



Examensarbete
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**The implications of diet composition and declining vole
supply on populations of vole eating raptors**

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The implications of diet composition and declining vole supply on populations of vole eating raptors

Konsekvenser av födoval och minskande sorkstammar för populationer av sorkätande ugglor och rovfåglar

Katie Andrie

Keywords: Tengmalm's owl, kestrel, breeding density, vole decline, food supply, small mammal specialization, predicted and observed trends

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Abstract

Breeding success for specialist avian predators in northern Fennoscandia is highly dependent on cyclic vole populations. The 3-4 year high amplitude vole cycles once regular to this region have shown significant long term declines in abundance since the 1970s. The vole decline in Sweden, detected by the National Environmental Monitoring Program, is suggested to have negative consequences on breeding performance for specialist raptors. Complete, long term monitoring data to show this on particularly northern owls are scarce. I compared Tengmalm's owl to the European kestrel, an increasing generalist, in northern Sweden, and used these as model species for comparing with other northern raptors. Diet compilation for 15 raptors revealed the snowy, great grey, hawk, long and short-eared owls are also small mammal specialists and were placed together with Tengmalm's owl in an 'owl' predator category; the hen harrier, common buzzard, kestrel, and eagle, tawny, Ural, and pygmy owls are generalists and were placed in a 'kestrel' predator category; and the rough-legged buzzard is an intermediate placed in a combined owl/kestrel category. I predicted trends for species based on degree of small mammal specialization and model predator category. I suggested those in the owl category should decline, those in the kestrel category should not decline, and rough-legged buzzard should probably decline. Population data for raptors from Sweden, including migration counts from Falsterbo and breeding density of Tengmalm's owl and kestrel in Västerbotten County, were analyzed against the spring and previous autumn vole food supply indices from Västerbotten County. Migration counts of the common and rough-legged buzzards showed a significant positive relationship with the spring vole index. Breeding density of Tengmalm's owl and kestrel showed significant positive relationships with the previous autumn vole index (and also spring for Tengmalm's owl), while mean annual brood size for kestrels was only dependent on the spring vole index. For species with data available from Sweden, only the kestrel showed an increasing population trend. However, breeding density of Tengmalm's owl, a vole specialist, has declined in northern Sweden since the 1980s. The specialists placed in the owl category are predicted show similar patterns as Tengmalm's owl and are the most likely species that have been and will continue to be adversely affected by significant declines in vole abundance.

Introduction

In Fennoscandia, Hansson and Henttonen (1985, 1988) distinguished three main zones according to population fluctuations of microtine rodents: 1) a southern zone (55° to 59° N) with seasonal and non-cyclic populations; 2) a transition zone (59° to 61° N) with weakly cyclic populations; and 3) a northern zone (above 61° N) with strong 3-4 year high-amplitude cyclic populations. They attribute this cyclic gradient to increasing snow cover from south to north, and an increased diversity of predators and alternative prey is thought to be the primary cause of non-cyclic vole populations in the southern zone (Erlinge et al. 1983; Hanski et al. 1991). Voles are the main prey source for many northern avian and mammalian specialist predators and their cycles directly affect predator population dynamics (Hörnfeldt 1978; Korpimäki 1984, 1994; Hörnfeldt et al. 1990, 2005).

When abundant, most raptors and mammalian predators consume voles, but many owls and other specialist avian predators are particularly dependent on peak vole years to produce sufficient numbers of offspring. Breeding density and performance of several species across Fennoscandia including Tengmalm's owl (*Aegolius funereus*), great grey owl (*Strix nebulosa*), short-eared owl (*Asio flammeus*), long-eared owl (*Asio otus*), Ural owl (*Strix uralensis*), rough-legged buzzard (*Buteo lagopus*), and European kestrel (hereafter "kestrel") (*Falco tinnunculus*) are positively correlated with small mammal density, and individuals consume larger proportions of these prey items during high density years than low ones (Pasanen and Sulkava 1971; Korpimäki 1984; Korpimäki and Norrdahl 1989, 1991; Hörnfeldt et al. 1990; Potapov 1997; Sundell et al. 2004; Hipkiss et al. 2008).

In times of vole scarcity, dietary shifts of generalist predators to alternative prey has been observed in kestrels (Korpimäki 1985b), Ural and eagle owls (*Bubo bubo*) (Korpimäki et al. 1990), and red foxes (*Vulpes vulpes*) (Angelstam et al. 1984). Many vole specialists, however, will not attempt to breed during low vole years (Newton 1979; Mikkola 1983). The kestrel however was considered to be a food generalist when compared to vole specialists including Tengmalm's, long and short-eared owls (Korpimäki 1985a); these three specialists were found to be much more restrictive and do not regularly take alternative prey even during low vole years (Korpimäki 1981, 1992a; Korpimäki and Norrdahl 1991). Specialists including Tengmalm's, hawk (*Surnia ulula*), great grey, snowy (*Nyctea scandiacus*), long and short-eared owls are generally nomadic and will disperse from areas of low to high abundance of voles and track their population fluctuations (Korpimäki 1985c, 1992b, 1994; Löfgren et al. 1986). The main factor explaining geographical synchrony of vole populations across Fennoscandia is thought to be caused by rapid tracking of voles by nomadic avian predators (Ydenberg 1987; Ims and Steen 1990; and Norrdahl and Korpimäki 1996).

Increasing irregularity and long term declines in density and amplitude of vole populations have been observed in northern Sweden and other regions in Fennoscandia (Hörnfeldt 1991, 1994, 1995, 2004; Henttonen 2000; see Hörnfeldt 2004 for review and references). Declines in bank voles (*Clethrionomys glareolus*), grey-sided voles (*Clethrionomys rufocanus*), and field voles (*Microtus agrestis*) revealed from population monitoring of voles in northern Sweden from 1971-2003 are largely related to their decreased winter survival (Hörnfeldt

2004). Overall population decline is most evident for spring densities. Lower winter survival rates have led to low amplitude cycles and a change from a gradual two year increase in spring density (leading to superabundant peaks found in the 1970s) to a more or less one year build up resulting in smaller spring densities (Hörnfeldt 2004). Decreased over-wintering success has coincided with a change in the North Atlantic Oscillation (NAO). In Scandinavia, negative NAO-index values are associated with cold and dry winters; however, high positive NAO-index values that are associated with mild and wet winters have occurred for long periods since the early 1980s (Hurrell 1995). This period of mild winters has caused temperatures to increase in Scandinavia since the 1980s (Alexandersson 2002), likely resulting in less stable winters with shorter periods of protective snow cover as well as more freezing and thawing periods creating icebark formation on the ground (Hörnfeldt 2004). These conditions have been shown to be detrimental to winter survival of voles (Aars and Ims 2002).

Declines in abundance of vole populations are likely to have significant negative consequences on breeding performance and abundance of their specialist avian predators (Hörnfeldt 1998, 2004; Strann et al. 2002). Declines in some raptor and mammalian predators have been observed in Fennoscandia, although there have been few studies attempting to link this change to declines in vole abundance. High quality, long-term monitoring data are scarce on regional breeding performance of raptors and on dynamics of regional vole populations. Tengmalm's owl is one exception, where breeding populations in northern Sweden have experienced significant declines in synchrony with vole populations since the 1980s (Hörnfeldt et al. 2005). Autumn migration counts at Falsterbo, Sweden, showed recovering populations of most raptor species in the 1970s due to decreased pesticide use and human persecution, but by the 1990s species including the hen harrier (*Circus cyaneus*), common buzzard (*Buteo buteo*), and rough-legged buzzard began to decline again. Declines in vole abundance were suggested to be a possible reason for reduced numbers of migrating hen harriers and rough-legged buzzards (Kjellén and Roos 2000). Lack of population data on other owls than Tengmalm's owl in northern Sweden makes it difficult to determine accurate population status and if any subsequent declines are related to the long term vole decline.

Resident generalist owl species are typically large, long-lived, monogamous, form strong pair bonds for several years to a lifetime, and are strongly territorial; nomadic or migratory specialists are generally smaller, short-lived, sometimes polygamous, form weak pair bonds and show weak territoriality (Mikkola 1983; summarized in Korpimäki 1992b). Nomadic specialists usually stay in Fennoscandia during winter, whereas migratory specialists including long and short-eared owls overwinter in central and western Europe. Tengmalm's owl is a cavity nester and probably the most common bird of prey in coniferous forests of Fennoscandia (Ulfstrand and Högstedt 1976, cited by Korpimäki and Norrdahl 1989), preferring spruce forests for breeding territories (Korpimäki 1981). Kestrels are adaptable hunters and consume a wide variety of prey which enables them to occupy a large geographical range in Europe (Village 1990). They are primarily open-country falcons that nest in a variety of structures including tree cavities, cliffs, old stick nests, ledges of buildings, and artificial nest boxes (Shrubb 1993). Kestrels tend to avoid dense forests unless clearings are present for hunting (Village 1990).

Aims of my study

The first aim of this study was to compare breeding density for Tengmalm's owl, a declining vole specialist (Hörnfeldt et al. 2005), to the kestrel, a stable/increasing generalist (Stefan Delin *pers. comm.*), and in relation to vole abundance.

The second aim was to group raptors of northern Sweden as more similar to Tengmalm's owl or kestrel based on diet selection in an attempt to infer possible effects of the long term vole decline on northern raptors, which is particularly important for most owls where population monitoring is not available. Raptors placed in the owl group based on diet selection are predicted to follow patterns similar to that of Tengmalm's owl, and those in the kestrel group less likely so.

The third aim was to investigate relationships between population data on migration of several other raptors and vole populations in northern Fennoscandia. This will enable a determination of which raptors show a relationship to the vole cycle, and the results will also hopefully allow us a better indication of which raptors may have been and will continue to be affected by declines in vole abundance.

Methods

Raptor population data

I used breeding density, expressed as the proportion of occupied nest boxes, of Tengmalm's owl and kestrel from areas around Umeå in Västerbotten County, Sweden, (approximately 64°N, 20°E) as indices of population trend. For both species, a breeding was defined by the presence of at least one egg. Nest boxes have been used to monitor Tengmalm's owl populations in Västerbotten County by Birger Hörnfeldt and colleagues since 1980. Owl nest boxes were placed at approximately 1 km intervals along roads in transects of normally 50 boxes. Boxes were visited at 3-4 week intervals (and more often if breeders were present) from March through June to monitor breeding performance. The number of boxes monitored varied from about 300 to 600 per year (more detail on study design in Löfgren et al 1986; Hörnfeldt et al. 1990, 2005). Since 1995, kestrel populations around Umeå have been monitored yearly by Stefan Delin using nest boxes. Nest boxes were checked from April through July to record presence of breeding pairs, number of eggs, and number of chicks. The number of boxes placed and monitored steadily increased from 27 in 1995 to 231 by 2009 (Stefan Delin *pers. comm.*).

Migration counts for honey buzzard (*Pernis apivorus*), hen harrier, common buzzard, rough-legged buzzard, and kestrel used in my analyses were obtained from Falsterbo Bird Observatory (Kjellén 2010). I selected these species because they are vole eating predators to some degree, except for honey buzzard. I included the honey buzzard because its drastic decline in migration counts from Falsterbo resembles the small mammal decline from northern Sweden and thought this potential relationship required further investigation.

Standardized counts from August 11 through November 20 in Falsterbo have been conducted since 1973 to cover the entire raptor migration (Kjellén and Roos 2000). The Falsterbo peninsula (approximately 55°23'N, 12°49'E) comprises the southwestern most point of Scandinavia where large numbers of migrants assemble during autumn, making it one of the best places to observe raptor migration in Europe.

Vole monitoring

To compare raptor populations to vole food supply, I used long term monitoring data on small mammal populations. Snap-trapping twice a year during late May and late September has been conducted in an 100 x 100 km² area in Västerbotten County, northern Sweden, since 1971 (Hörnfeldt 1978, 1994, 2004, 2005). Initiated at Umeå University, the small mammal monitoring in Sweden is now part of the Swedish Environmental Protection Agency's National Environmental Monitoring Program (Hörnfeldt 2011). Sampling was conducted in 58 regularly distributed 1 ha plots over three consecutive nights, and the data are presented as an index of number of individuals caught per 100 trap nights (for more detail on study design see Hörnfeldt 1978, 1994, 2004). I combined the number of bank voles, field voles, and grey-sided voles as an index of food supply in spring and autumn.

Diet Compilation

I searched the literature and compiled diet selection data for 15 raptors that are found in northern Sweden. I included the selected species with migration counts, as well as the snowy, eagle, tawny (*Strix aluco*), Ural, great grey, hawk, pygmy (*Glaucidium passerinum*), Tengmalm's, long-eared, and short-eared owls. I restricted diet studies to those within Fennoscandia, as diet can vary widely across geographical areas. I included mammals, birds, reptiles/amphibians, invertebrates, and other as prey categories. In addition, I summarized a break down of the mammal category to include 1) small mammals, with 'small microtines' and 'other small mammals' as subcategories, and 2) larger mammals. Small microtines included voles and lemmings, excluding only water voles (*Arvicola amphibius*). Even though water voles are microtine rodents, I chose to place them with larger mammals due to their size, and they were only found in any significant amount in the larger generalists (i.e. eagle and Ural owl). Rats, hares, squirrels, and mustelids were other prey items included in the larger mammal category. The other small mammals category included primarily shrews and mice. Even though diet compilation was confined to Fennoscandia, prey selection will inevitably vary across study areas, so I summarized the amount of variation for each prey category between studies as a range of percentage of the diet, and variance.

Data analysis

Population trends

Least squares regression was used to analyze population trends using breeding density of Tengmalm's owl and migration data on the honey buzzard, hen harrier, common and rough-legged buzzard, and kestrel. I added a quadratic and third order polynomial to the regression models and used Akaike's information criterion (AIC) to determine which model provided the best fit. Migration count data were natural log transformed for all species before analysis. Kestrel breeding density was based on the number of occupied and unoccupied nest boxes, so I used a generalized linear model (GLM) with a binomial distribution to assess the population trend for the kestrel population around Umeå.

Relationships to vole cycle

I used autocorrelation function (ACF) to indicate any cyclicity in the time series for breeding density of Tengmalm's owl and kestrel in Västerbotten and annual number of migrating raptors from Falsterbo that could be linked to the 3-4 year vole cycle. I also used ACF on mean annual brood size of kestrels in Umeå. All variables were natural log transformed before analysis.

Least squares regression was used to analyze the relationship between breeding density of Tengmalm's owl and migration count data to the vole food supply during current spring and previous autumn. In cases where significant autocorrelation was found within the model residuals, generalized least squares estimation (GLS) was used in order to include appropriate correlation structures. A GLM with a binomial distribution was used for analyzing breeding density of kestrels. I used mean annual brood size of kestrels as an additional response variable to compare to the food supply indices using regression. All response variables in the least squares regressions were natural log transformed prior to analysis. All calculations were performed in R version 2.13.0.

Results

Diet Compilation

Diet compilation showed that the percentage of small microtines varied considerably among the species considered to be vole specialists in this study (see Tables 1-3). Small microtines comprised 96%, 81%, and 70% for the vole specialists hawk owl, Tengmalm's owl, and long-eared owl, respectively; however, the small mammal category comprised 98%, 96%, and 98% for these species (Table 1). Similarly, some of the owl specialists showed large variation in percentage of small microtines across studies, but the percentage of small mammals varied very little. The range in small microtines was 53%-92% and 72%-93% for the great grey and Tengmalm's owl, respectively, but was 92%-97% and 95%-99% for small mammals across studies (Table 2). Due to the low variation and consistency of small mammals in the diet of the owl specialists, I concluded that this was a better way than using the small microtines

category to classify raptor specialization according to diet. The percentage of larger mammals in the diet only occurred in any quantity in the generalists. The eagle owl, tawny owl, Ural owl, and common buzzard had 38%, 9%, 25%, and 17%, respectively, of larger mammals in their diet (Table 1). The vole specialists all had less than 1% in this category, except the great grey owl, which due to its larger size is more capable to occasionally take larger mammals. In this case almost all larger mammals taken by great grey owls were water voles. Invertebrates comprised 96% and 25% of the diet for honey buzzard and kestrel, respectively, and did not occur more than 3% in any other species (Table 1).

To compare raptors based on diet selection, I grouped species into a predator category as more similar to Tengmalm's owl, labeled 'owl', or kestrel, labeled 'kestrel'. I made this decision based primarily on the percentage of small mammals in the diet. There were quite clear distinctions when looking at the small mammal category: it comprised at least 95% of the total diet for the snowy, great grey, hawk, Tengmalm's, long and short-eared owls (Table 1). According to this study, these six owl species are considered the small mammal specialists and are therefore placed in the owl predator category (Table 3). Rough-legged buzzard was the next closest species with 88%. I did not believe this percentage was high enough to be placed with the specialists, so I categorized this species as an intermediate in small mammal specialization and placed it in a combined kestrel/owl group. There was a fairly large gap between the specialized owl group and the intermediate rough-legged buzzard on one hand, and the rest of the raptors (excluding honey buzzard), which ranged from 21%-66% small mammals in their diet. These other species including hen harrier, common buzzard, kestrel, eagle owl, tawny owl, Ural owl, and pygmy owl, were considered small mammal generalists and were all placed in the kestrel predator category. The honey buzzard did not include any mammals in its breeding time diet; it is rather a specialist on bee and wasp larvae (Itämiel and Mikkola 1972) and was placed in its own category without small mammal specialization.

I made predictions of population trend based on the classification of the model predator category for each species. A species was given a 'decline' if in the owl category, a 'probable decline' for the rough-legged buzzard, and a 'no decline' if included in the kestrel category, (Table 3). Even though the honey buzzard was not included in a model predator category, it was given a 'no decline' because no small mammals were reported in the one diet study available for Fennoscandia. These predictions were made only for Fennoscandian populations that would be affected by changing vole dynamics in this region. Additionally, predictions are based solely on degree of small mammal specialization, and contradicting observed trends can be result of many other factors. Table 3 shows any reported population trends (including this study) for raptors in any Fennoscandian country and Europe. General trends in Europe are from BirdLife International (2004) that compiled data from organizations and research institutes across Europe. These conclusions are made with the best available data but in many occasions data are probably of poor quality.

Table 1. Summary of diet selection, expressed as a percentage of total diet, for 15 raptor species from studies within Fennoscandia. The mammal category is broken down into subcategories. ‘Small mammals’ and ‘larger mammals’ are a subset of the total mammals, and ‘small microtines’ and ‘other small mammals’ are a subset of ‘small mammals’. Small mammal specialization according to this study is also given: S=specialist, G=generalist, I=intermediate, N=none.

Prey Category	Honey Buzzard ^a	Hen Harrier ^b	Common Buzzard ^c	Rough-legged Buzzard ^d	Kestrel ^e	Eagle Owl ^f	Snowy Owl ^g	Tawny Owl ^h	Ural Owl ⁱ	Great Grey Owl ^j	Hawk Owl ^k	Pygmy Owl ^l	Tengmalm's Owl ^m	Long-eared Owl ⁿ	Short-eared Owl ^o
Total mammals	0	58.4	52.1	89.8	65.5	59.4	98.0	74.7	85.1	98.0	97.9	65.4	96.4	98.1	95.9
Small mammals	0	56.7	35.0	88.3	64.1	21.0	97.5	66.2	59.8	95.3	97.6	65.3	96.4	97.8	95.1
Small microtines	0	(55.8)	(30.4)	(82.9)	(43.9)	(18.8)	(97.2)	(40.8)	(49.1)	(86.5)	(95.7)	(57.3)	(80.5)	(70.3)	(85.9)
Other small mammals ¹	0	(0.9)	(4.6)	(5.4)	(20.3)	(2.2)	(0.3)	(25.4)	(10.7)	(8.8)	(1.9)	(8.0)	(15.8)	(27.5)	(9.2)
Larger mammals ²	0	1.8	17.1	1.5	1.4	38.4	0.5	8.5	25.3	2.7	0.3	0.1	0	0.3	0.7
Birds	1.5	40.0	32.3	9.8	8.5	36.2	1.5	14.3	10.1	0.8	1.4	33.4	3.6	1.8	1.8
Reptiles/Amphibians	2.5	0.4	10.9	0.3	1.3	3.4	0.3	9.0	4.7	0.3	0	0	0	0	0.2
Invertebrates	96.1	1.2	2.4	0	24.8	0.2	0.1	1.7	0.0	0.0	0.1	0	0.1	0.1	2.1
Other	0	0	2.5	0	0	0.9	0.2	0.3	0	1.1	0.6	1.2	0	0	0
Number of prey items	937	570	2980	3582	2934	15642	2726	9947	11930	12842	2167	4082	16448	17676	3030
Small mammal specialization	N	G	G	I	G	G	S	G	G	S	S	G	S	S	S

¹ includes primarily shrews and mice

² includes primarily rats, water voles, hares, squirrels and mustelids

Sources:

^a Finland (Itäemies and Mikkola 1972)

^b Norway (Hagen 1952)

^c Finland (Reif et al. 2001; Suomus 1952), Norway (Spidsø and Selås 1988)

^d Finland (Pasanen and Sulkava 1971; Tast 2010), Norway (Hagen 1952)

^e Finland (Korpimäki 1985a), Norway (Hagen 1952)

^f Finland (Korpimäki et al. 1990), Norway (Willgohs 1974), Sweden (Olsson 1979)

^g Finland (Hakala, Kaikusal and Rikkonen (*in litt.*) from Mikkola 1981), Norway (Løvenskiold 1947; Hagen 1960), Sweden (Andersson and Persson 1971)

^h Based on 13 studies in Finland, Norway, and Sweden summarized by Mikkola 1981, Sweden (Lundberg 1980)

ⁱ Finland (Korpimäki et al. 1990; Korpimäki and Sulkava 1987), Norway (Myrsterud and Hagen 1969), Sweden (Lundberg 1976, 1977)

^j Finland, Norway and Sweden (*cf.* Mikkola 1981), Sweden (Höglund and Lansgren 1968), Finland (Sulkava and Huhtala 1997)

^k Finland (Hublin and Mikkola 1977; Mikkola 1972), Norway (Hagen 1952; Nybo and Sonerud 1990)

^l Finland (Jussila and Mikkola 1973; Kaakinen and Mikkola 1972; Kellomäki 1969, 1977; Mikkola 1970; Mikkola and Jussila 1974), Norway (Solheim 1984)

^m Finland (Heinonen et al 1970; Klaus et al 1975; Korpimäki 1972; Rajala 1976; Rajala 1976; Sulkava and Sulkava 1971), Sweden (Hörnfeldt et al. 1990)

ⁿ Finland (Korpimäki 1992a), Sweden (Källander 1977)

^o Finland (Grönlund and Mikkola 1969; Mikkola and Sulkava 1969), Norway (Hagen 1952)

Table 2. Variation in diet across Fennoscandian studies for 15 owl and raptor species. Range (in percentage of diet) and variance for the most important prey categories are given (estimates rounded to nearest integer for those greater than 1). Small mammal specialization according to this study is also given: S=specialist, G=generalist, I=intermediate, N=none. There was only one study available for honey buzzard and hen harrier.

Species	Total mammals		Small mammals		Small microtines		Other small mammals		Larger mammals		Birds	
	Range	s ²	Range	s ²	Range	s ²	Range	s ²	Range	s ²	Range	s ²
Honey Buzzard, N											2	--
Hen Harrier, G	58	--	57	--	56	--	1	--	2	--	40	--
Common Buzzard, G	44-55	39	32-37	5	28-37	18	0.3-7	26	11-19	17	14-36	142
Rough-legged Buzzard, I	44-99	863	44-99	830	34-87	904	1-12	31	0.4-2	2	1-56	852
Kestrel, G	65-71	17	63-70	25	36-45	38	19-34	123	0.3-2	*	3-9	16
Eagle Owl, G	41-87	580	12-30	80	10-29	88	1-4	2	17-58	408	10-51	497
Snowy Owl, S	97-99	2	96-99	3	96-99	3	0.3-0.5	*	0.1-1	*	1-2	*
Tawny Owl, G	70-84	57	55-69	44	26-46	103	16-25	229	8-28	103	9-19	28
Ural Owl, G	85-86	*	50-79	209	40-67	180	10-12	1	6-36	225	10-15	7
Great Grey Owl, S	93-99	7	92-97	5	53-92	334	5-39	265	1-4	2	0.6-1	*
Hawk Owl, S	96-99	3	96-99	4	93-98	8	0.2-3	2	0.1-1	*	0.6-3	1.1
Pygmy Owl, G	54-89	599	54-89	602	50-74	292	5-15	56	0.1	--	11-44	538
Tengmalm's Owl, S	95-99	9	95-99	9	72-93	221	6-23	139			1-5	9
Long-eared Owl, S	98-98	*	97-98	*	67-81	92	16-31	113	1.4	--	1.6-2	*
Short-eared Owl, S	96-98	2	95-98	5	84-95	56	3-11	29	1	--	2-2	*

* variance < 1

-- only reported in one study, no variance estimate

Table 3. Small mammal specialization, model predator category (owl, kestrel, combined, or none), prediction of population trend based on model predator category, and reported population trends (Fennoscandia and Europe) based on the results of this study and any other known trends for the 15 selected raptors.

Species	Small mammal specialization	Model predator category	Prediction of population trend based on model predator category	Reported population trend in Fennoscandia	Reported overall population trend in Europe ^f
Honey Buzzard	None	None	No decline	Decreasing ^{abf}	Stable
Hen Harrier	Generalist	Kestrel	No decline	Decreasing ^{abf}	Decreasing
Common Buzzard	Generalist	Kestrel	No decline	Decreasing ^{abd}	Increasing
Rough-legged Buzzard	Intermediate	Kestrel/Owl	Probable decline	Decreasing ^{ab} Stable ^d	Fluctuating
Kestrel	Generalist	Kestrel	No decline	Increasing ^{ad}	Decreasing
Eagle Owl	Generalist	Kestrel	No decline	Increasing ^f Decreasing/stable(Finland) ^e	Stable
Snowy Owl	Specialist	Owl	Decline	Fluctuating ^f	Fluctuating
Tawny Owl	Generalist	Kestrel	No decline	Stable ^{ef}	Stable
Ural Owl	Generalist	Kestrel	No decline	Increasing ^{ef} Stable ^f	Stable
Great Grey Owl	Specialist	Owl	Decline	Fluctuating ^f	Unkown
Hawk Owl	Specialist	Owl	Decline	Fluctuating ^f	Fluctuating
Pygmy Owl	Generalist	Kestrel	No decline	Stable ^{ef}	Stable
Tengmalm's Owl	Specialist	Owl	Decline	Decreasing ^{ace} Fluctuating ^f	Stable
Long-eared Owl	Specialist	Owl	Decline	Decreasing ^e Fluctuating ^f	Stable
Short-eared Owl	Specialist	Owl	Decline	Fluctuating ^f Decreasing ^{ef}	Fluctuating

^a Sweden (this study)

^b Sweden (Kjellén and Roos 2000)

^c Sweden (Hörnfeldt et al. 2005)

^d Finland (Saurola 2005)

^e Finland (Saurola 2009)

^f Europe (BirdLife International 2004)

Population trends

The spring vole index in Västerbotten has experienced significant reductions in peak densities, the last major one being in 1978, but has more or less remained stable at a lower abundance since then (Fig. 1a). Due to large variation in cyclic fluctuations for breeding density of Tengmalm's owl, which displayed similar low densities but declining peak densities throughout the time series, strong autocorrelation was found in the regression model residuals and no significant population trend was found when all data were used in the analysis. However, when only peak densities were used ($n=10$) from 1982-2008, there was a strong significant negative trend ($p < 0.001$) and no autocorrelation was present in the residuals (Fig. 1c). AIC showed that the best fit for kestrel and honey buzzard was the quadratic model. The kestrel showed significant increasing trends for both breeding density around Umeå and migration counts from Falsterbo (Table 4; Figs. 1d, 2a). Significant negative trends were found for migration counts of honey buzzard, hen harrier, common buzzard, and rough-legged buzzard (Table 4). No autocorrelation was found in the residuals for these models. However, the R^2 was low for the hen harrier, common and rough-legged buzzard; only 11-12% of the variation was explained by these models (Table 4).

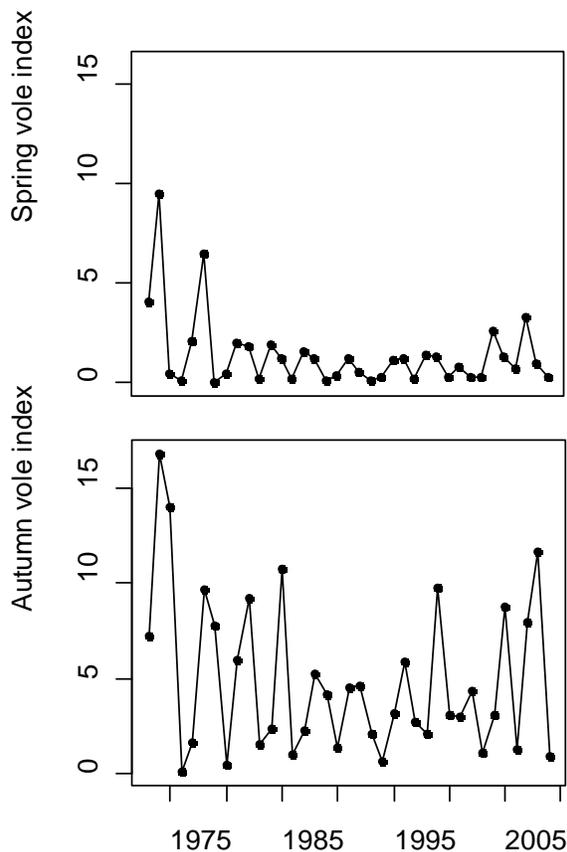


Figure 1. Vole indices in a) spring and b) autumn (1973-2009), and breeding density of c) Tengmalm's owl (1980-2009) and d) kestrel (1995-2009) in Västerbotten, Sweden. Dashed lines represents significant relationships from regression analysis, see text for further explanation.

Figure 2. Population trends for the annual autumn migration counts for a) kestrel, b) common buzzard, c) hen harrier, d) rough-legged buzzard, and e) honey buzzard from Falsterbo, Sweden. Dashed lines represent significant relationships from regression analyses, see text for further explanation.

Table 4. Results of least squares regression testing for trends in breeding density of Tengmalm's owl from Västerbotten and migration counts of raptors from Falsterbo, and from a generalized linear model for kestrel breeding density around Umeå. Coefficients, t values, R^2 , and significance (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$) are given for explanatory variables Year and Year². Only trends for kestrel and honey buzzard migration counts included a quadratic term.

Species	Period	Year	t	Year ²	t	R^2	Trend
Tengmalm's owl	1980-2009	-0.02	0.759 ns			0.02	
Tengmalm's owl (peak densities n=10)	1982-2008	-0.02	-5.64***			0.80	Declining
Kestrel breeding density	1995-2009	0.08	2.63*			NA	Increasing
Kestrel migration count	1973-2009	-7.1	-3.03**	1.8×10^{-3}	3.03**	0.34	Increasing
Honey buzzard	1973-2009	-6.3	-2.77**	1.6×10^{-3}	2.75**	0.64	Declining
Hen harrier	1973-2009	-0.01	-2.23*			0.12	Declining
Common buzzard	1973-2009	-0.01	-2.11*			0.11	Declining
Rough-legged buzzard	1973-2009	-0.02	-2.17*			0.12	Declining

Relationships to vole abundance

Autocorrelation function showed a significant positive correlation at lag 3, indicating a 3 year cyclicity, for breeding density of Tengmalm's owl ($r=0.59$, $p < 0.001$) and annual autumn migration counts for rough-legged buzzard ($r=0.43$, $p < 0.01$), and hen harrier ($r=0.37$, $p < 0.05$) (Fig. 3). This 3 year cyclicity roughly corresponds to the vole cycle length in Västerbotten (Figs. 1a, b). ACF of kestrel brood size indicates a similar, but not significant, cyclicity as for breeding density and migration counts above. No significant ACFs were found for breeding density of kestrel, or migration counts for honey buzzard, common buzzard, and kestrel.

When analyzing the relationship between raptor population data and vole food supply, significant autocorrelation was found in the residuals for Tengmalm's owl and rough-legged buzzard regression models (Figs. 1, 2). Therefore, I used generalized least squares estimation (GLS) and a moving average order 3 correlation structure, MA(3), and an autoregressive order 1 correlation structure, AR(1), for the respective species, to correct for this. Visual inspection of autocorrelation plots of residuals was used to determine if autocorrelation structures remained in the residuals. Furthermore, the residuals were examined to ensure the validity of the rest of the models. Note that the GLM used for breeding density of kestrel and GLS used to correct for autocorrelation do not compute an R^2 (Tables 4, 5). The previous autumn vole index was removed as an explanatory variable in the regression models for kestrel brood size and migration counts of common buzzard, as it was not significant and its removal increased significance of the current spring vole index. Breeding density of Tengmalm's owl was positively dependent on vole food supply during spring and the previous autumn (Table 5). Breeding density of kestrels showed a significant positive relationship with the previous autumn vole index, but not with the current spring. In contrast, mean annual brood size for kestrel was positively dependent on the spring vole index. Interestingly, the common and rough-legged buzzards showed a positive dependence on the

spring vole index, but the honey buzzard showed a positive dependence on the previous autumn vole index (Table 5). Migration counts for kestrel and hen harrier did not show any significant relationships to food supply.

It should be noted that breeding densities used here for Tengmalm's owl and kestrel are not reliable measures of population size as the term implies, and are only indices of population size. During years with low proportions of breeding individuals it is difficult to explain the status for the rest of the population, as very little is known about the nomadic movements of vole specialized owls.

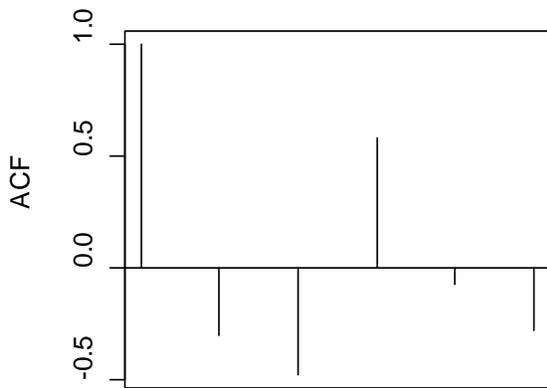


Figure 3. Autocorrelation function for a) breeding density of Tengmalm's owl (1980-2009) in Västerbotten, b) mean annual brood size for kestrel (1995-2009) in Umeå, and annual autumn migration counts (1973-2009) for c) rough-legged buzzard and d) hen harrier from Falsterbo, Sweden. Dashed lines indicate 95% confident intervals.

Table 5. Results of least squares regression of the effects of spring and previous autumn vole food supply on breeding density of Tengmalm's owl and kestrel in Västerbotten, mean annual brood size for kestrel around Umeå, and migration counts of raptors from Falsterbo. Coefficients, t values, R^2 , and significance (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$) are given for explanatory variables.

Species	Period	Spring	t	Previous autumn	t	Model R^2
Tengmalm's owl	1980-2009	0.90	3.96***	0.14	2.9**	NA
Kestrel breeding density	1995-2009	0.12	1.03 ns	0.09	2.81*	NA
Kestrel brood size	1995-2009	0.07	2.63*	-	-	0.35
Kestrel migration count	1973-2009	-0.06	-1.2 ns	0.04	1.68 ns	0.09
Hen harrier	1973-2009	0.05	0.22	-1.7×10^{-4}	0.99	0.06
Common buzzard	1973-2009	0.09	3.3**	-	-	0.24
Rough-legged buzzard	1973-2009	0.21	3.53**	-0.002	-0.08 ns	NA

Discussion

Tengmalm's owl versus kestrel

Long-term studies of northern owls are relatively limited, and few studies have observed population decline and further quantitatively linked it to declines in vole abundance. Tengmalm's owl is the only species for which there are high-quality data in northern Sweden. Hörnfeldt et al. (2005) presented a shift in vole-predator dynamics with cycles of Tengmalm's owl and its prey changing from the typical 3-4 year high-amplitude cycles towards annual fluctuations, resulting in lower breeding densities of owls since the early 1980s. In accordance with other studies in northern Fennoscandia (Korpimäki and Norrdahl 1989; Hörnfeldt et al. 1990, 2005; Saurola 2009), my results also show significant declining trends and strong dependence of Tengmalm's owl populations on both spring and previous autumn food supply.

One can argue that breeding density of Tengmalm's owl (Fig. 1c) showed significant declines only after the loss of major spring vole peaks in the 1970s (Fig. 1a). Spring vole indices remained relatively stable, albeit at lower densities throughout the rest of the time series after this shift. The lack of owl data before 1980 prevents a comparison of trends when there were higher spring vole densities, but it appears that a decline in Tengmalm's owl is showing a delayed response to food supply. Strong autocorrelation indicating a 3 year cyclicality in breeding density of Tengmalm's owl implies that they cycle with and are significantly correlated with vole abundance even if there is a time lag. This is not a very long lived owl, but six year olds have been captured in northern Sweden (Birger Hörnfeldt *pers. comm.*) and some probably live up to 10 years. This suggests that poor breeding success during the early years of the vole decline was likely and consequently reduced numbers of breeding adults, which became evident several years later in breeding densities. Hagen (1969) suggested that a trap index of less than 2 small mammals per 100 trap-nights was more or less a threshold where below this point in boreal Norway vole eating raptors did not settle and breed. The peak spring indices in Västerbotten since 1981 have somewhat stabilized around 2, and in

most peak years just under (Fig. 1c). If this threshold in Norway is any indication for Tengmalm's owl in Sweden, the current spring peaks are barely above a potential limit and could explain a steady decline over time.

I have shown that breeding density and migration counts for the kestrel have shown a significant increase in Sweden, confirming Stefan Delin's observations of populations around Umeå. Their dramatic increase, completely the reverse of Tengmalm's owl, suggests that kestrels do not rely on vole populations as extensively as Tengmalm's owl in northern Sweden. A 32-78% nest box occupancy since the program's initiation in 1995 around Umeå suggests kestrels are very capable of breeding even with a low vole supply. Breeding density and mean annual brood size for kestrels were related to food supply, but if kestrels were as specialized on voles as owls they would most likely not increased as they have, despite increases in available nest boxes. Increases in kestrel populations in Sweden and Finland (Saurola 2005) are also most likely attributed to successful implementation of nest boxes. On the other hand, Tengmalm's owls readily accept artificial nest boxes (Hörnfeldt et al. 1990), but the plethora of unused boxes suggests lack of nesting sites is not cause for their decline. In addition, no difference was found between occupancy of new versus old nest boxes in Sweden, so avoidance of old nest boxes cannot be an explanation of declining owl breeding densities (Gustafsson 2008). Thus, their observed decline is very real and has serious implications for Tengmalm's owl and raptors with a similar food niche.

Differences in breeding ecology and the migratory strategy of the kestrel could partly explain its success. Kestrels are more able to build up energy reserves before the breeding season in their wintering grounds regardless of the vole supply in Västerbotten. Tengmalm's owl and other specialists must endure situations of low food supply and subsequently may be in poorer breeding condition whereas kestrels might have a head start being in better condition.

Reported trends in Europe for Tengmalm's owl are listed as stable, and may be due to more constant rodent populations or a higher diversity of prey. Tengmalm's owl was found to be a resident generalist predator in central Europe consuming a greater diversity of prey southwards (Korpimäki 1986). Populations may have already undergone a significant historical decline and occur at low numbers, making any further observation of decline extremely difficult. In the rest of Europe, kestrel populations have declined and lack of available nest sites may be a limiting factor. Abundance of breeding kestrels has been found to increase when nest boxes were provided, and individuals sometimes prefer them (Cavé 1968; Fargallo et al. 2001). Furthermore, the lack of available nest sites was the primary limiting factor breeding density of kestrels in the UK (Village 1993). Pesticides (Kjellén and Roos 2000) and an agriculture dominated landscape lacking hedgerows, small woodlands, etc., in much of Europe (Butet et al. 2010) may also be contributing factors to declines.

Classifications based on diet

Grouping species according to diet can be rather subjective and some species may be difficult to place, especially when diets can vary widely across geographical areas. The vole specialized owls were fairly straightforward to classify, all having greater than 95% of small

mammals in the diet and very low variance across studies clearly separating them from all other species (Tables 1, 2). The snowy, great grey, hawk, Tengmalm's, long and short-eared owls are all widely known to be small mammal specialists (Mikkola 1983) and no further discussion is required here. The rough-legged buzzard was a difficult species to place as it is generally considered to be a vole specialist. However, Tast et al. (2010a, b) suggested the rough-legged buzzard can be regarded as a generalist when a higher diversity of prey is available, particularly birds, but are highly specialized on microtine rodents in their study area in northern Finland and in other tundra habitats in Norway, Sweden, and Russia (Hagen 1952, 1969; Potapov 1997; Nyström 2004; Tast et al. 2010a). Hanski et al. (1991) categorized the rough-legged buzzard as a generalist predator, and one study in Finland found successful breeding of rough-legged buzzards during a crash vole year where birds comprised 84% of its diet (Pasanen and Sulkava 1971), further suggesting it is not always restricted to small mammals. I would argue that rough-legged buzzards are closer to the owl than the kestrel category, but their diet consisting of 88% small mammals was not in the same league as the owls above, and therefore I considered it an intermediate in small mammal specialization.

The kestrel predator category comprised of the seven small mammal generalists included a higher proportion of birds, insects, larger mammals, or reptiles/amphibians in addition to small mammals in their diets (Table 1). Raptors in this group may primarily eat voles during superabundant years but continue to take other prey, and they will generally eat very few voles during low years by switching to alternative prey. The higher percentage of larger mammals for the generalists illustrates the importance of alternative mammalian prey in their diets. Eagle and Ural owls and common buzzards partially switch to small game, lagomorphs and grouse (common adders (*Vipera berus*) also important for buzzards), as alternative prey when voles decline (Korpimäki et al. 1990; Reif et al. 2001). Pygmy owls consume a substantial amount of birds in addition to small mammals (Mikkola 1983, Kullberg 1995).

Some studies have reported or considered the kestrel to be a small mammal specialist (Hanski et al. 1991; Kjellén and Roos 2000); however, my diet compilation and many studies classify the kestrel as generalist due to the importance of birds, insects, and other small mammals including shrews and mice in their diet (Yalden and Warburton 1979; Itämies and Korpimäki 1987; Korpimäki 1985a, b). Insects particularly represent an important alternative prey. There are high food niche overlaps between kestrels and the vole specialists Tengmalm's owl, long and short-eared owls (Korpimäki 1987), but kestrels can reduce interspecific competition when voles are scarce by consuming larger quantities of insects, while the specialists must continue hunting voles (Itämies and Korpimäki 1987).

The hen harrier was another difficult species to classify, as there was only one diet study I found within Fennoscandia (Hagen 1952). I classified the hen harrier as a generalist as small mammals seemed to be an important prey group comprising 57% of its diet, but birds were also significant 40%. Diet studies from Europe report small mammals ranging from 4% and 6% in the UK (Redpath and Thirgood 1999; Picozzi 1980) to 64% in France (Millon et al. 2002), the rest included birds and lagomorphs. Clearly, this species consumes voles and other small rodents when available, but the range in their diet to almost entirely birds does not suggest it is a typical vole specialist. The honey buzzard is a specialist on wasps and bees,

both larvae and adults (Itämies and Mikkola 1972), and obviously received ‘none’ for small mammal specialization. However, honey buzzards are reported to take small mammals (and other prey including worms, spiders, birds and reptiles) to supplement its diet early in the breeding season (Génsbøl 2008), so small mammals might possibly be important during that early critical time before breeding.

Predictions of population trends for other raptors

Population trends were predicted for the 15 raptors species in my study based on the model predator category (Table 3). Based on the trend for Tengmalm’s owl, I argue that the other five owl specialists in this group are very likely to show similar patterns and will decline or continue to decline if vole peaks remain at their current reduced levels. Many studies have demonstrated the dependence of specialist owls on regional vole abundance for hawk owl (Korpimäki 1994), long-eared owl (Village 1981; Korpimäki and Norrdahl 1991; Korpimäki 1994), short-eared owl (Village 1987; Korpimäki and Norrdahl 1991; Korpimäki 1994), and snowy owls only breed when lemmings are abundant (Mikkola 1983; Hakala et al. 2006). Average brood size of great grey owls was found to be positively correlated with vole food supply and consequently this has decreased in relation to declining vole populations in northern Sweden (Hipkiss et al. 2008). This evidence for owl dependence on voles indicates that population decline is a likely effect even if data to support this is limited or of poor quality. I predicted the intermediate rough-legged buzzard would probably show a decline due to its high dependence on voles described above. Generalists are predicted to show no decline based solely on their small mammal specialization. These species should be able to take alternative prey during years of low vole abundance, so even if they show a positive association with vole supply, they should not show a significant negative response over time. The honey buzzard, having no small mammal specialization, is also not predicted to decline based on diet.

Relationships of migration counts for other raptors to vole abundance

It was expected that I found a significant 3 year cyclicity in migration counts for rough-legged buzzard. However, it is interesting that hen harrier also showed a 3 year cyclicity but did not show any relationship with the food supply in the regressions. In contrast, breeding density of hen harriers appeared to fluctuate with spring vole densities in Norway (Hagen 1969) and Finland (Korpimäki 1984), although the maximum number of breeding pairs in Finland was only three. Others have suggested the importance of microtines in Sweden (Kjellén and Roos 2000), and a study in the UK reported strong correlation of hen harrier abundance to regional vole indices (Redpath et al. 2002). However, further research is needed to determine the relationship of hen harrier abundance with food supply in more detail for northern Europe.

Common and rough-legged buzzards showed a positive relationship with the spring vole index. This is not a surprising finding for rough-legged buzzard as breeding success is dependent on and fluctuates with small mammal densities in northern Fennoscandia and Russia (Hagen 1969; Potapov 1997; Tast et al. 2010a). Though common buzzards are generalists, they take advantage of small mammals during peak years and studies have found

breeding performance to be positively correlated with abundance of voles in Fennoscandia and Poland (Spidsø and Selås 1988; Jedrzejewski et al. 1994; Reif et al. 2004), while one study in the UK found lagomorphs as the primary influencing prey (Graham et al. 1995). Over an 18 year period in Finland, 26-57% of common buzzard territories were occupied and 44-95% of active nests were successful (Reif et al. 2004), suggesting that common buzzards were relatively successful even in poor vole years when typical specialists would rarely breed.

A criticism of using migration data is that I am comparing local vole populations in Västerbotten County to counts of raptors coming from a wide range of localities in Fennoscandia. Ringing recoveries have shown that most raptors migrating through Falsterbo are from Sweden, with some individuals coming from Norway, Finland, and occasionally northwest Russia (Stolt et al. 1995, cited by Kjellén and Roos 2000). Strann et al. (2002) reported that even though a decrease in cyclicity and cycle amplitude in vole populations across Fennoscandia is evident, dynamics of vole cycles may be quite different over short distances within Fennoscandia. Raptors across northern areas can therefore show various responses depending on regional vole dynamics and be less relatable to vole indices in Västerbotten. However, in absence of monitoring programs for most species in the study area, migration counts are the best available data I am aware of. The proportion of juveniles, instead of total population that includes non-breeders, would be a better measure to compare to vole abundance.

I do not have an explanation for the significant relationship of honey buzzard to the previous autumn vole index ($p < 0.05$) (not listed in Table 5); it is most likely a spurious correlation. Year was an explanatory variable used to remove some slight autocorrelation in model residuals. Although using year removed slight autocorrelation, it explained most of the variation in the model ($R^2 = 0.62$ compared with only 0.17 when only previous autumn was included), suggesting the relationship to vole supply is rather misleading. If anything, I predicted honey buzzard might have shown a relationship to the current spring index, but this was not the case.

Observed versus predicted population trends

Predicted and reported population trends in Fennoscandia and Europe are summarized in Table 3, and whenever I discuss ‘reported trends’ for a species I am referring to this table. Trends were generalized for all of Europe by BirdLife International (2004). For several species, ‘fluctuating’ was given for the trend. This implies that breeding densities were highly fluctuating over the study period, and therefore any accurate determination of trend was impossible. It is often difficult to monitor trends in species with regularly fluctuating populations (i.e. small mammal specialists) without extensive international cooperation (see also Saurola 2005), so this basically means that their status is relatively unknown.

The Finnish Ringing Centre has been monitoring northern owls since 1982 in Finland (Saurola 2009), and probably represents one of the most comprehensive owl monitoring programs in Fennoscandia. In line with predictions above, they report a significant declining long-eared owl population, although they can only assume a strong decline in short-eared

owls. Due to insufficient data consisting of low sample size and very large annual variation in number of active nests, no trends could be confidently suggested for owls including great grey owl, hawk owl, short-eared owl, and snowy owl in Finland. Similarly, other reported trends in Fennoscandia for the nomadic specialists are fluctuating or unknown, implying that the status for these owls remains largely unknown. Reported trends in Europe for long and short-eared owls are listed as stable, and reasons explained above for Tengmalm's owl (also stable populations reported in Europe) are most likely applicable to these species.

In line with predictions above, rough-legged buzzard has declined in some areas but its status is not completely certain. Numbers of migrating birds have declined in Sweden, but overall trends for Fennoscandia and Russia have been reported to be stable (BirdLife International 2004). Kjellén and Roos (2000) suggest a likely explanation to declining numbers of rough-legged buzzard migration counts at Falsterbo beginning in the 1980s may be due to the lack of significant vole peaks during this time and continued poor vole supply since then.

In line with predictions above, the generalist owls were either stable or increasing from reported trends from Fennoscandia and Europe. In Finland, population trends were significantly positive for Ural owl, while tawny and pygmy owls were considered stable (Saurola 2009). Decreasing populations of eagle owls reported in Finland was attributed to 90% closure of open dump sites, which previously provided an ample food supply of rats (Saurola 2009), so this decrease is probably stabilizing the population to more natural levels and should actually be considered stable over declining.

In contrast with predictions above, hen harrier and common buzzard showed population declines in my analysis of migration counts (see also Kjellén and Roos 2000) and in other reported studies within Fennoscandia. Population declines for common buzzard have also been observed in Finland (Saurola 2005), and in migration counts from Gibraltar, Spain (Bensusan et al. 2007). Interestingly, the rest of Europe shows general increasing trends for common buzzard.

The honey buzzard was not predicted to decline as it is not specialized on small mammals. Their decline is quite evident in Fennoscandia, but interestingly, their overall trend in central Europe is considered to be stable and increasing in some countries (BirdLife International 2004). Reasons for their observed decline in Fennoscandia may be due to destruction of their wintering habitat (Ahlén and Tjenberg 1996), or transformation of preferred deciduous forests to conifer plantations in Sweden (Amcoff et al. 1994; Ahlén and Tjenberg 1996). Low vole numbers may be an additional factor, especially during spring, when honey buzzards are the most likely to consume voles when insect prey may not be readily available yet. However, there is no evidence to support this and further research is needed to determine what has caused declines of honey buzzards in Fennoscandia.

Why declining trends in hen harrier and common buzzard?

The hen harrier and common buzzard have declined in Fennoscandia when they were predicted to remain stable, and thus were the only two species to show opposite trends to

predictions. These migratory species are probably partly affected by additional factors to the vole decline. However, stable or increasing trends in Europe for breeding common buzzards suggest that Fennoscandian birds wintering in Europe is not a likely reason for their decline. Hen harriers on the other hand have experienced a significant historical decline and are classified as a depleted population in Europe (BirdLife International 2004). Both may be dependent on voles during a critical point during the breeding season, or they may be more dependent on voles at northern latitudes due to lower prey diversity there compared to southern areas. This difference in prey availability may be extremely important and cause generalists to be more dependent on voles than they otherwise would be, even if they still take alternative prey. Kjellén and Roos (2000) suggest declines in hen harrier migration counts since the 1980s are probably a result of poor vole supply. No explanations for observed declines in common buzzards in Fennoscandia have been given (Kjellén and Roos 2000; Saurola 2005); however, a possible reason may be shortened migration distances due to climate change which would be more pronounced in short-distance migrants (Møller et al. 2010). Moreover, Visser et al. (2009) found hen harriers and common buzzards among others had reduced their migrating distance over a 70 year period in the Netherlands. Also, some hen harriers and common buzzards already overwinter in southern Sweden and Finland, so perhaps an increased percentage of birds are staying and not migrating past Falsterbo, thus biasing comparison of annual migration counts over time. This could also be an explanation for rough-legged buzzard, where some individuals winter in southern Scandinavia (Kjellén 1992). Clearly, more research is needed to rule out these issues.

General conclusions

My analysis and classification of diet specialization revealed that the owl specialists will be the most negatively affected by a decline in abundance of vole populations in northern Sweden. Rough-legged buzzard has shown declines, but some stable populations suggest it may be more robust than the owl specialists in Fennoscandia. The owl generalists should not respond as negatively based on their more varied diet, and reported trends from Fennoscandia and Europe have confirmed this. Decline in common buzzard is not as likely due to vole supply based on diet, but this cannot be ruled out. Hen harrier is more uncertain, its ACF of migration counts suggests a link to the vole cycle, so vole declines may have a potential impact even if diet specialization does not predict this outcome. If vole dynamics in northern Fennoscandia remain in its current state, characterized by a long period lacking historically high-amplitude peaks and progressing towards small annual fluctuations as at southern latitudes, all northern vole eating raptors will probably show a negative response. Prey diversity is much lower at northern latitudes, and even generalists that take other food items still depend on small microtines as a significant proportion of their diet. A significant long lasting reduction in this important food source is likely to affect breeding performance and abundance even in generalist vole eating raptors.

Climate change has been suggested as the likely reason for the collapse of high-amplitude vole cycles in northern Europe, and as temperatures are predicted to continue increasing, specialist vole predators are likely to experience further population declines (Hörnfeldt 1998, 2004; Strann et al. 2002; Solonen 2004; Hörnfeldt et al. 2005; Ims et al. 2008). This problem

is not limited to northern raptors; mammalian vole specialists have also declined in recent years. The arctic fox population in northern Sweden has experienced major declines since the early 1980s, which has been linked to declining vole and lemming peaks in the region (Angerbjörn et al. 1995). International cooperation and directed quantitative studies across northern Europe are crucial if we are to assess accurate status for different vole eating predators and continue working towards their conservation (see also Saurola 2005).

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