Forum

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Do eagle owls select larger water voles?

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Optimal foraging theory predicts that a hunter should hunt the energetically most profitable prey, often the larger size classes. The eagle owl is a formidable hunter of water voles. Measurements of mandibles of voles eaten by eagle owls indicated a size frequency distribution more skewed toward larger individuals than could be expected, suggesting a selection of voles by the owls.

Key words: prey selection, *Arvicola terrestris*, *Bubo bubo*, Norway

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Optimal foraging theory predicts that a predator should maximize energy efficiency, both in short (season) and long (fitness) terms (Krebs 1978, Innes & Houston 1997). Maximizing energy gain and minimizing energy spent during a hunt may involve many different trade-offs (Krebs 1978). Optimal foraging can involve both selective and opportunistic foraging (Altringham 1996). A selective hunter will take only the most profitable prey, but may spend a lot of time (and energy) looking for them. An opportunist will spend little time looking for particular prey, but hunt any that comes within reach. An optimal forager will adjust the time and energy it spends to maximize its net energy intake (Altringham 1996). Search, capture and handling times will all be a part of the energy balance. In addition come transportation costs. For a hunter of small rodents, prey size and abundance (density) may be the most important limiting factors, but the behaviour of prey and the habitat may play a role. A predator must continually update its estimates of capture rates and availability in order to make optimal decisions (Krebs 1978). However, a hunter may be unable to conform to the rules of optimal foraging because of other factors, such as avoiding being eaten itself (Krebs 1978, Altringham 1996).

The eagle owl *Bubo bubo* has a broad food niche and eats what animals it can catch and kill (Haftorn 1971). The water vole *Arvicola terrestris* is likely to be a common prey where the two species coexist. This small rodent is relatively large, weighing up to 350 g. The water vole's distribution in Norway is not continuous, and it seems to live in discrete populations along the coast of northern Norway. Populations are known to fluctuate widely, as water voles do elsewhere, but little research has been done on this species in Norway where its population ecology is virtually unknown. The population of eagle owls in Norway has been greatly reduced, but is now slowly recovering (Solheim 1994). The number of sites where the two species coexist in Norway may be limited. The coast of Helgeland in Nordland county is one such region, where both predator and prey live on islands. On many of these islands, the water vole is the only herbivore and the eagle owl is their major predator. This represents a unique and interesting situation, well suited for a predator-prey study. It may be more profitable for eagle owls to hunt larger water voles, but smaller individuals are usually more numerous during the summer. In Finland tawny owls *Aegolius funereus* seem to select smaller individuals of small rodents, perhaps because these are more vulnerable and easier to catch (Koivunen et al. 1996).

In this study, I examine the age classes of water voles killed by eagle owls. This may give some information about the water vole, but also about a possible selection of prey made by the eagle owl. Do eagle owls hunt water voles selectively or randomly?

Owl pellets and water vole mandibles

This study resulted from an invitation to participate in a general faunistic survey of some islands on Helgeland in June 2002, during a banding of eagle owl nestlings. I used the opportunity to collect lower mandibles of water voles and some owl pellets. Most of the material was collected from owl nests and a small area surrounding the nest, but some were collected at old abandoned nest sites and from a few adult resting places. The content of eagle owl pellets becomes nest substrate, which in this area mainly consists of the fur from water voles. Embedded in this fur are also bones that have been regurgitated, of which the lower mandible is the least damaged. I collected all mandibles that could be found without disturbing the nest during the brief visit. Many of these were from previous years, so the collection represented an unknown number of breeding seasons. Only the right mandible was measured, and those from nests were combined with those from the pellets to make a single sample. Three measurements were taken using a binocular with eye-piece reticle (Figure 1). The sum of these three represented mandible length (n=177) and correlated better with body measurements (see below) than any singular mandible measurement. Thus, only the sum is used in the analyses. The original measurements were used in statistical analyses, but were converted to mm for the figures.

To examine the relationship between mandible length and body size a collection of water voles from Bliksvær (a different island further north in Nordland county) was used. Body mass and total and tail lengths were known, and their right mandibles were measured. Body length was calculated as total length minus tail length. These water voles had been trapped in September (n=13) and November (n=16) 1999, a year with a large population on Bliksvær.

The owl pellets (n=22) and fragments of owl pellets collected were broken up to study their contents. Water vole fur and bones were identified, as well as feathers and bones from birds. The result is given as a percentage of the total number of voles and birds found in the pellets.

Which water voles were eaten?

Of the pellets and pellet fragments analysed, only one did not contain any remains of water voles, containing only bird remains. In total, 33 water vole skulls and 65 mandibles (both right and left) were identified in the pellets, and remains of five birds were found. Water voles made up 86.8% and birds 13.2% of the prey.

Mandible length correlated well with body measurements in water voles from Bliksvær (Table 1, Figure 2). The relationship between mandible length (ML, here in cm) and body mass (BM, in g) was calculated as a power curve estimation (regression, sensu Le Cren 1951) resulting in the equation: $BM = 2.82 * (ML^{5.21})$, r^2=0.60. The relationship between mandible and total lengths (TL, in mm) was calculated as a linear regression (Figure 2) resulting in the equation: $TL = -278 + 25.8 * ML$. These equations were used to estimate body mass and total length of water voles eaten by eagle owls in Helgeland (Table 2).

Table 1. Pearson's correlation coefficients between mandible length, body mass, total length, tail length and body length in water voles from Bliksvær (n=27-29, p<0.01).

	Mandible length	Body mass	Total length	Tail length
Body mass	0.79			
Total length	0.82	0.94		
Tail length	0.68	0.82	0.91	
Body length	0.82	0.91	0.94	0.71

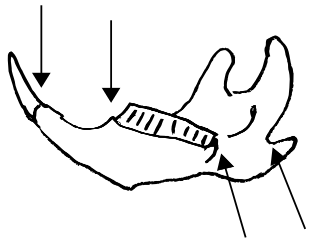

Figure 1
Lower jaw of water vole. Three measurements were made (between the arrows), and were summed as a measure of mandible length.

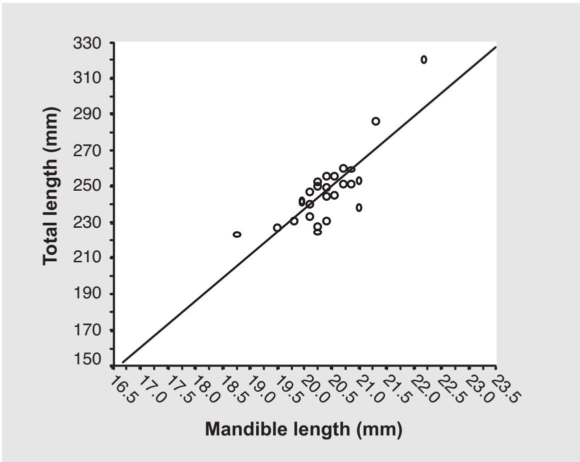

Figure 2
Regression of mandible length ML against total length TL for water voles from Bliksvær (TL=-278+25.8*ML, r^2=0.67). The regression line is extrapolated to include the variation in water voles from Helgeland.

Table 2. Mean, standard deviation, minimum and maximum mandible length, body mass and total length of water voles trapped at Bliksvær and eaten by eagle owls in Helgeland (values in italics are estimated, see text). Results of t-test between the two regions are given below each variable.

	Mandible length (mm)				Body mass (g)				Total length (mm)			
	$\bar{X}$	SD	Min.	Max.	$\bar{X}$	SD	Min.	Max.	$\bar{X}$	SD	Min.	Max.
Bliksvær	20.4	0.63	18.8	22.2	118.6	24.8	80.1	186.1	248.1	19.6	223.0	320.0
Helgeland	20.8	1.05	17.0	23.3	*132.1*	*31.9*	*43.9*	*227.7*	*256.0*	*27.0*	*156.4*	*317.8*
	t=2.15, p=0.03				t=2.18, p=0.03				t=1.52, p>0.05			

The mean mandible length was significantly larger for water voles eaten by eagle owls than for those trapped at Bliksvær (Table 2). Median was 21.0 and 20.4 mm, respectively. The difference was not large, but still clear, as can be seen from the frequency distribution (Figure 3). The mean estimated body mass of voles eaten in Helgeland was also significantly greater than the mean mass of voles trapped at Bliksvær (Table 2, Figure 4), but the mean total lengths were not significantly different. The voles from Bliksvær had been trapped late in the autumn when they should all be of subadult or adult size, while the voles collected at eagle owls nests were likely to have been caught during summer when younger and smaller voles normally greatly outnumber adults. Thus, the size distribution of water voles eaten by eagle owls was more skewed toward larger size classes than could be expected. This suggests a selection of larger voles by eagle owls.

A possible bias could be that mandibles of very young voles are likely to be more readily dissolved in the stomach than those of older voles. Of the total of 201 mandibles found and measured, 24 were excluded from the analysis because all tree measurements could not be taken (giving the sample size of 177). Several of these may possibly have been from younger animals. The most anterior measurement was lacking in only one vole, hence this was used to test for size differences in the two groups of voles; excluded voles (n=23) and included voles. The excluded mandibles were significantly smaller than those included (Wilcoxon test, z=3.02, p=0.003), and would have skewed the sample of voles eaten to be 0.1 mm smaller (in this measurement) than those trapped. Consequently, this bias did influence the results slightly, but marginally compared to the hypothesis that voles eaten at the nest were much smaller than voles trapped in the autumn.

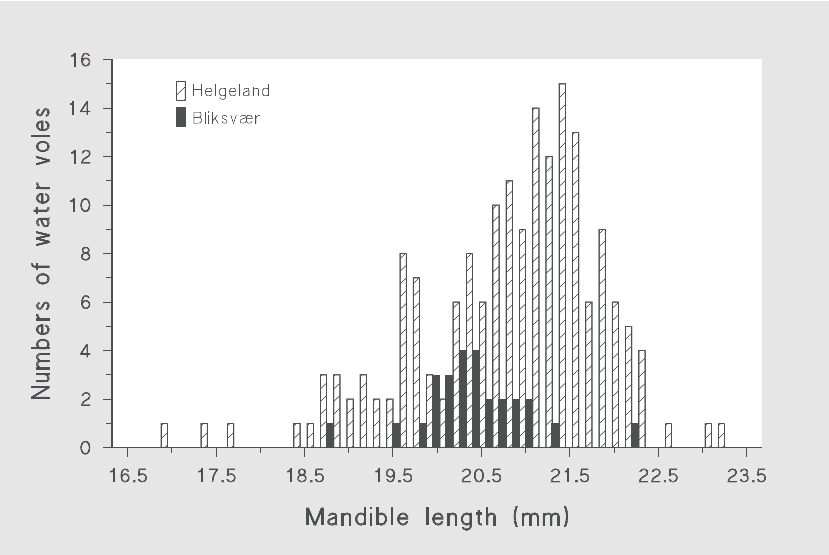

Figure 3
Histogram of water vole mandible length from Helgeland (eaten by eagle owls) and Bliksvær (trapped), North Norway.

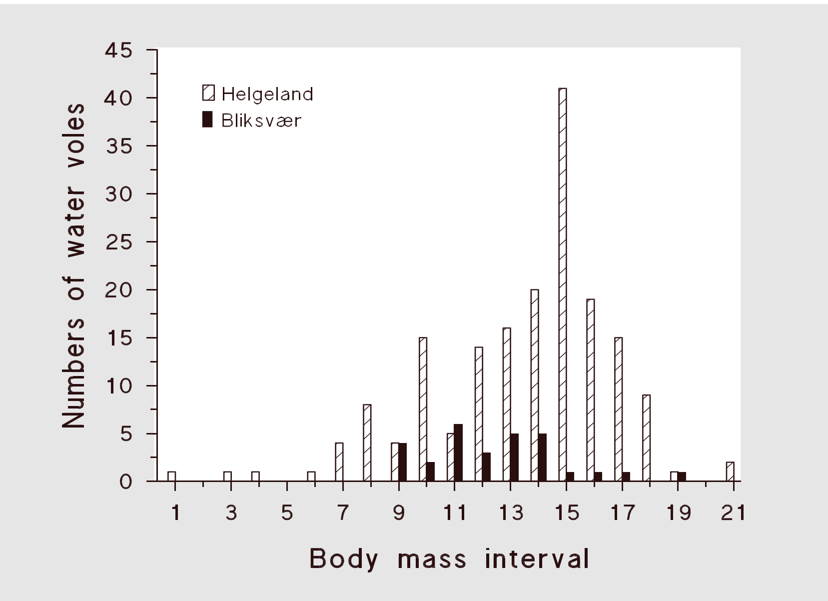

Figure 4
Histogram of water vole body mass from Helgeland (eaten by eagle owls, mass estimated) and Bliksvær (trapped), North Norway. The mass is given in intervals of 10 g (compare with min. and max. in Table 2).

Factors that may influence vole selection by eagle owls

Optimal hunting. Do eagle owls actually prefer to hunt larger voles? A larger prey animal represents more food, but may be more difficult to catch and may be found in smaller numbers. Smaller (and younger) animals are often more easy to catch and may, at least during the summer, occur in higher numbers. Each individual will, however, represent less food. In order to optimise the energy balance of a hunting effort, one would expect the eagle owl to hunt optimally with respect both to size and number of individuals in each size class. I assume here that a hunt was not influenced by the size of the nestlings, i.e. that the female owl will divide into parts voles that are too large to be swallowed whole by the young. This hypothesis implies a careful screening of the water vole by the owl before it attempts to catch it.

Population cycles. Was the water vole population increasing or decreasing? The production and number of young voles are higher when populations are increasing (sensu Stenseth & Ims 1993, Giraudoux et al. 1997). If the eagle owl hunts indiscriminately, voles should be taken according to their numbers in each size (age) class. It may also prefer to hunt the size classes that are most numerous. When the vole population is low, the eagle owl may possibly shift to other prey (birds). These factors would imply that the eagle owl should catch more young voles during the summer. The material collected here probably represented several different stages in the population cycles.

On offer. At what age and size do water voles leave their safe underground nesting sites and start to venture above ground? In many small rodents, the young may leave their nest when they are still very small and before they are weaned, but there is a minimum age or size for such agility. This age may vary much, probably also within a species according to food availability. Different age and sex classes may also differ in their degree of activity and use of cover. When the young are weaned, they must feed more and more outside the burrow, and become vulnerable to avian predators. Migrating animals suffer significantly more from predation than resident animals (Saucy 1994, Koivunen et al. 1996). The largest water voles, those that are grown-up and established on the better sites, may be more difficult to catch. They may also have learned to avoid the eagle owl's activity periods (sensu Halle 2000). Dispersal appears to be a key factor in water vole population dynamics (Aars et al. 2001, Telfer et al. 2003).

Synchronized reproduction. To what degree are the reproduction in water voles and eagle owls synchronized? Eagle owls in this region normally hatch from the middle of May until the beginning of June, and the owlets start to move away from the nest in the last part of June, rarely in the middle of June (Espen Dahl, pers. comm. 2003). According to Haftorn (1971) they still stay close to their nest, but some may also move several hundred meters away (Frode Johansen, pers. comm. 2003). It is therefore probable that the owlets usually stay within the area surrounding the nest where the material was collected. It is however also possible that the material mostly originated during the period from the middle of April (female incubation) to the middle of June. Are young voles available to eagle owls in this period? In England, the first water voles are born in April (Woodroffe 1996), but this is likely to take place at least one month later in northern Norway.

Optimal transportation. Does the male eagle owl eat the smaller voles himself, and only transport larger ones to the nest? The female incubates alone and stays in the nest when the young are small, leaving the male to do all the hunting (Haftorn 1971). The latter may optimise transportation costs by bringing only larger voles to the nest. Most of the material collected had probably been eaten by the female and young, hence the distribution of water voles may have been skewed toward larger voles. This may explain why so few small water voles were found in this sample. However, the male is able to transport several voles simultaneously and the flight distances to the nest are short (small home ranges). Even if the optimal transportation hypothesis is correct, he still must have caught a relatively high proportion of large voles to deliver to the nest. Evidence of optimal transportation has been found in e.g., otters *Lutra lutra*, when the mother fed her cubs larger fish than she ate herself (Kruuk et al. 1987, Heggberget & Moseid 1994).

Active selection of prey?

I would have expected eagle owls to eat predominantly smaller water voles, i.e. the young born during the summer (compare Koivunen et al. 1996). However, the size distribution was clearly skewed toward larger voles, and the voles eaten by owls on Helgeland were even larger than those captured late in the autumn on Bliksvær (although the difference was only 0.4 mm in average mandible length). This suggests some kind of selection of voles, but when and how such a selection is made is unknown. Any or a combination of the hypotheses mentioned could apply. The eagle owl may even show temporary variation in its foraging strategy. Of the hypotheses mentioned, the problems of asynchronized breeding between predator and prey and optimal transportation may seem the more likely ones to explain the results of this study.

Most of the water voles captured on Bliksvær were born during the previous summer, and would have reached adult or near-adult size by the time they were caught in the autumn. But what is the adult size of water voles? This species varies a lot in size, and, as in other small rodents, may have two "adult" sizes: prebreeding adult size and breeding adult size. Only those born early in the summer may reproduce the same year (Strachan 1998), the minimum in England being 38 days old and 77 g (Woodroffe 1996) . Breeding voles are the largest, have greater energy requirements and may need to spend more time foraging outside their safe burrows. Siivonen (1976) states that pregnant females are minimum 230 mm in total length (body length 140 mm), and Collett (1912) found one pregnant female to be 296 mm and states that adult water voles are normally 280-300 mm in total length. All voles from Bliksvær were more than 220 mm and may be considered adults. Hence, most of the voles eaten by owls on Helgeland were also adults. The maximum length of water voles also varies between localities, but most values given are in the range 300-380 mm (Collett 1912, Siivonen 1976, Reichstein 1982, Semb-Johansson & Ims 1990, Macdonald & Barrett 1993). The largest vole on Bliksvær was 320 mm in total length. The largest vole on Helgeland was estimated to be 317.8 mm and the smallest 156.4 mm.

According to Strachan (1998) water voles in England must reach 170 g to survive the winter. Very few of the voles in this study were that large, but Strachan (1998) also states that the "water" form of the water vole is larger than the "fossorial" form, to which the Norwegian populations are supposed to belong (sensu Reichstein 1982). According to Woodroffe (1996, see also Reichstein 1982), the body mass of the youngest water voles captured by scientists varies much between studies, from 42 to 150 g (3-15 weeks old). Water voles are weaned at two weeks and may then be thrown out of the nest. This means that young have to forage for themselves at a young age, and when venturing outside the burrow would be at risk of predatory owls. The eagle owl at Helgeland had eaten only four voles smaller than 70 g and 200 mm (mandible length less than 18.5 mm, Figure 3). This is remarkably few, considering that during the summer the majority of the population would be young voles. This suggest a selection of larger water voles by eagle owls either during hunting or transportation, or perhaps more likely, eagle owls start breeding earlier than water voles. Intense hunting of adult pre-breeding voles could have a significant impact on their population growth, and may even suppress their potential summer population size. Further studies into this predator-prey relationship and its significance for prey selection, reproduction in both species and behavioural strategies and population cycles in water voles could be very interesting, both in terms of ecology and conservation.

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Sammendrag

Foretrekker hubro større vånd?

Optimal furasjering forutsetter at en jeger jakter på det byttedyret som er energetisk mest lønnsomt. Dette er ofte større individer. Hubroen *Bubo bubo* er en effektiv jeger med vånd *Arvicola terrestris* på menyen. På Helgeland i Nordland ser det ut som om hubroen i stor grad er avhengig av vånd, og at den samtidig er våndens viktigste predator. Jeg samlet inn underkjever (n=177) av vånd fra hubroreir og gulpeboller (n=22 + endel fragmenter) i juni 2002. Vånd utgjorde 86.8 % av byttedyrene i gulpebollene, mens fugler utgjorde 13.2 %. Høyre underkjeve ble målt, noe som viste at de våndene som ble spist av hubro var relativt store. Svært få små vånd var spist, selv om disse om sommeren ofte både finnes i større antall og kan være lettere å fange enn store og voksne dyr. Totallengden på det største individet ble estimert til 318 mm. Vånd (n= 29) fra ei anna øy i Nordland, Bliksvær, ble brukt som referanse der både kjevelengde, vekt, totallengde, halelengde og kroppslengde var kjent. Kjevelengde korrelerte godt med alle andre mål. Disse våndene hadde blitt fanget om høsten og burde være av voksen eller tilnærmet voksen størrelse, selv om få av dem hadde reprodusert. Underkjevene fra Helgeland representerte flere år og ikke en enkelt sesong, og var signifikant større enn kjevene fra Bliksvær selv om forskjellen var liten. Dette støtter hypotesen om at hubroen velger ut større vånd. Imidlertid er det mulig at ugleungene forlater reiret (hvor det meste av materialet ble samlet) før de unge våndene blir store nok til å forlate sitt trygge reir under bakken og blir tilgjengelige som byttedyr. En annen hypotese er at uglehannen optimaliserer transport av føde til reiret, ved kun å transportere større vånd og spise de minste selv.

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