Clutch Size Variation in Tawny Owls (*Strix aluco*) from Adjacent Valley Systems: Can This be Used as a Surrogate to Investigate Temporal and Spatial Variations in Vole Density?

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Abstract.—Research on Tawny Owls (*Strix aluco*) in Kielder Forest, northern England, since 1981 demonstrated that field voles (*Microtus agrestis*) were their most important food. Here, field voles exhibited a 3-4 year cycle of abundance, and mean clutch size in Tawny Owls was significantly related to vole abundance in March. In this analysis we use variations in clutch size as a surrogate to explore whether vole abundance was synchronized over a larger spatial scale, in this case between Kielder Forest and another forest (Kershope) in an adjacent valley system. We show that mean clutch sizes were synchronized between study areas during 1987-1992, but not subsequently (1993-1996). Synchrony was broken in 1993 when voles in Kielder experienced an extended low phase to the cycle resulting in 4 years between peaks, whereas vole cycles in Kershope continued with 3-year periodicity. Thus, since 1993 vole cycles in the two valley systems have been out-of-phase by 1 year. We discuss possible mechanisms whereby vole abundance in nearby areas can oscillate in- and out-of-phase with one another.

In Europe, numerous species of owls feed on rodents with populations that undergo multi-annual fluctuations in abundance (Korpimäki 1992). Owls that are dependent on rodents for food have thus developed numerous strategies to live through food shortages in years when rodents are scarce. Some species are highly mobile, such as Short-eared Owl (*Asio flammeus*) and Snowy Owl (*Nyctea scandiaca*). These owls are able to track changes in rodent abundance over large areas and settle to breed wherever food is most abundant (Korpimäki 1992). Whereas sedentary species, such as Tawny Owl (*Strix aluco*) and Ural Owl (*Strix uralensis)*, remain on territory but cease to breed in poor rodent years (Pietiäinen 1988, Southern 1970). In this paper we concentrate on the Tawny Owl.

The Tawny Owl is a sedentary, nocturnal rodent hunter with its range largely concentrated in the temperate broadleaved forest zone of Europe and Asia. It is replaced by the larger Ural Owl in boreal and alpine conifer forests (Cramp 1985, Lundberg 1980). The Tawny Owl has shown a remarkable flexibility to man-induced changes to European landscapes, having colonized urban habitats (Bevan 1964, Goszczynski *et al*. 1993) and well able to exist in farmland with few trees (Redpath 1995). In Britain, it has readily colonized extensive areas of man-made conifer forest established over the last 75 years, from which Ural owls are absent (Petty and Avery 1990, Petty 1992).

Considering just how abundant the Tawny Owl is in Europe, there is a dearth of studies on its reproduction, compared, for instance, to the vast literature on diet (summarized in Mikkola 1983 and Cramp 1985). Only three studies in Britain have investigated its reproduction in relation to food-supply. Two were in lowland broadleaved woodland near Oxford, southern England where bank voles (*Clethrionomys glareolus*) and woodland mice (*Apodemus sylvaticus* and *A. flavicollis*) were the main prey (Hirons 1976, Southern 1970), and the third was on farmland in Aberdeenshire, northern Scotland, where field voles (*Microtus agrestis*) were more important (Hardy 1977, Hardy 1992).

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There has been much recent interest in the causes and consequences of multi-annual cycles of microtine rodents in Scandinavia (Hanski *et al*. 1991, Hanski and Henttonen 1996, Hansson and Henttonen 1985). This has been largely concerned with temporal patterns, but more recently with spatial aspects (Steen *et al*. 1996). Few studies have been designed to investigate the spatial dynamics of multi-annual rodent cycles, but the literature generally indicates that vole cycles are synchronized over large geographical areas (Hanski *et al*. 1991). So, vole-dependent predators suffer either heavy mortality in trough years between cycle peaks unless other prey are available, or they are highly mobile and "track" high vole densities, and may thus have a synchronizing effect on vole abundance over large areas (Ims and Steen 1990; Korpimäki 1986, 1992; Norrdahl and Korpimäki 1996; Ydenberg 1987).

More recently, Petty (1992) has investigated how Tawny Owls have adapted to man-made conifer forests in northern England. Here the owls fed largely on field voles, which were most abundant on clearcuts, and all demographic measurements of the owl population were significantly related to vole abundance. Vole abundance fluctuated on a 3-year cycle but with some spatial asynchrony. This meant that at any one time, vole numbers could be declining in some parts of the forest while increasing in others. In this analysis, we use clutch size variation in Tawny Owls as a surrogate to investigate if vole abundance was synchronized over a larger spatial scale, in this case adjacent valley systems that straddle the border between England and Scotland.

MATERIALS AND METHODS

Study Areas

The two study areas, in Kielder and Kershope Forests, are situated in the border area between England and Scotland (fig. 1). These forests lie in adjacent valley systems separated by a higher area of treeless moorland, and form part of a much larger area of man-made conifer forest planted over the last 70 years. The forest in both areas comprise largely Sitka spruce (*Picea sitchensis)* and Norway spruce (*Picea abies)* managed on a clearcutting system (40-60 year rotation length), which over the last 25 years has created a mosaic of different-aged stands of trees in older parts of each forest (Petty *et al*. 1995). Clearcuts ranged in size from 5 ha to more than 100 ha, with the smallest in valley bottoms. The current clear-cutting program in Kielder Forest District, which included both our study areas, is around 1,000 ha per year. The center of the Kielder study area (55°13′ N, 2°33′ W) was 17.7 km NE of the center of the Kershope study area (55°08′ N, 2°47′ W). The main differences between study areas were that Kielder was higher and

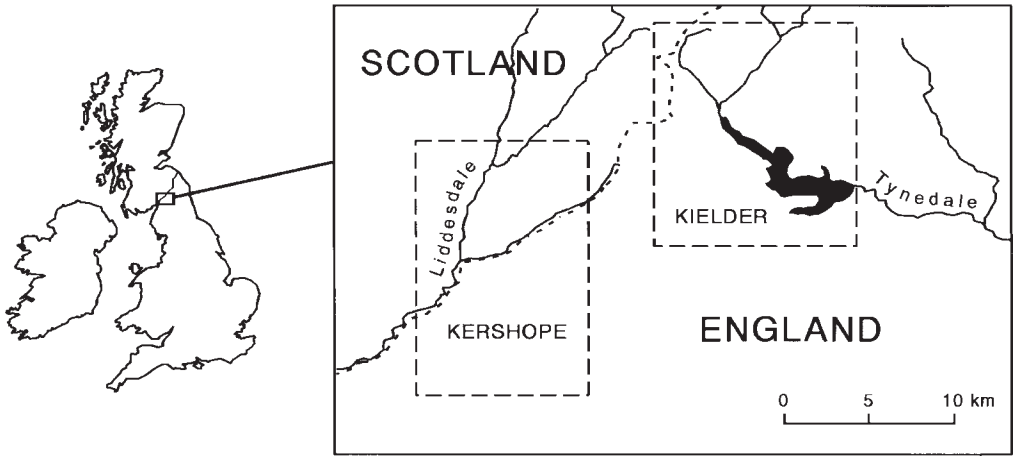

Figure 1.—*Location of the Kielder (180 km²) and Kershope (170 km²) study areas in the border area between England and Scotland. The study areas were defined by the smallest rectangle that included all Tawny Owl nest sites based on 1 km square of the national grid. Not all ground in each study area was monitored for Tawny Owls.*

contained more forest than Kershope. In Kershope, over 50 percent of the study area was farmland (mainly grass pasture) and moorland, compared to less than 25 percent in Kielder which was mostly heather (*Calluna vulgaris*) moorland.

Tawny Owl Numbers and Breeding Performance

Nest Visits and Number of Pairs Used in the Analysis

Within both study areas, owls bred largely in nest boxes provided for them (Petty 1987, Petty *et al*. 1994). Checks of potential nest sites (nest boxes and natural sites) commenced in March, with subsequent visits timed to obtain the data required with the minimum of disturbance. In Kershope we had no data on the number of territorial pairs present each year, just those that laid. Petty (1992) showed that, in Kielder, the percentage of the territorial population that laid varied from 84-96 percent in years when voles were abundant to less than 30 percent in the trough years between vole cycles (see below). Therefore, the sample used in this analysis is based on the number of pairs that laid at least one egg. This amounted to 565 clutches from Kielder during 1981-1996 and 187 clutches from Kershope during 1987-1996 (table 1).

Table 1.—*Number of Tawny Owl (*Strix aluco*) pairs laying at least one egg in the Kieder and Kershope Forests along the border area between England and Scotland*.

Year	Kielder	Kershope
1981	41	-
1982	34	-
1983	10	-
1984	43	-
1985	44	-
1986	4	-
1987	48	20
1988	50	19
1989	14	5
1990	51	23
1991	63	25
1992	22	1
1993	27	29
1994	50	27
1995	35	6
1996	29	32
Total	**565**	**187**

Clutch Size

On the first visit to a nest with eggs, each egg was marked with a unique code using a black spirit-based felt-tip pen. Egg lengths (l) and breadths (b) (at the widest point) were measured to the nearest 0.01 cm with plastic dial calipers. Each egg was weighed (W) in a small polythene bag with a 50 g pesola balance, to the nearest 0.1 g. A density index (DI) was calculated for each egg when DI = W/(0.507*b *l) (Petty 1992). The DI decreases through incubation as eggs lose weight (Furness and Furness 1981). Any clutch with a DI for any egg of > 1.060 could have been incomplete, so was revisited to obtain the complete clutch. Clutches where all eggs had a DI < 1.059 were considered to be complete. Most Tawny Owls laid from mid-March to mid-April (Petty 1992).

There were no predators in either study area, such as pine martens (*Martes martes*), that could remove eggs from owl nests in boxes or elevated natural sites. Foxes (*Vulpes vulpes*) were potential predators of ground nests, but only two such nests were found once nest boxes had been provided, and neither were predated (Petty *et al*. 1994). Red squirrels (*Sciurus vulgaris)* were present in both study areas, and were considered capable of removing eggs from nests but this was never recorded. Squirrels occasionally built dreys on top of deserted owl eggs, but eggs always remained unbroken.

Nest Desertions Due to Observer Disturbance

Some female owls deserted complete or incomplete clutches following observer visits (Kielder 1981-1996, n = 66; Kershope 1987-1996, n = 10). Most desertions followed the first visit to the nest (Petty 1992). Desertion during egg-laying often resulted in the clutch being continued without interruption at another nest site within the territory. Of the females which deserted after incubation commenced, about half laid a second clutch at a new nest site, but after an interval much longer than normal between eggs. Generally the more advanced the nesting cycle when the failure occurred, the less the chance of a relay. Pairs which failed with chicks older than 6 days never relaid. Virtually all repeat clutches were considered to result from first-clutch desertions caused by the observer. Therefore, to avoid using two or more clutches from the same female in a year, the following procedure removed these observer effects. Incomplete and complete clutches that

were deserted were excluded and substituted by the replacement clutch. There was no significant difference between completed first and repeat clutch sizes (Petty 1992). When deserted first clutches were not replaced, or when these were replaced and subsequently failed, then clutch size from the first clutch was used.

Tawny Owl Diet

In Kielder Forest, field voles were the main prey of Tawny Owls (Petty 1989, 1992). Field voles comprised 72 percent of 2,429 prey items found in pellets collected at roost sites during 1980-1989, and 66 percent of 991 prey items identified in owl nests during the same period. We have no comparable data from Kershope, but field voles were the most frequent prey in owl nests.

Estimating Field Vole Abundance

A Vole Sign Index (VSI) was used to estimate the abundance of field voles on clearcuts throughout the Kielder study area. The VSIs were done on around 20 grass-dominated sites in March from 1985 until 1996. At each site, a 25 cm^2 quadrat was thrown 25 times along a similar route, and the presence or absence of fresh (green) grass clipping in vole runs recorded. Thus calculated, the VSI for each site ranged from 0 to 25. In this analysis we use the mean VSI value from all sites. The accuracy of this method for assessing vole abundance had previously been checked by trapping voles on one vole sign assessment site, at the same time that the VSI was done in March during 1985-1990, to provide a vole trapping index (VTI) (Petty 1992). The VTI was equivalent to the number of voles caught per 100 snap trap nights. Each trapping session comprises 576 trap nights. There was a significant relationship between the VSI and VTI in March (fig. 2).

RESULTS

Relationship Between Vole Abundance and Clutch Size

In Kielder during 1985-1996, 77 percent of variation in clutch size of Tawny Owls was accounted for by the March VSI (fig. 3). Thus, a comparison of annual mean clutch sizes in Tawny Owls in Kielder and Kershope should reflect variation in vole abundance between study areas in March.

Clutch Size Variation Between Study Areas

The longer-term data set on mean clutch sizes from Kielder indicated regular 3-year vole

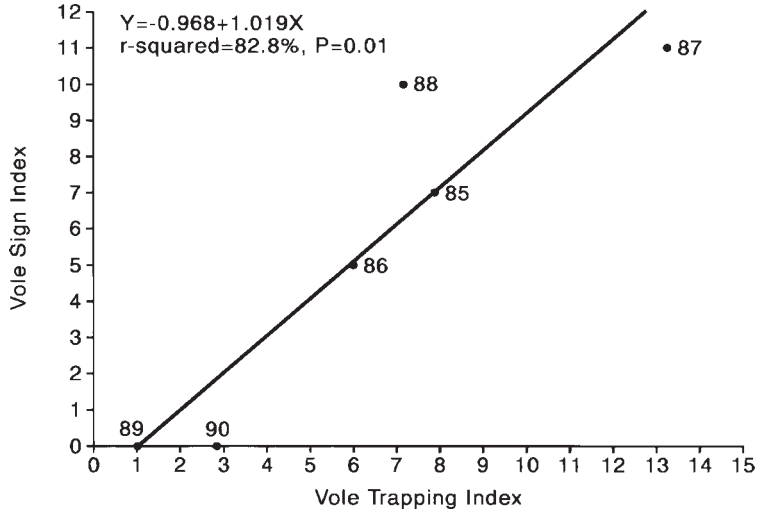

Figure 2.—*The relationship between the Vole Trapping Index and the Vole Sign Index in March in the Kielder study area in the border area between England and Scotland.*

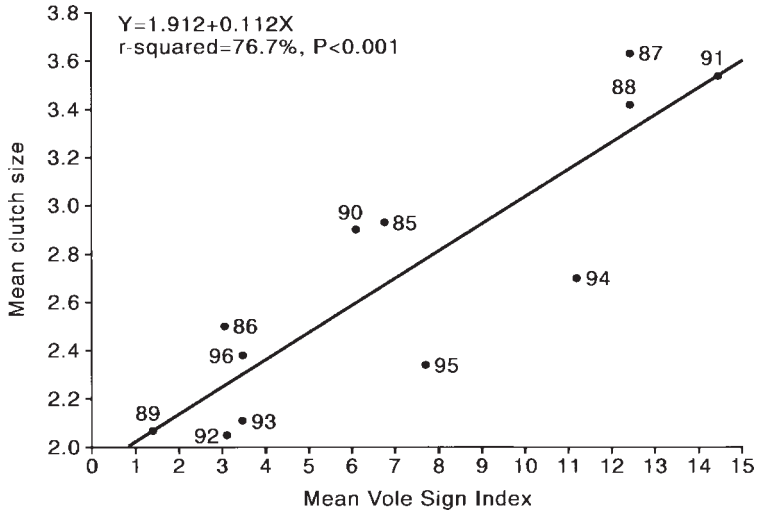

Figure 3.—*Relationship between the mean Vole Sign Index in March and mean clutch size in Tawny Owls (*Strix aluco*) in the Kielder study area in the border area between England and Scotland.*

cycles from 1981 until 1992, with trough years in 1983, 1986, 1989, and 1992, and higher clutch sizes in intervening years (fig. 4). The Kershope data started in 1987, and from then until 1992 it tracked clutch size variation of Tawny Owls in Kielder (r = 0.85, df = 5, P = 0.03), but not during 1993-1996 (r = -0.30, df = 3, P = 0.70). Since 1992, the data from Kershope indicated that vole abundance continued to cycle at 3-year periodicity with high amplitude. Whereas in Kielder the overall amplitude declined, with both lower peaks and

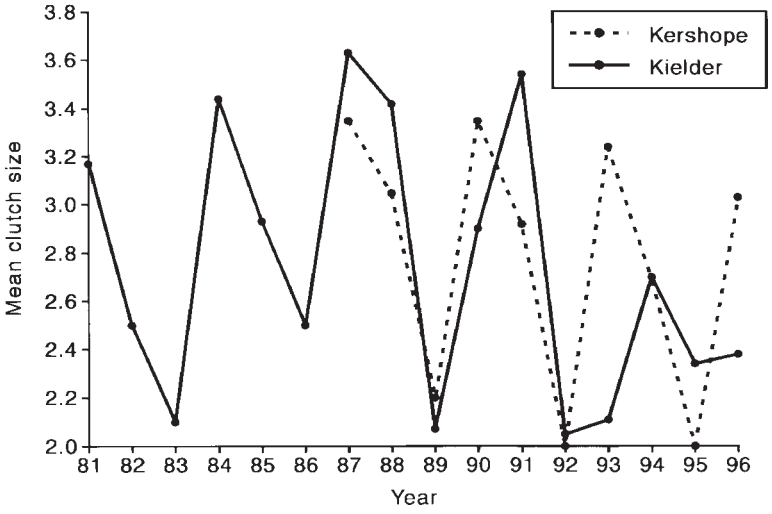

Figure 4.—*Annual variation in mean clutch size of Tawny Owls (*Strix aluco*) in the Kielder(1981-1996) and Kershope (1987-1996) study areas in the border area between England and Scotland.*

higher troughs, and the 1992 trough extended into 1993, resulting in the study areas being out-of-phase by one year since 1993.

Clutch Size Variation in Relation to Vole Abundance

Excluding the years 1993-1996 in Kielder, a typical 3-year vole cycle in our study areas comprised: (1) a spring when vole numbers were low (low phase), before starting to increase in late summer, but after the owls breeding season; (2) a spring with vole numbers continuing to increase (increasing phase); (3) a spring when voles declined from a winter peak (declining phase). In four out of five cycles in Kielder and all three cycles in Kershope, clutch sizes peaked in the increasing phase and declined in the following year (fig. 4).

There was little difference between study areas in mean clutch size in each of these "vole year classes" (fig. 5). Median clutch sizes were similar in Kielder and Kershope in the low and increasing phases of the vole cycle (low phase, Mann-Whitney, Z = 0.16, P = 0.88; increasing phase, Mann-Whitney, Z = 0.57, P = 0.57), but were significantly higher in the declining phase in Kielder than in Kershope (Mann-Whitney, Z = 2.47, P = 0.01). In both study areas the modal clutch size was three in increasing and declining years and two in low years.

DISCUSSION

Hanski *et al.* (1991) indicated that in Fennoscandia, vole cycles decreased in periodicity from around 5-year intervals at 70°N to 3-year intervals at 56-60°N, with no clear evidence of multi-annual cycles further south. The amplitude of the cycles also showed a declining gradient from north to south. Hanski *et al.* (1991) also explored the role of predators in vole cycles and concluded that their results were consistent with the hypothesis that cycles were driven by specialist predators, and that generalist predators could modify cycles. Other studies indicated that a lack of multi-annual cycles in rodent populations in Southern Sweden could be the result of predation (Erlinge 1987; Erlinge *et al.* 1983, 1984, 1988). In such fragmented habitats, generalist predators were abundant. These fed on alternative prey when voles were scarce, but increased their predation on voles once voles started to increase, to the point where numbers then decreased. In this way they kept voles at a fairly stable level and so prevented the development of multi-annual cycles. In contrast, in northern Scandinavia with pronounced 3-5 year vole cycles,

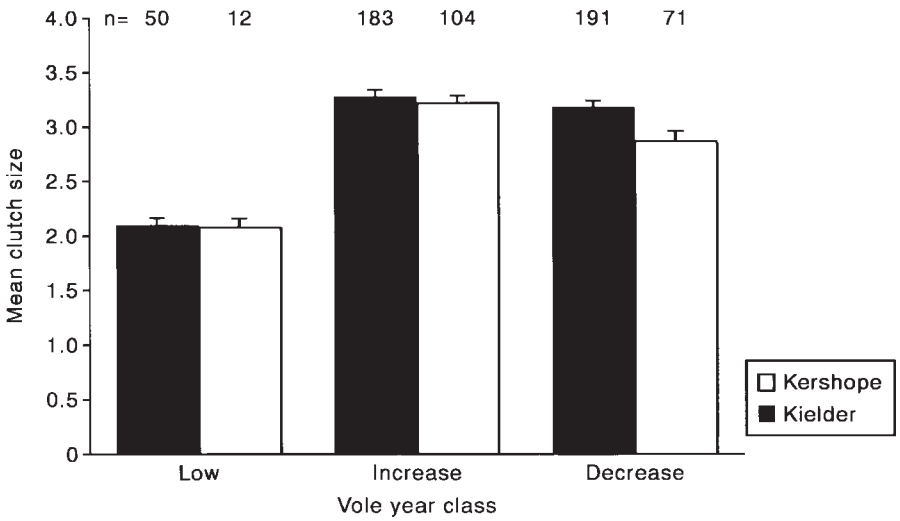

Figure 5.—*Comparison of mean clutch sizes (with SE bars) of Tawny Owls (*Strix aluco*) between the Kielder and Kershope study area, in the border area between England and Scotland, in three vole year classes that typify one vole cycle.*

generalist predators were scarce or absent, and vole numbers were able to increase rapidly from the low point in the cycle, because there was little predation to delay an increase in numbers (Hanski *et al.* 1991; Korpimäki 1985, 1986; Korpimäki and Norrdahl 1991). Only when voles became abundant did specialist predators (mainly mustelids and nomadic owls) start to exploit them and reduce numbers.

The temporal trends in vole abundance identified from our analyses indicated cycle lengths of 3 years, which at 55°N was similar to that from cyclic populations at 56-60°N in southern Fennoscandia. However, the most interesting aspect to emerge from our study was that vole cycles in adjacent valley systems oscillated in- and out-of-phase with each other. There was also some indication that the amplitude of cycles in Kielder had reduced, due to increasing local asynchrony[2]. Thus, within the same valley system, it appears possible for vole population in different patches to switch between synchronous and asynchronous fluctuations. So, what causal factor(s) from the current batch of hypotheses could explain these phenomena?

First though, it is easier to reject hypotheses that cannot explain the pattern of cyclicity we have reported. In our study areas, generalist predators such as badger (*Meles meles*), Buzzard (*Buteo buteo*) (in Kershope only), fox, mink (*Mustela vison*), stoat (*Mustela erminea*) and Tawny Owl were far more abundant than specialist avian vole predators such as Long-eared Owl (*Asio otus*), Short-eared Owl, and Kestrel (*Falco tinnunculus*). We suspect the weasel (*Mustela nivalis*) was abundant, but we have no data on its density or distribution. Therefore, from the predator assemblages present in our study areas which comprised mostly generalists, the prediction from the predator hypothesis would be that our vole population should be non-cyclic, but this was not the case.

Most species of predator present in both study areas were relatively sedentary. So, there were unlikely to be movements between study areas. For instance, many Tawny Owl chicks have been ringed in both study areas over the course of the study, but none have been recovered as breeding adults in a different study area to that in which they were ringed (Petty 1992). Thus, voles and their predators in the two study areas were largely independent of each other. If this was the case, then why were cycles in Kershope and Kielder in-phase for part of the study (1987-1992), unless just by chance?

Nor can any of the weather/climate-related hypotheses explain our observations (Hansson and Henttonen 1985). Weather patterns are unlikely to vary over such a small spatial scale, so if weather was a causal factor, then vole abundance should have been synchronized between valleys.

So, what could explain our observations? The key may lie in trying to understand why the pattern of multi-annual cycles appears to have changed since 1993 in Kielder but not in Kershope. Our approach has been to try and identify any habitat differences between valleys that may explain this change.

Both valleys have large areas of man-made spruce forest where patch clearcutting is now widespread. Clearcuts provide the most important vole habitat within each forest, particularly on surface water gley soils in valley bottoms and on lower slopes. On these sites, grassy vegetation, dominated by *Deschampsia caespitosa*, develops within 1-3 years of clearcutting, and then remains suitable for voles until the new tree crop starts to shade out the ground vegetation, from 12-15 years after replanting (Petty 1992). Clearcuts at higher elevation are usually on peaty gley soils or blanket peats where re-colonization by vegetation is slower and often dominated by *Calluna vulgaris*. Such sites provide poorer habitat for field voles. Clearcuts are usually separated from each other by closed-canopy stands of close-grown spruce with little ground vegetation apart from bryophytes. So, they provide islands of vole habitat within a larger matrix of unsuitable habitat (spruce forest).

During the early part of our study in Kielder, most clearcutting was in the older forest at lower elevations, and these were on soil types that produced the best vole habitat. Recently, the pattern of clearcutting has altered the configuration of habitat mosaics at the landscape scale, with less clearcutting at lower elevations and more on the upper slopes and watersheds. So, the gross amount of good vole habitat may

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have declined, and it may also have become more patchily distributed. This corresponds to: (1) a change in the territorial population of Tawny Owls, from 44 pairs in 1981, to a peak of 66 pairs in 1991, followed by a decline to 54 pairs in 1996[3] (Petty 1992); and (2) declining synchrony in vole abundance within Kielder. Whereas in Kershope, there are still numerous large clearcuts suitable for voles, and unlike Kielder, the forest is in closer contact with extensive areas of farmland (unimproved or improved pasture) where voles are abundant and cycles synchronized.

Jansen (1995) has recently shown from modeling that patch dynamics may have an important influence on population fluctuations. For example, prey populations in small patches were more likely to fluctuate asynchronously than prey in large patches, and fluctuations in small patches were able to flip in- and out-of-phase with each other. This generates a pronounced cycle during an in-phase oscillation, but the amplitude is dampened during an out-of-phase oscillation. There are analogies here with changes that have occurred in Kielder, in both patterns of clearcutting and in the periodicity and amplitude of vole cycles.

Steen *et al*. (1996) studied spatio-temporal patterns in bank vole population cycles in Norway, and concluded that these were not related to habitat. However, from our results we feel that the scale and distribution of habitat have crucial influences on rodent population fluctuations. This hypothesis does not of course rule out other factors. For instance, habitat quality, predation, and intrinsic factors within rodent populations, may help to shape the pattern of population fluctuations, but in a proximate rather than ultimate manner. There are two predictions from our hypothesis. First, synchronized multi-annual cycles should occur only in suitable large-scale habitats (large patches). Suitability of the habitat being very important, for instance, heavy grazing can operate as a proximate factor to dampen synchronized multi-annual cycles in otherwise suitable habitat. Such a process has frequently been observed when heavily-grazed grasslands in the British uplands are converted over a short period of time into extensive conifer forests. Prior to afforestation, rodents populations are non-cyclic and occur at low density (Charles 1981). Domestic stock are then excluded by fencing prior to tree planting, grass growth recovers and field vole numbers dramatically increase to generate 1-3 multi-annual cycles before tree growth makes the habitat again unsuitable (Charles 1956, Chitty 1952, Goddard 1935, Lockie 1955, Petty 1996, Petty and Avery 1990). Second, overall synchrony in multi-annual cycles should break down in fragmented habitats (small patches) because; either individual patches are out-of-phase with each other, even though cycles are still multi-annual, or cycles become annual with rodent numbers increasing from spring to autumn because over-winter predation (acting as a proximate factor) reduces numbers to a low point by the following spring.

Our results indicate that clutch size variation in Tawny Owls can be used to investigate not only temporal but also spatial variations in vole abundance. It is often laborious to obtain estimates of vole abundance at the same time from trapping or vole signs indices at a landscape scale or regional scale. Therefore, future comparisons of breeding performance of vole-eating raptors appear to offer a promising method to explore more fully the spatial dynamics of multi-annual rodent cycles.

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