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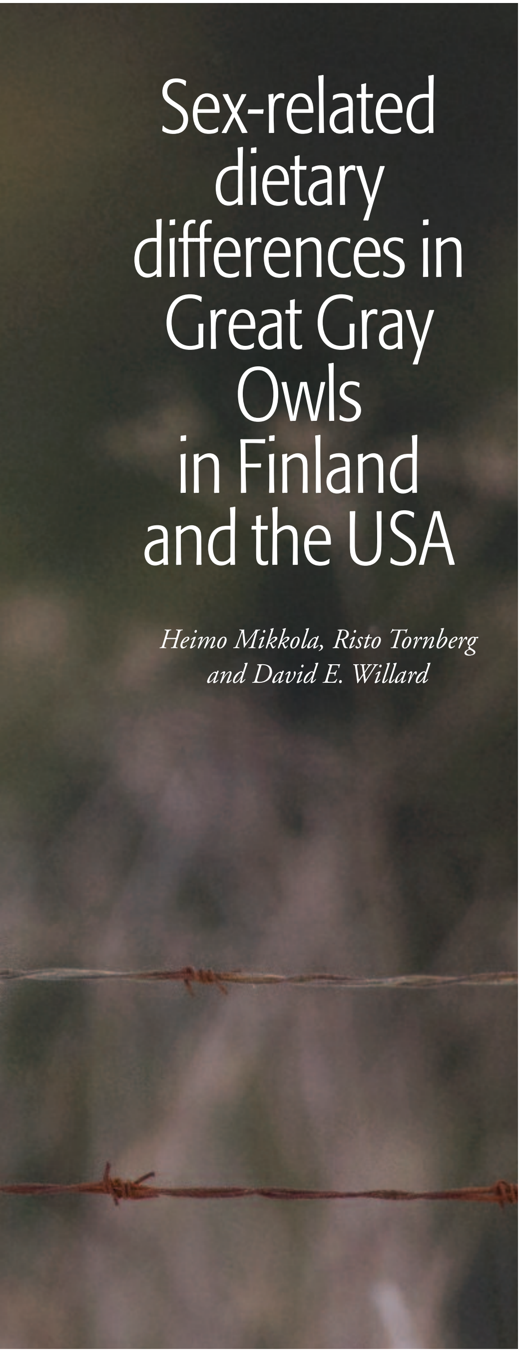
Great Gray Owl listening for prey from a barbed wire fence. *Photo: J. Spallin*



Sex-related dietary differences in Great Gray Owls in Finland and the USA

Heimo Mikkola, Risto Tornberg and David E. Willard

Introduction

The Great Gray Owl (*Strix nebulosa*) is a large nocturnal raptor of the boreal zone, ranging south through coniferous mountain regions. It is the only member of the genus with populations in both the Old and New Worlds (Bull and Duncan 1993), with nominate *nebulosa* found in North America and *lapponica*, differing in plumage characters (Mikkola 2012), in Eurasia. The species exhibits high reverse sexual size dimorphism (RSD) with females clearly larger than males. Based on specimens at the University of Oulu, Finland, female owls from Finland had an average weight of 1165 g (N=89), while male weights averaged 894 g (N=50). Values from North America were remarkably similar (based on specimens at the Field Museum of Natural History, Chicago). Mean female weight was 1168 g (N=356) and males averaged 902 g (N=272). On both continents, the largest females were nearly three times as heavy as the smallest males. The Reversed Size Dimorphism (RSD) index of the European Great Gray Owls is 11.8 (calculated as in Amadon (1943) and Earhart and Johnson (1970) by using the cube root of body mass to compare to indices of linear measurements). This is the highest value of all European owls (Mikkola 1983).

There are many studies of owl diets based on analysis of prey remains found in pellets (summarized in Marti *et al.* 1993). Pellets of Great Gray Owls at breeding sites have provided information on overall diet (Mikkola and Sulkava 1970, Bull and Henjum 1990, Duncan 1992, Sulkava and Huhtala 1997), but because it is difficult to be certain which sex produced the pellet, and because the male is almost exclusively responsible for prey deliveries to the nest, these studies cannot address the question of sexual differences in diet or prey selection. With the large amount of sexual size dimorphism in this species, it seems logical to hypothesize that females should take larger prey, minimizing intraspecific competition, as seen in studies of diurnal raptors (Temeles 1985, Krüger 2005).

Two large samples of Great Gray Owls allow us to test whether there are dietary differences between the sexes. HM and RT analyzed a sample from Finland found dead along roads or confiscated after illegal hunting over a 78 year span, 1927–2005 (specimens in collections of taxidermist Pentti Alaja, Vesanto and the University of Oulu); DW worked with birds from Minnesota and Wisconsin found dead during the huge irruption of the winter of 2004-2005 (Svingen and Lind 2005). The source of many of these irruptive owls in Minnesota and Wisconsin would have undoubtedly referred to breeding populations in the boreal forest regions of Ontario and Manitoba.

Materials and Methods

One hundred and fifty Great Gray Owls from Finland and 675 from Minnesota and Wisconsin were sexed internally and the contents of their stomachs identified. In Finland, 312 prey items were identified from 59 females and 46 males, while there were 1225 prey items from 203 female and 148 male stomachs in North America. The remainder of stomachs were either empty or contained no identifiable prey items. The samples from Finland were collected over several decades in years of variable prey abundance, whereas those from Minnesota and Wisconsin were all collected in a single winter, during an irruption when prey was abundant.

For the Finnish prey items, we used average weights given by Siivonen (1967) and Jensen (1994) for small mammals, and for birds, we used Von Haartman *et al*. (1963-1972). Average weights for Minnesota and Wisconsin prey items were taken from on-line data provided by the Smithsonian Institution.

We tested differences in the diet between sexes in both countries by Chi-square χ^2 tests. We arranged the data according to prey weight classes in order to have sufficient numbers of prey in each cell of the contingency table. These weight categories were: a) < 15g (mostly shrews); b) 16-30g (mostly smaller rodents); c) 31-50g (larger voles, frogs, thrushes); d) 51g and above (water voles, weasels, large birds, hare).

To calculate diet width, we used Levins' index (Levins 1968) $B=1/\sum Pi^2$, in which Pi is the proportion of the i^{th} prey or prey group.

Table 1. Sexual differences in the diet of Great Gray Owls in the USA based on 351 stomach contents (148 male and 203 females). The average weight of prey species calculated from minimum and maximum weights given by Smithsonian Institute and/or Wisconsin University on the internet.

Prey species of *Strix nebulosa nebulosa*	Average Prey item Weight (g)	Female Prey Number %	Female Prey Weight %	Male Prey Number %	Male Prey Weight %	Total Prey Number %	Total Prey Weight %
Arthropod	2	0.13	0.01	0.20	0.01	0.16	0.01
Sorex cinereus/hoyi Masked / Pygmy Shrews	5	4.88	0.55	8.62	1.09	6.37	0.76
Sorex arcticus Arctic Shrew	8	3.79	0.69	6.36	1.29	4.82	0.91
Aves sp. small Birds	12	0.41	0.14	-	-	0.25	0.08
Peromyscus sp. Deer Mice	16	0.41	0.15	2.26	0.92	1.14	0.43
Blarina brevicauda Short-tailed Shrew	24	3.52	1.92	3.08	1.87	3.35	1.90
Clethrionomys gapperi Southern Red-backed Vole	28	1.49	0.95	4.11	2.92	2.53	1.68
Synaptomys cooperi Southern Bog Lemming	36	0.68	0.55	0.82	0.75	0.74	0.63
Microtus pennsylvanicus Meadow Vole	48	82.38	89.86	71.87	87.51	78.20	88.99
Rana sp. Frogs	50	0.54	0.61	0.21	0.26	0.41	0.48
Unidentified prey	50	0.81	0.92	1.85	2.34	1.22	1.45
Condylura cristata Star-nosed Mole	59	0.54	0.73	0.41	0.62	0.49	0.69
Scalopus aquaticus Eastern Mole	80	-	-	0.21	0.42	0.08	0.17
Tamiasciurus hudsonicus Red Squirrel	227	0.14	0.70	-	-	0.08	0.44
Mustela frenata Long-tailed Weasel	250	0.14	0.77	-	-	0.08	0.48
Mustela erminea Ermine	467	0.14	1.44	-	-	0.08	0.90
Total		100	100	100	100	100	100
Prey Item Numbers/ Total Weights (g)		738	32476	487	19198	1225	51674
Average Prey Size (g)			44.0		39.4		42.2
Diet Niche Breadth			1.462		1.899		1.681

Results

In the sample from Minnesota and Wisconsin (Table 1), the most common prey for both male and female owls was the Meadow Vole (*Microtus pennsylvanicus*). Shrews of several species were also commonly eaten (12% of female, 18% of male prey items), but by weight, their contribution was considerably less important. Only females were documented taking prey over 80 g: Red Squirrel (*Tamiasciurus hudsonicus*), Long-tailed Weasel (*Mustela frenata*) and Ermine (*Mustela erminea*). Previous studies have also documented Ermine in Great Gray Owl diet (Brunton and Reynolds 1984).

In the USA, the average weight of the 738 prey items taken by females was 44.0 g, while the average weight of male prey based on 487 items was 39.4 g. These differences are statistically significant (χ^2=20.702, p<0.001, Figure 1).

The sample for Finland comprises 312 prey items, with 180 of those taken by females and 132 by males (Table 2). Short-tailed and Root Voles (*Microtus agrestis* and *M. oeconomus*) were the most common prey (40% of total prey, 52% by weight), but shrews were taken nearly as often (39% of total, but only 11 % by weight). The average prey weight for both sexes in the Finnish sample is 33 g which

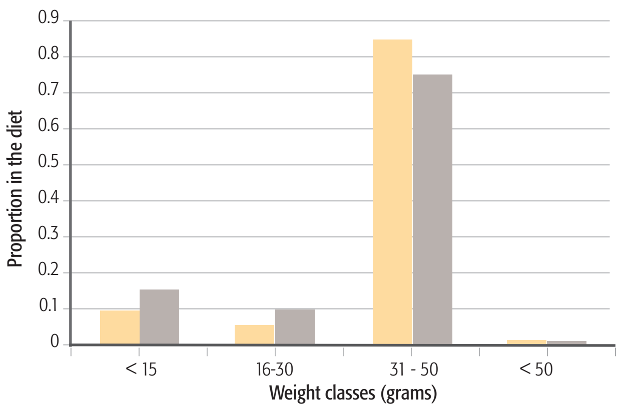


Figure 1. Proportion of prey specimens found in stomachs of male and female Great Gray Owls collected in Minnesota and Wisconsin, USA in winter 2004-05. Prey specimens are categorized into weight classes.

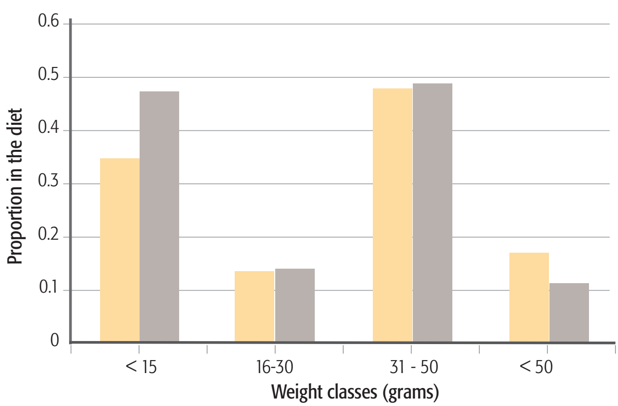


Figure 2. Proportions of prey specimens found in stomachs of male and female Great Gray Owls collected in Finland during 1929-2005. Prey specimens are categorized into weight classes.

Table 2. Sexual differences in the diet of Great Gray Owls in Finland based on 105 stomach contents (46 males and 59 females). Average weights calculated from Siivonen (1967) and Jensen (1994) for small mammals, and from Von Haartman *et al.* (1963-1972) for birds.

Prey species of *Strix nebulosa lapponica*	Average Prey item Weight (g)	Female Prey Number %	Female Prey Weight %	Male Prey Number %	Male Prey Weight %	Total Prey Number %	Total Prey Weight %
Sorex minutissimus Least Shrew	3	0.55	0.04	3.02	0.36	1.60	0.15
Sorex minutus Pygmy Shrew	5	0.55	0.07	3.78	0.75	1.92	0.29
Sorex caecutiens Laxmann's Shrew	7	0.55	0.10	-	-	0.32	0.07
Sorex sp.	9	5.56	1.29	9.85	3.51	7.37	2.01
Sorex araneus Common Shrew	10	26.67	6.89	25.76	10.19	26.28	7.96
Sorex isodon Taiga Shrew	11	0.55	0.16	-	-	0.32	0.11
Neomys fodiens Eurasian Water Shrew	15	0.55	0.21	0.76	0.45	0.64	0.29
Aves sp. (small)	20	0.56	0.28	-	-	0.32	0.19
Mus musculus House Mouse	20	0.56	0.28	-	-	0.32	0.19
Clethrionomys glareolus Bank Vole	24	12.22	7.58	10.61	10.07	11.54	8.38
Myopus schisticolor Wood Lemming	29	0.56	0.42	2.27	2.61	1.28	1.13
Clethrionomys rufocanus Grey Red-backed Vole	35	2.22	2.01	-	-	1.28	1.36
Cricetidae sp.	35	1.67	1.51	4.55	6.29	2.89	3.06
Microtus agrestis Short-tailed Vole	40	26.67	27.55	28.79	45.56	27.57	33.38
Microtus oeconomus Root Vole	48	15.00	18.60	9.85	18.71	12.82	18.63
Turdus pilaris (juv.) Fieldfare	50	1.11	1.43	-	-	0.64	0.97
Rana temporaria Common Frog	50	1.11	1.43	0.76	1.50	0.96	1.46
Arvicola terrestris European Water Vole	150	2.22	8.62	-	-	1.28	5.82
Lagopus lagopus Willow Ptarmigan	600	0.56	8.62	-	-	0.32	5.82
Lepus timidus (carrion) Mountain Hare	900	0.56	12.91	-	-	0.32	8.73
Total		100	100	100	100	100	100
Prey Item Numbers/ Total Weights (g)		180	6969	132	3336	312	10305
Average Prey Size (g)			38.7		25.3		33.0
Diet Niche Breadth			5.417		5.407		5.412

is identical to that found in a large (N=5177) sample of prey material from pellets studied in Fenno-Scandia (Mikkola 1981). Mean weight of prey for females in this study was 38.7 g and for males 25.3 g, and although they were more dramatically different in an absolute sense than the American sample, owing to smaller sample size, they did not differ significantly (χ^2=3.938, n.s., Figure 2).

Many owl stomachs (40% in Minnesota and Wisconsin and 30% in Finland) were empty or contained only hair or a few unidentified bones, but some individuals had remarkable numbers of prey items in their stomachs. A stomach from a Finnish female contained 13 prey items: 7 Common Shrew (*Sorex araneus*), 1 Pygmy Shrew (*S. minutus*), 1 Least Shrew (*S. minutissimus*) and 2 Bank Voles (*Clethrionomys glareolus*). Total weight of these prey animals was 126 g. Another female had 7 Root Voles in the stomach. Total estimated weight of these voles was 336 g, helping to explain why this female owl was the heaviest ever weighed in Finland (1900 g). The highest number of prey in one stomach from Finland came from a male which had 17 items: 13 Common Shrew, 1 Pygmy Shrew, 1 Common Frog (*Rana temporaria*), 1 Bank Vole and 1 Short-tailed Vole. Total weight of this stomach content was about 250 g. There were similar individuals in the Minnesota and Wisconsin sample. One female had 13 items (8 Meadow Voles, 2 Southern Red-backed Voles (*Myodes gapperi*), 2 Cinereous Shrews (*Sorex cinereus*), 1 Short-tailed Shrew (*Blarina brevicauda*) and 1 Star-nosed Mole (*Condylura cristata*); another female stomach contained remains of 12 Meadow Voles, for which the total weight was estimated to be even 576 g. The most prey items recorded in a single stomach in the North American sample came from a male with 18 items (10 Arctic Shrews (*Sorex arcticus*), 3 Cinereous Shrews, 3 North American Pygmy Shrews (*S. hoyi*), 1 Southern Red-backed Vole and 1 Star-nosed Mole). Several male stomachs contained more than 10 Meadow Voles.

When comparing Finnish material with that collected in Minnesota and Wisconsin, size class 30-50 g, *i.e.* the size of large voles, was found more frequently in the USA material, while smaller size classes were relatively better represented in Finnish material (Figure 3). The difference is statistically highly significant (χ^2 = 262,333, df = 3, $p < 0.001$).

Levin's index of dietary niche breadth in Finland was almost the same between males and females (Table 2); in Minnesota and Wisconsin, that measure was slightly lower for females than males (Table 1). The niche breadth of the Finnish sample was considerably higher than that for Minnesota and Wisconsin.

Discussion

Reversed sexual dimorphism may have evolved to allow members of a pair to capture different prey types and/or sizes and thus more efficiently exploit the local food resources and reduce competition between the sexes (Snyder and Wiley 1976, Hakkarainen and Korpimäki 1991, Tornberg *et al.* 1999). Studies of temperate owls have generally failed to show this (Mikkola 1981, Lundberg 1986). The two data sets presented here give some indication of niche partitioning of this sort, with female owls on both continents

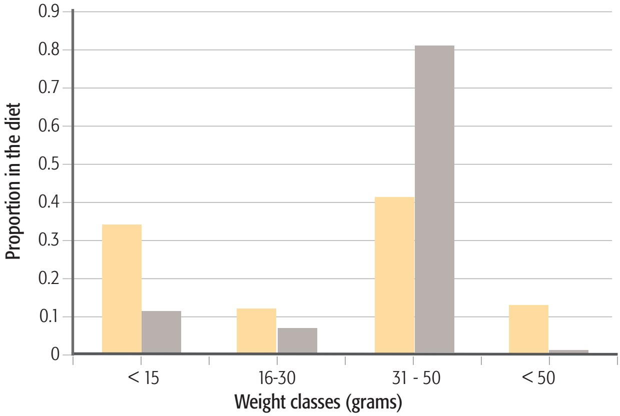


Figure 3. Proportion of prey specimens found in stomachs of Great Gray Owls collected in Finland and Minnesota and Wisconsin, USA during 1929-2005. Prey specimens are categorized into weight classes.

taking slightly larger prey and a broader variety of prey species although the differences were only statistically significant in the Minnesota and Wisconsin sample (owing to the larger sample size). Greater differences may be masked by the nature of the samples. Since we are dealing with partially digested stomach contents, we have to rely on average weights of the prey items for this analysis. For most of the prey identified there was a range of weights (*e.g.* Meadow Voles range in weight from 33 to 65 g), so there is still the possibility that males and females specialize at either end of the range.

There is some indication of a pattern like this in the shrews in both the European and North American samples. In Minnesota and Wisconsin, shrews 8 grams and less make up 15 % of the male prey items, but only 8.7% of the female diet, while the larger Short-tailed Shrew (24 g) is about equally represented in the diets of both sexes. In the Finnish sample, nearly 7% of the male prey items were shrew species weighing less than 5 grams, with only 1.1% of this size in female stomachs, but females were taking equal numbers of the larger Common Shrew. Whether smaller males can better justify the energy expended on capturing small prey, whether they may be pushed to microhabitats with reduced availability of larger prey or some other explanation needs further observation and testing.

The fact that the average weight of prey in the Minnesota and Wisconsin sample is somewhat larger than that in Finland (42 *vs.* 33 g) may simply reflect the available prey base. In studies from the western USA, average prey size was greater than in either the Minnesota and Wisconsin or Finnish samples. In Oregon, pocket gophers (*Thomomys* spp.) comprised one third of the prey items and 69% of the biomass taken by Great Gray Owls, making the average prey weight 54.4 g (Bull *et al.* 1989). Pocket gophers were an even greater component of the diet in California and Idaho, where average prey size was over 80 g (Winter 1986, Franklin 1987). These western pocket gopher specialists recently have been described as a third subspecies, *Strix nebulosa yosemitensis* (Hull *et al.* 2010).

Great Gray Owl
Ken Newcombe

The much greater niche breadth in Finland may reflect the longer duration of that study, representing samples collected over decades and including birds from years when voles were scarce and shrews were plentiful. The samples from Minnesota and Wisconsin represent a one-time irruption; all collected over one winter when Meadow Voles were abundant.

Owl diets in general are fairly well known, owing to the ease of finding regurgitated pellets from known species and analyzing prey remains in those, but usually there is no way of determining which sex produced them, so they cannot be used to address the question of sexual differences.

Snowy Owls (*Bubo scandiacus*) are one of the few owl species that can be sexed with some accuracy by plumage, making them a candidate for a field study of prey partitioning. Boxall and Lein (1982) showed that wintering female Snowy Owls in southern Alberta consumed a greater diversity of prey than males which preyed almost exclusively (85 per cent in numbers) upon North American Deer Mouse (*Peromyscus maniculatus*) and Meadow Vole (61% and 24%, respectively). By numbers, mice were also the most common prey of females (45%) and voles next (34%), but in addition they preyed upon eleven Gray Partridges (*Perdix perdix*), and four weasels (*Mustela* spp.). Three pellets from females contained remains of White-tailed Jackrabbits (*Lepus townsendii*), the largest prey taken by Snowy Owls in that study. None of the pellets from males included remains of any of these larger prey items.

The Boreal Owl (*Aegolius funereus*) is another species with high RSD, but there is very little evidence for dietary separation between sexes (Korpimäki and Hakkarainen 2012). However, in Idaho, USA, wintering female Boreal Owls captured Northern Flying Squirrels (*Glaucomys sabrinus*) more than males did (Hayward *et al.* 1993). Of twelve flying squirrels (body mass 140 g) found in prey remains, only one was captured by a male. Flying squirrels represented 45 per cent of the female prey weight. While the sample is too small to be statistically significant, it represents another example among owls where the largest prey is taken by females.

The Great Gray Owl specimens used in the current study represent a somewhat serendipitous sample, but salvaged birds such as these may provide the best avenue to address sexual dietary differences in species where internal examination is the only sure way to determine gender. Salvaged specimens can provide information for a variety of studies; the same USA sample served as the basis for a study on nutritional stress and body conditions (Graves *et al.* 2012).

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