unidentifed	70	4.5	145	2.6	215	3.0
Reptiles (Reptilia)	18	1.1	23	0.4	41	0.6
Snakes (Serpentes)	15	1.0	23	0.4	38	0.5
Lizards (Squamata)	2	0.1	0	0.0	2	0.0
Turtles (Testudines)	1	0.1	0	0.0	1	0.0
Amphibians (Amphibia)	75	4.8	353	6.4	428	6.0
Frogs (*Rana* spp.)	10	0.6	250	4.5	260	3.7
Frogs (*Rana* spp.) or toads (*Bufo* spp.)	12	0.8	0	0.0	12	0.2
Frogs (*Rana* spp.) or salamanders (Urodela)	49	3.1	85	1.5	134	1.9
Salamanders (Urodela)	4	0.3	6	0.1	10	0.1
Unidentifed	0	0.0	12	0.2	12	0.2
Fish (Osteichthyes)	52	3.3	82	1.5	134	1.9
Earthworms (Annelida)	71	4.5	2	0.0	73	1.0
Snails, slugs (Gastropoda)	11	0.7	5	0.1	16	0.2
Insects (Insecta) and spiders (Arachnida)	149	9.5	308	5.6	457	6.5
Crayfish (*Cambarus* spp.)	9	0.6	164	3.0	173	2.4
TOTAL	1573	100.0	5504	100.0	7077	100.0
% of all samples		22.2		77.8		

[a] References used are listed in Appendix.

[b] Prey from observations of prey captures or deliveries, camera-documented food deliveries, intact prey at nest, prey remains at nest, and prey in stomachs.

documented 7077 individual prey items via direct observations, camera-documented prey deliveries to a nest, intact prey at nests, prey remains at nests, stomach contents, and pellets (Table 7). More than 75% of all samples were pellets (Table 8). The distribution of prey items by taxonomic group obtained from pellets differed significantly from those obtained by other means ($\chi^2_8 = 414.76$, $P < 0.001$, Table 7, 8), due especially to more earthworms in non-pellet samples than in pellet samples.

Among ecoregion domains, the distributions of the six types of prey samples (Table 7) differed significantly (χ^2_{10} = 521.14, $P < 0.001$) largely due to the high number of prey remains at nests in the humid temperate domain (17.6%) vs. polar (0%) and dry (0.8%) domains. The distributions of the eight taxonomic groups of prey (Table 7) also differed significantly among ecoregion domains (χ^2_{14} = 1824.39, $P < 0.001$) as a result of greater numbers of amphibians in the polar domain (62.8%, primarily from a single study, Mazur et al. 1997c) than in the humid temperate (4.5%) and dry (2.8%) domains, and correspondingly fewer mammals in polar studies.

Comparing the historic vs. expanded ranges, the distributions of the six types of prey samples differed significantly (χ^2_5 = 702.16, $P < 0.001$) due to high numbers of pellets in the west (97.9%) vs. the east (70.1%) and high number of prey remains at nests in the east (18.2%) vs. the west (0.7%). The distributions of taxonomic groups of prey also differed between eastern and western studies (χ^2_7 = 378.36, $P < 0.001$), with more amphibians (10.5%) in the western regions than in the eastern (4.4%) and fewer crayfish in the western region (0% vs. 3.4% in the east).

Taxonomic groups of prey differed seasonally as well: more mammals were identified in the winter diet (98.4%) than in the non-winter months (58.9%), and far greater numbers of birds (11.9%), insects or spiders (11.4%), amphibians (10.7%), earthworms (2.3%), fish (2.0%), and crayfish (2.0%) were eaten in non-winter months (χ^2_7 = 743.05, $P < 0.001$, N = 4631 prey items that could be placed into these two seasons). Virtually all (99.6%) winter data were from pellets, whereas approximately two-thirds (61.7%) of non-winter data were from pellets.

Barred Owls in some areas during some years ate large amounts of fish, salamanders, frogs, crayfish, and earthworms (e.g., Errington and McDonald 1937, Bosakowski and Smith 1992, Hamer et al. 2001, J. Hobbs pers. comm.). For example, of the 231 prey items identified by pellets or prey remains in a study in Saskatchewan, 147 (63.6%) were frogs (Mazur et al. 1997c). During a 20-yr study in Missouri, annual diet volume of crayfish was 0–31.1%, that of fish was 0–8.4%, and that of insects was 0–7.6%; during the only yr in which salamanders were eaten, they comprised 4.3% of diet volume (Korschgen and Stuart 1972). In Nova Scotia, a female Barred Owl fed earthworms to her young at least once every 10 min during rainy nights (Elderkin 1987).

DISCUSSION

Although this review is not an attempt to map the complete distribution of Barred Owls, the locations of the studies included herein (Fig. 1) do approximate the entire distribution of the many thousands of mapped Barred Owl detections throughout their historic and expanded ranges (T. Fleming and K. Livezey unpubl. data). This synthesis is not a result of a stratified random sampling of habitats or prey throughout the range of the Barred Owl. However, from the data presented here, it is evident that Barred Owls survive and reproduce in most of the mature or older deciduous, coniferous, or mixed forests of North America, from those in remote, undisturbed areas to those close to human development with high amounts of fragmentation. Barred Owls use similar locations for natural nests throughout North America, and prey almost exclusively on small mammals in the winter and on a wide variety of animals including mammals, birds, reptiles, amphibians, and invertebrates during non-winter months.

In the west, available evidence indicates that Barred Owls prefer forests located in lower, flatter areas. In the mountainous forests of southern Alberta, southern British Columbia, western Washington, western Oregon, and northern California, Barred Owls used sites during the nesting season in low and/or flat areas in all three preference studies, all eight description studies, and all three comparison studies (relative to Northern Spotted Owls) that addressed these variables. A long-term study in Olympic National Park, an area largely free from human influences including timber harvest, demonstrated this preference (Gremel 2005). Early sightings of Barred Owls in various portions of the Olympic peninsula and park from 1985–1990 were in floodplain forests, near lakes, or in riparian areas (Gremel 2005). Through time, Barred Owls increased their numbers while extending their distribution farther up valleys and higher in elevation (Gremel 2005). Mean elevation of Barred Owl site-centers significantly increased from 1987–2003 (r^2 = 0.57, N = 17, $P < 0.001$, S. Gremel pers. comm.). Number of Barred Owl site-centers below 343 m in elevation increased from two in 1987 to 13 in 2006 whereas those above that elevation increased from zero in 1987–1989 to 20 in 2006 (S. Gremel pers. comm.).

The Barred Owl studies presented mixed results concerning proximity to water. The reason for this may be that definitions of ''water'' or ''riparian areas'' and distances required to be ''near'' these areas differed among studies, and what meaningfully constitutes a wetland for Barred Owls might differ from that for other species and possibly differs for Barred Owls across the range of habitats in North America. Consequently, it seems reasonable for investigators to undertake exploratory analyses of the statistically explanatory effects of ''water'' by analyzing the power of alternative definitions (e.g., ephemeral, seasonal, or permanent bodies) using residuals after removing variation attributable to directly measurable variables. Such explorations in which ''water'' was treated *a posteriori* could then identify optimally informative definitions of wetlands for Barred Owls in various parts of the species' range and be used in subsequent analyses no differently than directly measured variables.

Use of wetland or lowland areas by Barred Owls in some areas may be related to availability of amphibian and fish prey (Yannielli 1988, Buchanan et al. 2004), and to larger nest trees that are often found in these areas because of decreased frequency of fires (Hinam 2001, Hinam and Duncan 2002) and faster growth rates of trees. Frequent use of black cottonwood (*Populus trichocarpa*) and balsam poplar as nest trees may be due to the presence of these species in moist, lowland areas. Cottonwoods are the fastest-growing native tree in North America (Elias 1980, Burns and Honkala 1990); they are early successional species that rapidly grow large trunks (Millet et al. 1999), are relatively short-lived, and have weak wood, so they frequently produce cavities and broken limbs that provide nesting opportunities for Barred Owls.

According to the studies reviewed here, Barred Owls apparently preferred mature or older forests, possibly because of greater availability of nest sites, lower stem densities in the understory that allow unimpeded visibility and travelways for foraging, and dense canopies that provide thermally neutral microclimates and protection from mobbing birds (Haney 1997). Barred Owls used young forests when nest boxes were provided (Elderkin 1987). Because Barred Owls are generalist predators, habitat selection may be influenced more by prey availability than by strong affinity for any specific type of forested habitat (Olsen 1999). The greater use of coniferous trees for nests in the west probably merely reflects the greater availability of coniferous forest there, and demonstrates the ability of Barred Owls to use different forests in their expanded range. Additional research in fragmented, younger forests, such as those done in suburban studies in North Carolina (Harrold 2003, Mason 2004), would provide a more complete understanding of the use of such habitats by Barred Owls.

The lack of significant differences among the natural nest locations in studies in humid temperate vs. dry domains and eastern vs. western regions suggested that Barred Owls used similar nest locations throughout North America. The vast majority of the natural nests (>75%) were placed in the most productive locations: cavities. In Michigan, Barred Owls that nested in cavities ($N = 49$) and boxes ($N = 52$) produced young 80% of the time, whereas only 31% of breeding attempts in hawk nests and other open sites ($N = 13$) were successful (Postupalsky et al. 1997).

Breeding-season home ranges of adult Barred Owls averaged only 250–300 ha, and densities ranged as high as 0.21–0.25 sites/km^2. Annual home ranges of sympatric Northern Spotted Owls were 3–4 times larger than those of Barred Owls in the western Cascade Mountains of Washington (Hamer pers. comm.), probably due to the more-varied prey base of Barred Owls (Hamer et al. 2001, Forsman et al. 2004, this review).

Barred Owls' diet consisted almost exclusively (98–99%) of small mammals during winter months, but included other types of prey (41–43%) as available during other times of the year. The differences in distributions of prey types among ecoregion domains and between east and west were significant primarily because of a few studies with large numbers of amphibians in pellets (Mazur et al. 1997c), crayfish in pellets (Korschgen and Stuart 1972), or earthworms documented by camera (Elderkin 1987) or observations (J. Hobbs. pers. comm.). These studies provided important data on the varied diet of Barred Owls and underscored the need for additional research to thoroughly understand the Barred Owl diet in North America throughout the year.

Different methods used to document Barred Owl diet yielded markedly different results. For example, 97.3% of the 73 records of Barred Owls eating earthworms were from camera-documented food deliveries or visual observations; only 2.7% were from pellets. The amount of soft-bodied prey such as earthworms eaten by Barred Owls probably was greatly underestimated in the pellet studies presented here due to the rapidity with which such prey decomposes and because such prey do not contain durable materials such as bones, feathers, hair, and exoskeletons necessary in pellet analysis. Because diet information gathered through pellet analysis can be biased toward some prey groups, such data should be used with data obtained through other, complementary methods (Yom-Tov and Wool 1997, Marchesi et al. 2002, Bonvicino and Bezerra 2003, Torre et al. 2004).

Barred Owls began their range expansion westward beginning more than 100 yr ago according to early reports (T. Fleming and K. Livezey unpubl. data). The range expansion apparently was facilitated by increased distribution of trees in the northern Great Plains (Maini 1960, Moore 1972, Bragg and Hulbert 1976, Grant and Murphy 2005) brought about by exclusion of fires historically set by Native Americans (Sauer 1950, Lewis 1980, Pyne 1983, Higgins 1986, Kimmerer and Lake 2001), suppression of fires (Arno 1980, Pyne 1982, Williams 1989), planting of trees (Droze 1977, Williams 1989), and other factors (T. Fleming and K. Livezey unpubl. data). Barred Owls have approximately doubled the size of their range during this time, and are now living in forests and preying on wildlife of central and western North America. Thus, there are abundant opportunities to study their use of various habitats and prey, as well as their effects on other raptors including Northern Spotted Owls (Kelly et al. 2003, Pearson and Livezey 2003, Gremel 2005, Olson et al. 2005) and Western Screech-Owls (*Otus kennicottii*; Elliott 2006), especially if they increase their densities in newly colonized areas and further expand their range.

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Appendix. Study numbers, references, ecoregion province (EP) numbers, and samples sizes (*N*) of studies of Barred Owl habitat or prey.

				NESTING HABITAT				PREY				
								STOMACHS[d]			PELLETS	
STUDY NO.[a]	REFERENCE	LOCATION	EP NO.	NEST SITES	SITES	MAN-MADE NESTS[b]	RADIO-TAGGED OWLS	OBSERVATIONS, ETC.[c]	SAMP	IND	SAMP	IND
Nesting habitat or prey												
1	Allin (1944)	ON	132	2								
2	Apfelbaum and Seelbach (1983)	N. Amer.	–	31	6							
4	B. Woodbridge (pers. comm.)	CA	M261	5	3							
5	Bent (1938)[e]	MA	221a	38								
6	Blackburn and Harestad (2001)	BC	M242b		115							
7	Blakemore (1940 in Elody 1983)	MN	221b						81	np		
8	Bosakowski and Smith (1992)	NJ, NY, CT	221a								np	243
9	Bosakowski et al. (1987)	NJ	221a	3	59						34	31
10	Boxall and Stepney (1982)	AB	132, M331	8	79							
11	Breedlove (1992)	IN	221b	1								
12	Brock (1994)	IN	221b	1				1(o)				
13	Brown (1980)	KY	221b		1							
14	Buchanan et al. (2004)	WA	M241	10								
15	Cahn and Kemp (1930)	IL, IN	221b								68	33
16	Carter (1925)	NJ	221a	1								
17	Cook (1992)	NY	221a						1	1		
18	Coon (1917)	PA	221a								40	74
19	Craighead and Craighead (1969)	MI	221b	6								
20	Crosby (1912)	NY	221a			1(b)						
21	D. Gibson (pers. comm.)	AK	M242b	1								
22	D. Rock (pers. comm.)	OR	M241		51		1m,1f					
23	Devereux (1982), Devereux and Mosher (1984)	MD	M221	8							np	82
24	Devine et al. (1985)	FL	231					2(o)				
25	Dingle (1926)	SC	231		3							
26	Dodd and Griffey (1997)	FL	231					1(o)				
27	Dunbar et al. (1991)	BC	M242b		57							
28	Duncan and Kearns (1997)	MB	211		28							
29	Dunstan and Sample (1972)	MN	211	1	np							

Appendix. Continued.

				Nesting Habitat				Prey				
								Stomachs[d]			Pellets	
Study No.[a]	Reference	Location	EP No.	Nest Sites	Sites	Man-made Nests[b]	Radio-tagged Owls	Observations, etc.[c]	Samp	Ind	Samp	Ind
30	Elderkin (1987)	NL	211					178(c), 105(i), 740(r)			198	635
31	Elody and Sloan (1985)	MI	211				7np					
32	Errington (1932)	WI	221b					12(r)			156	319
33	Errington and McDonald (1937)	IO	251								305	np
34	Falk (1990)	CT	M221b	21								
35	Fisher (1893)	ON, East[f]	–						109	114		
36	Franz (1992), Franz and Shea (1993)	FL	231	8								
37	Fuller (1979)	MN	221b	1			1m, 3f, 3j					
38	Fullerton and Meekins (2004), S. Fullerton and D. Meekins (pers. comm.)	CA	263		1							
39	Gehlert (1970)	SK	132	1								
40	Gibbs (1988)	SC	232			1(u)						
41	Gibson et al. (1998)	WI	211					1(o)				
42	Goelitz (1916)	IL	251	1								
43	Grant (1966)	BC	M331	1	35							
44	Graves and Niemi (2006)	MN	211					1(o)				
45	Green (1990)	NE	251		1			1(o)				
46	Gremel (2005)	WA	M241		64							
47	Hamer (1988), Hamer et al. (1989), Hamer (pers. comm.)[g]	WA	M241				9m, 14f					
48	Hamer et al. (2001)	WA	M241								np	265
49	Hamerstrom and Hamerstrom (1951)	MI	221b					174(r)			59	168
50	Haney (1997)	PA	211	6	1							
51	Haney and Lydic (1999)	TN	221b		1							
52	Harris (1968)	SD	251		1							
53	Harris (1972)	SK	132		2							
54	Harrold (2003)	NC	232	20		1(n), 3(b)	5m, 4f					

Appendix. Continued.

				NESTING HABITAT				PREY				
								STOMACHS[d]			PELLETS	
STUDY NO.[a]	REFERENCE	LOCATION	EP NO.	NEST SITES	SITES	MAN-MADE NESTS[b]	RADIO-TAGGED OWLS	OBSERVATIONS, ETC.[c]	SAMP	IND	SAMP	IND
55	Herter and Hicks (2000)	WA	M241		53							
56	Hertzel (2003)	MN	251					1(o)				
57	Hester (1954)	NC	232					1(o)				
58	Hinam (2001), Hinam and Duncan (2002)	MB	132		76							
59	Hobbs (2005), J. Hobbs (pers. comm.)	BC	M242b	6	95			8(o)				
60	Hodges (1947)	IO	251					1(o)				
61	Hoffman (1882)	ND	332		1							
62	Holt and Hillis (1987)	MT	M331	5	7							
63	Holt and Bitter (2007)	MT	M331								np	1153
64	Houston (1961)	SK	251	1								
65	Houston (1999)	SK	132			1(b)						
66	Iverson (1993, 2004)	WA	M241		13							
67	J. Buchanan, J. Acker, D. Garcia (pers. comm.)	WA	241		18							
68	J. Schaberl (pers. comm.)	WA	M241		33							
69	Jensen et al. (2004)	CA	263		2							
70	Johnson (1987)	MN	221b	8		14(n)						
71	Johnson and Follen (1984)	MN	211, 221b	5		12(n)						
72	Jones (1956)	AB	132						1	4		
73	Jones (1966, 1987)	AB, BC	132, M331	2	14							
74	K. Hulbert and A. Taylor in Taylor and Forsman (1976)	OR	M332		1							
75	Kelso (1939)	VA	232	2				6(r)			18	22
76	Kilham (1930)	NH	M211b						1	10		
77	Kinch (1963)	NE	331		1							
78	Korschgen and Stuart (1972)	MO	251								700	1185
79	Kuntz and Christophersen (1996), R. Christophersen (pers. comm.)	WA	M241		42							
80	L. Diller (pers. comm.)	CA	263	7	27							
81	Laidig and Dobkin (1995)	NJ	221a		37							
83	Le Duc (1970)	MN	221b	1							np	17

Appendix. Continued.

				NESTING HABITAT				PREY				
								STOMACHS[d]			PELLETS	
STUDY NO.[a]	REFERENCE	LOCATION	EP NO.	NEST SITES	SITES	MAN-MADE NESTS[b]	RADIO-TAGGED OWLS	OBSERVATIONS, ETC.[c]	SAMP	IND	SAMP	IND
82	Leder and Walters (1980)	WA	241	1				2(r)			np	5
84	Leskiw and Gutiérrez (1998)	CA	263					1(o)				
85	Lloyd (1887)	TX	314		np							
85	Marks et al. (1984)	MT	231								37	107
87	Martin (2001)	MD	231	1								
88	Mason (2004)[h]	NC	232	64	4	19(n), 1(b)	22j					
89	Mazur (1997), Mazur et al. (1998)	SK	132				4m, 11f					
90	Mazur et al. (1997a)	SK	132		25							
91	Mazur et al. (1997b)	SK	132	15								
92	Mazur et al. (1997c)	SK	132								60	230
93	Mazur et al. (2000)	SK	132				9ad					
94	McGarigal and Fraser (1984)	VA	M221		40							
95	Mendall (1944)	ME	211						136	178		
96	Nicholls and Warner (1972), Nicholls (1973)	MN	221b				2m, 2f, 5np					
97	Olsen (1999, 2004), Olsen et al. (2006)	AB	132, M331	10			5m, 4f					
98	Olson (1999)	SD	331		1							
99	Olson et al. (1978)	ID	332		2							
100	Pearson and Livezey (2003), R. Pearson (pers. comm.)[i]	WA	M241	36	113							
101	Peterson (1989)	MS	232						1	1		
102	Piorecky (2003), Piorecky and Prescott (2004)	AB	M331		74							
103	Postupalsky et al. (1997)	MI	211	61		52(n), 1(p)						
104	Price (1942)	IN	221b								np	11
105	R. Gerhardt (pers. comm.)	OR	241	5								
106	Rand (1944)	BC	M132b		2							
107	Reichard (1974)	WA	241	1								
108	Rhodes (1974)	TN	221b					1(o)				
109	Robertson (1959)	FL	411	1								

Appendix. Continued.

				NESTING HABITAT				PREY				
								STOMACHS[d]			PELLETS	
STUDY NO.[a]	REFERENCE	LOCATION	EP NO.	NEST SITES	SITES	MAN-MADE NESTS[b]	RADIO-TAGGED OWLS	OBSERVATIONS, ETC.[c]	SAMP	IND	SAMP	IND
110	Rubey (1927)	MD	231		1	1(n)						
111	S. Waycheschen in Houston (1959)	SK	251		1							
112	Schmelzer and Phillips (2004)	NL	131		2							
113	Schmidt (2005), K. Schmidt (pers. comm.)	CA	263		34							
114	Seamans et al. (2004), M. Seamans (pers. comm.)	CA	M261		1							
115	Shackelford and Earley (1996)	TX	232	1								
116	Shea (1974)	MT	M331		13							
117	Shupe (1985)	NE	251	10								
118	Sindelar (1969)	IL	221b						1	1		
119	Singleton et. al (2005)	WA	M241	5			8m, 8f					
120	Smith (1952)	NC	M221						1	1		
121	Smith (1978)	CT	221a		14							
121	Smith (1978)	NH	M211b		11							
122	Smith et al. (1983)	FL	231					1(o)				
123	Soucy (1976)	NJ	221a	1								
125	Stein (1930)	MN	221b	1								
126	Stewart (1975)	ND	251, 331		2							
127	Sutton and Sutton (1986)	NJ	221a		37							
128	Swanson and Liknes (1992)	SD	251		1							
129	Sweeny (1959)	NC	231		1			np(o)				
120	T. Minkova and T. Fleming (pers. comm.)	WA	241, M241		np							
131	Takats (1996, 1998)	AB	M331	6	20		1m, 1f	14(o), 11(r)			78	143
132	Takats Priestley (2004)[j]	AB	132, M331	28		4(n), 1(p)						
133	Trapp (1989)	IO	251		1							
134	Van Ael (1996)	ON	211		43							
135	Wetmore (1930)	NC	231		1							
137	Wilson (1938)	MI	221b	1	np						249	781
138	Winton and Leslie (2004)	OK	331		11							
139	Wright and Hayward (1998)	ID	M332		12							

Appendix. Continued.

				NESTING HABITAT				PREY				
								STOMACHS[d]			PELLETS	
STUDY NO.[a]	REFERENCE	LOCATION	EP NO.	NEST SITES	SITES	MAN-MADE NESTS[b]	RADIO-TAGGED OWLS	OBSERVATIONS, ETC.[c]	SAMP	IND	SAMP	IND
140	Yannielli (1988)	CT	221a	6	16							
Totals for nesting habitat and prey				466	1411	103(n), 6(b), 2(p), 1(u)		35(o), 178(c), 105(i), 945(r)	332	310	2002	5504
Roosting habitat												
3	Applegate (1975)	IL	251		1							
9	Bosakowski et al. (1987)	NJ	221a		1							
37	Fuller (1979)	MN	221b				1m, 3f, 3j					
93	Mazur et al. (2000)	SK	132		16		9ad					
96	Nicholls and Warner (1972), Nicholls (1973)	MN	221b				2m, 2f, 5np					
131	Takats (1998)	AB	M331		25							
Foraging habitat												
3	Applegate (1975)	IL	251		1							
37	Fuller (1979)	MN	221b				1m, 3f, 3j					
96	Nicholls and Warner (1972), Nicholls (1973)	MN	221b				2m, 2f, 5np					
131	Takats (1998)	AB	M331		11							
Non-nesting season detections												
85	Marks et al. (1984)	MT	M331		3							
136	Weydemeyer (1927)	MT	M331		1							
Dispersing male detection												
124	Steger et al. (2006)	CA	M261		1							

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[a] Studies are ordered alphabetically by the last name of the first author.

[b] Nests in: nest boxes (n); buildings (b); platforms (p); under bridges (u).

[c] Prey determined by: observations of prey captures or deliveries (o), including Gibson et al. (1998); camera-documented deliveries (c); intact prey at nests (i); remains of prey at nests (r).

[d] Samp = no. of stomachs or pellets; Ind = no. of individual prey identified.

[e] Bent (1938) also described a nest in Florida, but did not provide its location.

[f] ON, Washington DC, and 19 eastern states.

[g] Hamer (1988) and Hamer et al. (1989) are being revised by T. Hamer, E. Forsman, and E. Glenn (Hamer pers. comm.); when there were differences between the earlier works and Hamer (pers. comm.), I used results from Hamer (pers. comm.).

[h] Mason (2004) also included 3 nests in buildings (house chimneys) that were reported in Harrold (2003; R. Bierregaard pers. comm.); sample sizes for nest sites and nests were provided by R. Bierregaard (pers. comm.).

[i] 98 sites in Pearson and Livezey (2003), 113 sites and 36 nest sites in R. Pearson (pers. comm.).

[j] The nests in Takats Priestley (2004:Table 3) included here were only those that were not presented elsewhere in this review.