

COMMISSIONED REPORT

Commissioned Report No. 099

The ecology and conservation of water voles in upland habitats

(ROAME No. F99AC320)

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The ecology and conservation of water voles in upland habitats

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Background

The water vole *Arvicola terrestris* is in a state of rapid decline across the UK due to the combined influence of habitat degradation and predation by feral American mink. Approximately 40% of the UK population is now thought to occur on Mainland Scotland and many of these remaining animals are living in upland habitats.

In order to conserve these upland populations a thorough knowledge of water vole ecology in such habitats is required. To this end the Deeside Water Vole Project was undertaken between June 1999 and September 2002 with a view to obtaining data on aspects such as population dynamics, habitat preference and diet. These data are presented in this report, and together with the results of other published studies are used to identify practical conservation measures.

Main findings

- Water vole populations in the Geldie & Bynack sub-catchments declined over the period 1999–2002. Further monitoring is required to determine whether this decline is part of a natural regional scale population cycle or an intermediate stage on the road to extinction.
- Preferred habitat comprised well-vegetated mosaics of sedge, rush, grass and ericoids adjacent to slow flowing, shallow burns with penetrable banks and relatively gentle bank angles. Such habitats are localised and in consequence populations of water voles in upland habitats tend to be naturally highly fragmented.
- Spring, summer and autumn diet, as assessed from plant remains at feeding stations, was dominated by species belonging to the sedge, rush and grass families. Rushes were selectively exploited, sedges eaten in proportion to availability and grasses avoided relative to their abundance in the general environment.
- Colonies comprised a mean of 4.6 animals (range 1–15). First and last conceptions were estimated to have occurred on 3rd April and 25th August respectively, giving a breeding season of 144 days and the potential for females to produce four litters. This reproductive potential was not achieved: on average only 1 litter was produced, with a maximum of three being recorded.
- Monitoring of water vole populations would be best achieved by undertaking latrine counts together with surveys of % site occupancy, providing indices of abundance and snap-shots of spatial distribution respectively.

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It was a privilege being given the opportunity to learn more of the life of water voles in an upland environment. It is to be hoped that the results of this study will contribute in a small way to the conservation of an animal whose survival in such a hostile environment commands the greatest of respect. However, this study could not have been undertaken in isolation and I would like to record my gratitude to all those concerned for their assistance, encouragement and forbearance. Particular thanks are due to Ewen Cameron, Mairi Cole, Emma Philip and Rob Raynor (Scottish Natural Heritage); Alister Clunas, Stewart Cummin, Peter and Liz Holden (National Trust for Scotland); Chris Gibbins and Xavier Lambin (University of Aberdeen); and Drew Aitken, Mike Davidson and Roger Owen (Scottish Environment Protection Agency).

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1 WATER VOLE DISTRIBUTION AND ABUNDANCE 1998–2001

1.1 Introduction

The upland environment is not homogeneous. Habitats vary both spatially and temporally in their ability to provide the conditions necessary to sustain a given animal species. In consequence, a species may occur as a series of local populations occupying favourable habitat patches, separated from similar populations by areas of unsuitable land. Such patchy animal distributions may arise naturally. Alternatively, they may arise as a consequence of the process of habitat fragmentation, whereby formerly more extensive favourable habitats are reduced to remnant "islands" within surrounding areas of unfavourable terrain.

Relative to large populations, small local populations are more vulnerable to extinction by virtue of their greater sensitivity to chance (stochastic) variations in demography (eg birth rate, death rate, sex ratio), genetics (eg inbreeding depression), and environment (eg food resources, flooding, predation).

However, providing that sufficient movement occurs between local populations to supplement declining numbers, to add new genes, or to ensure that the rate of recolonisation exceeds the rate of local population extinction, the population will survive at the regional scale. Individual local populations may go extinct, but are replaced by recolonisation from other sub-populations.

Regional populations of a species, which comprise a set of smaller sub-populations maintained by frequent dispersal between them, are referred to as "metapopulations". Metapopulations are analogous to a constellation of twinkling stars blinking on and off. Some stars may dull (local extinction) while others appear (local colonisation). Thus, while the pattern of reflected light (animal distribution) changes over time, the overall stability of the spectacle (regional population) is maintained.

Water voles living in upland habitats appear to conform to the metapopulation concept outlined above. In essence, a metapopulation comprises a set of distinct local populations connected by movements of animals. It is conceivable that an isolation threshold exists, such that isolated sites are unlikely to become colonised. Areas where the average distance between patches is too large are unlikely to experience sufficient dispersal to support a metapopulation (Hanski 1991). Therefore, an understanding of the spatial characteristics and dynamics of water vole colony distribution is likely to be a key element in defining conservation requirements for the species. Accordingly, this chapter explores aspects of spatial distribution and changes over time in relation to water vole colonies in the Geldie and Bynack sub-catchments.

1.2 Study area and methods

Data were collected from the Geldie and Bynack sub-catchments, both of which constitute headwater tributaries of the River Dee, and are located in the Cairngorm Mountains, Scotland. Some previous survey work had already been undertaken, particularly in the Bynack sub-catchment (Lambin *et al.*, 1998) and this, together with relative ease of access, influenced the selection of study sites.

Surveys for the presence of water voles were undertaken during the periods August-October 1999, April-October 2000, and April-October 2001. Burns were systematically walked and surveyed for evidence of occupation by water voles based on the following indicators:

- faeces: water voles produce characteristic blunt-ended faeces, which they deposit on runways or at points of entry to, or exit from, water;
- latrine sites: comprising concentrations of faeces near nests, home range boundaries or on runways;
- runways: comprising regularly travelled corridors of trampled and grazed vegetation, usually within 2m of water;
- entrances to subterranean burrows in banks adjacent to water;
- feeding stations, comprising piles of cut grass, sedge or rush stems, rush pith and leaves;
- nests, comprising woven surface structures;
- footprints;
- sightings.

Colonies were considered to be occupied if fresh water vole signs (droppings, latrines, footprints, sightings, feeding stations) were found. No surveys were undertaken while burns were in spate following periods of heavy rain. Flooding temporarily removed signs of occupation by water voles and a 2 or 3 day post-spate period elapsed before surveys of affected burns were resumed. In those cases where burns were obscured by dense plant cover, vegetation was parted in order to expose the water and banks beneath. This is considered to be crucial, since a high proportion of vole signs are obscured and could easily be missed.

Wherever possible, the beginning and end of water vole colonies were determined using a hand-held Geographical Positioning System. The limits of a colony were defined by the positions of the first and last latrine sites. Latrine sites separated by less than 200m were considered to belong to the same colony on the basis that this is within the home range length of adult males (Sah 1998).

Nearest-neighbour distances between occupied colonies were measured from 1:25,000 Ordnance Survey maps. Euclidean distance, rather than the distance along waterways, was used. Although little is known about the movement of dispersing animals there is some evidence to suggest that dispersal can take place overland (Telfer 2000).

In comparing occupancy rates between years, only burns surveyed in both years were included in the analyses.

1.3 Results

The burns surveyed and the distribution of active water vole colonies for the years 1998–2001 inclusive is shown in Figures 1.1–1.6. The precise burns surveyed in any year reflected logistical constraints. The 1998 data are derived from Aars *et al.* (2001). Using only those waterways surveyed in each of the years 1998–2001, the annual proportion of burns with fresh signs of occupation by water voles is shown in Figure 1.7. From the latter it can be seen that in both catchments, the proportion of positive burns declined during the period of study from 73–9% and 78–39% for the Bynack and Geldie catchments respectively. By 2001 only 1 of 11 burns monitored throughout the study retained water voles in the Bynack, and 9 of 23 burns in the Geldie.

The decline in the proportion of watercourses occupied by water voles over the period 1998–2001 was not the consequence of a redistribution of animals elsewhere within the two catchments. Considering all surveyed water courses (not just those counted in each year), the percentage length of burn occupied by extant water vole colonies declined from 20–5% and from 18–6% in the Bynack and Geldie catchments respectively (Figure 1.8). The number of water vole colonies per kilometre of watercourse surveyed also declined as shown in Table 1.1.

Table 1.1 The number of active water vole colonies per kilometre of watercourse surveyed, 1998-2001. The colony count for 1999, which is partly derived from Aars *et al.* (2001), is likely to be conservative. The number of colonies per kilometre of watercourse appears to have declined, particularly in the Geldie catchment. nd = no data.

		Number of extant colonies per kilometre (number of colonies)		
Year	Length of watercourse surveyed (km)	Bynack catchment	Geldie catchment	
1998		nd	nd	
1999	34 (Bynack);	0.35 (c.12)	nd	
2000	15.5 (Bynack); 46 (Geldie)	0.32 (5)	0.78 (36)	
2001	14.5 (Bynack); 28 (Geldie)	0.28 (4)	0.29 (8)	

Table 1.2 shows a comparison of the mean length of watercourse occupied by extant water vole colonies in 2000 and 2001. Colony extent was estimated from the location of latrines. Assuming similar spacing and marking behaviour within subpopulations, colony length provides an index of the relative size of subpopulations. Data for the Geldie and Bynack catchments have been combined. Although it would appear that the median size of colonies declined from 200–185m between 2000 and 2001, the differences are not significant (U = 161, P>0.05, Mann-Whitney U-Test).

Table 1.2Mean length of watercourse occupied by extant water vole colonies in each of the
years 2000 & 2001. Data for the Bynack and Geldie catchments combined.
The apparent decline in median colony length between 2000 and 2001 is not
statistically significant (U = 161, P>0.05, Mann-Whitney U-Test).

Year	No. of colonies	Median colony length (m)	Min	Мах
2000	29	200	50	700
2001	12	185	50	450

Combining data for both catchments and the two years 2000 and 2001, median colony length was 200m (range 50–700m). Of the 41 colonies, 26 (63%) were 250m or less in length.

Table 1.3 shows mean nearest neighbour distances between extant colonies in the Geldie catchment. In a lowland study area Telfer *et al.* (2001) provided evidence that dispersal between colonies is not confined to waterways and that straight-line overland distances better explain colony distribution patterns. Accordingly, straight-line overland distances between colony centres were measured in the present study from 1:25,000 scale maps. Table 1.3 indicates that over the period 2000–2001 there was a progressive increase in the mean nearest neighbour distance.

Table 1.3 Mean nearest neighbour distances between extant water vole colonies in the Geldie catchment for the years 2000 and 2001. Straight-line overland distances were measured from 1:25,000 scale maps. Over the period of study, colonies became progressively more isolated.

Period	Sample size	Mean nearest neighbour distance in metres (Standard Error)
April-October 2000	36	454 (33.1)
April-May 2001	5	765 (191.8)
June-October 2001	4	1050 (417.3)
April-October 2001	8	584 (122.5)

An indication of colony turnover rate is given in Table 1.4. Using only those watercourses surveyed in each year, for both the Bynack and Geldie catchments c.80% of active colonies present in 2000 were abandoned in 2001. Allowing for the establishment of new colonies in 2001, the effective rate of colony loss was 70% and 75% for the Bynack and Geldie catchments respectively.

Table 1.4 Colony turnover rate in the Bynack & Geldie catchments, April-October 2000 to June-October 2001. Only those watercourses surveyed in each year are used in the analysis. Allowing for the establishment of new colonies in 2001, the effective rate of colony loss relative to 2000 was 70–75%.

Catchments	No. of colonies in 2000	No. (%) of Year 2000 colonies surviving in 2001	No.of new colonies established in 2001	No. (%) of colonies abandoned between 2000–2001	Effective colony loss relative to 2000 ((d – c)/a x 100)
Geldie	16	3 (19%)	1	13 (81%)	75%
Bynack	10	2 (20%)	1	8 (80%)	70%

1.4 Discussion

Evidence from the present and previous studies (eg Lambin *et al.*, 1998; Aars *et al.*, 2001), suggest that upland water vole populations are naturally highly fragmented comprising small, widely scattered colonies. Much of this fragmented distribution can be explained by the highly localised nature of preferred habitat (Aars *et al.*, 2001; habitat preference section, this study).

The degree of fragmentation reflected by water vole distribution in the Geldie-Bynack catchments does not appear to be unusual. In 1998/99, Aars *et al.* $(2001)^1$ found that median nearest neighbour distances between occupied colonies ranged from 0.3–1.1km (Mar Lodge and Balmoral Estates) and from 0.2–1.6km (Assynt). The equivalent figures for the Geldie catchment in 2000/2001 ranged from 0.4–0.7km (this study).

¹Other than the studies by Aars *et al.*, 1998 and Lambin *et al.*, 1998 and Telfer *et al.*, 2001, no detailed ecological work on water voles in upland habitats in Scotland has been undertaken.

The virtual loss of water voles from the Bynack catchment over the period 1999–2000 is likely to have been associated with predation by American mink *Mustela vison*. In 1998, Aars *et al.* (2001) recorded that this sub-catchment was totally saturated, with every single patch surveyed occupied by water voles. In 1999, the population in this sub-catchment crashed, coincident with the arrival of mink sometime during the summer. The first mink field signs located during the present study were found on the 23rd August 1999, in the form of a partially eaten and decapitated grouse carcass, which had been dragged into a water vole burrow. Mink tracks and scats were also found elsewhere in the Bynack catchment during the same month. Possible mink scats were found on the 17th May 2000, but no further signs were found thereafter.

The colonisation of Britain by mink has had a dramatic adverse impact on water vole populations, and colony extinction frequently follows the arrival of this introduced predator (eg Woodroffe *et al.* 1990a; Strachan and Jefferies, 1993; Strachan *et al.*, 2000; Telfer, 2000). The River Dee, into which the Bynack and Geldie catchments flow, is permanently occupied by mink (Lambin *et al.*, 1998). With respect to Mar Lodge Estate, the last time mink were successfully trapped was in 1997, when two were caught on the River Dee at Inverey (Stewart Cumming *pers. comm.*). In the same year, mink signs were recorded as far up the River Dee as White Bridge (c. 3km north east of the Bynack) and in the sub-catchment of the Clunie (c. 15km east of the Bynack) (Lambin *et al.*, 1998).

The occurrence of mink in the Bynack catchment appears to have been transitory. In addition, no evidence was found for the presence of mink in the Geldie catchment at any stage of the present or previous studies (Aars *et al.*, 2001). This suggests that only a small number of mink were involved (perhaps a single individual) and that conditions were inadequate to support a resident animal. The lack of alternative prey, such as rabbit *Oryctolagus cuniculus* could be crucial in this respect. Although rabbits have previously been recorded at Bynack Lodge (Stewart Cummin *pers. comm.*) none were seen here or in the Geldie during the present study.

Despite the absence of mink predation, the Geldie water vole population, like that at Bynack, also declined over the period of study. Were these independent or linked events? It is conceivable that the demise of water vole colonies in the Bynack as a consequence of mink predation resulted in some isolation threshold being exceeded such that dispersal was no longer sufficient to maintain the Geldie metapopulation (Hanski, 1991). However, in addition to the Bynack, the Geldie sub-catchment is surrounded by upland habitat known to support water vole populations, albeit patchily distributed eg in the Glen Feshie, Glen Dee, Glen Derry and Glen Lui catchments (Lambin *et al.*, 1998; WildCRU, 2004). In the absence of cumulative mink impacts on these peripheral populations it is perhaps difficult to see how the loss of the Bynack water vole colonies could have resulted in the hypothesised isolation threshold being exceeded.

Alternatively, it is possible to invoke the "core-satellite" scenario to explain the simultaneous decline in the Geldie-Bynack water vole populations. Under this scenario, core populations are those whose size confers immunity to stochastic extinction. They are therefore a constant source of dispersing animals which sustain satellite populations elsewhere (Harrison, 1991). The Bynack catchment is known to have supported one relatively large water vole colony in 1998, comprising c.12 breeding females on the Allt an t-Seilich tributary. Most habitat patches occupied by water voles contained single numbers of individuals, with only 29% and 37% of occupied patches holding more than a single breeding female or male respectively (Aars *et al.*, 2001). However, despite its relatively large size, even this colony is unlikely to have been immune from the effects of stochastic extinction and its function as a core population is therefore open to doubt.

The observed decline in the Geldie water vole population may have occurred independently of any indirect effects of mink predation in the Bynack catchment. Aars *et al.* (2001) provide evidence that even in the absence of mink, water vole populations appear to fluctuate on a regional scale (>25km²), with synchrony within regions but not between them. Thus, in the Assynt area in northwest Scotland, colony occupancy increased over the period 1998–1999, while the opposite trend was noted in the Grampian Mountains. It is speculated that these regional changes in colony extinction and colonisation rates may be part of multi-annual fluctuations such as those reported for fossorial water vole populations in the Alps (Saucy 1994). Under the above scenario, water vole populations in the Bynack catchment may have declined in synchrony with those of the Geldie catchment even in the absence of mink. However, the arrival of the latter predator will have been catastrophic, influencing both the speed and scale of subsequent decline, at least in the Bynack.

In conclusion, it would appear that water vole populations in the uplands are naturally highly fragmented: the scattered small colonies we see today are not necessarily the remnants of a formerly more continuous population. Further, given that water vole populations appear to undergo natural fluctuations in abundance on a regional scale, population declines can occur even in the absence of mink. Nevertheless, these natural fluctuations can reduce water vole colony density to very low levels and it is at such times that the effects of mink predation are likely to be potentially devastating. Within the sub-catchments comprising the upper reaches of the River Dee, such as the Geldie and the Bynack, mink predation is likely to be intermittent as long as alternative prey, such as rabbits, do not become established. Whether water vole populations can sustain such intermittent predation in the long term is debatable, depending as it does on factors such as mink predation and water vole colonisation rates.

Postscript:

A repeat water vole distribution survey was undertaken in July 2002 in the Geldie and Bynack sub-catchments. The results of this survey are given in Appendix 1 to this chapter.

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Figure 1.1 Distribution of water vole colonies in the Bynack catchment, June-October inclusive, 1998. Data from Aars *et al.* (2001). No data available for the Geldie catchment. Red: occupied watercourses. Yellow: surveyed but unoccupied watercourses.



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Figure 1.2 Distribution of water voles in the Bynack catchment, June-October inclusive, 1999. Data from Aars *et al.* (2001) and this study. No data available for the Geldie catchment. Red: occupied watercourses. Yellow: surveyed but unoccupied watercourses.



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Figure 1.3 Distribution of water vole colonies in the Bynack and Geldie catchments, April-October inclusive, 2000. Red: occupied watercourses. Yellow: surveyed but unoccupied watercourses.



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Figure 1.4 Distribution of water vole colonies in the Bynack and Geldie catchment, April-October inclusive, 2001. Red: occupied watercourses. Yellow: surveyed but unoccupied watercourses.



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- Figure 1.5 Distribution of water vole colonies in the Geldie catchment, April-May inclusive, 2001. Red: occupied watercourses. Yellow: surveyed but unoccupied watercourses.

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Figure 1.6 Distribution of water vole colonies in the Geldie catchment, June-October inclusive, 2001. Red: occupied watercourses. Yellow: surveyed but unoccupied watercourses.



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Figure 1.7 The % of burns with fresh signs of occupation by water voles for each of the years 1998-2001 (Bynack catchment) and 2000-2001 (Geldie catchment). Only those burns surveyed in each of the respective years are included in the analysis. Sample size ranged from 11 burns (Bynack) to 23 burns (Geldie). Data labels show actual percentages. In both catchments, the proportion of burns with active vole signs declined over the period of study. By 2001, in the Bynack catchment, only one of the 11 burns surveyed in each year retained fresh signs of use by water voles. Data for 1998 were derived from Aars *et al.* (2001).



Figure 1.8 The length of waterway with fresh water vole signs expressed as a percentage of the total length of waterway surveyed in the Bynack and Geldie catchments, 1997-2001. Data for 1997 from Lambin et al. (1998). 1998 and some 1999 data derived from Aars et al. (2001). Data labels show actual percentages. In both catchments the percentage of occupied waterway has declined. Lengths of waterway surveyed in the Bynack catchment: 14.4km (1997); 32.5km (1998); 34km (1999); 15.5km (2000); 14.5km (2001). Lengths of waterway surveyed in the Geldie catchment: 46km (2000); 28km (2001).



APPENDIX 1 – water vole surveys in the Bynack and Geldie catchments, Mar Lodge Estate, 2002

Introduction

Water vole surveys conducted in the Bynack & Geldie sub-catchments of the River Dee during the period 1998–2001 provided evidence for a substantial population decline.

In order to establish whether or not this decline continues, repeat surveys of a sample of burns were undertaken between the 24th and 28th June 2002.

Methods

Burns were systematically walked and surveyed for evidence of occupation by water voles based on the following indicators:

- faeces: water voles produce characteristic blunt-ended faeces, which they deposit on runways or at points of entry to, or exit from, water;
- latrine sites: comprising concentrations of faeces near nests, home range boundaries or on runways;
- runways: comprising regularly travelled corridors of trampled and grazed vegetation, usually within 2m of water;
- entrances to subterranean burrows in banks adjacent to water;
- feeding stations, comprising piles of cut grass, sedge or rush stems, rush pith and leaves;
- nests, comprising woven surface structures;
- footprints;
- sightings.

Colonies were considered to be occupied if fresh water vole signs (droppings, latrines, footprints, sightings, feeding stations) were found. In those cases where burns were obscured by dense plant cover, vegetation was parted in order to expose the water and banks beneath. This was considered essential, since a high proportion of vole signs are obscured and can be easily missed.

Results

The surveyed burns and the locations of occupied water vole colonies are shown in Figure 1. Water vole signs were found on 5 burns in total with details being given in Table 1.

Table 1Details of burns surveyed during the period 24th-28th June 2002 on which fresh
water vole signs were found. The locations of all burns surveyed (both positive
and negative) are shown in Figure 1.

CATCHMENT	BURN LOCATION	EVIDENCE
Geldie	NN985883	Signs found at 6 locations between NN985880 & NN987886, comprising droppings and 1 latrine.
Geldie	NN981888	Signs found at 9 locations between NN982884 & NN98008926, comprising droppings, 2 latrines & several active burrows. Fresh water vole gut remains found at one location: source of predation unknown.
Geldie	NN976890	Droppings found at 1 location between NN977890 & NN975890.
Allt an t-Seilich	NN002853	Droppings found at 1 location between NN001831 & NN021884
Bynack	NN973843	3 active burrows & fresh feeding station found between NN975843 & NN971843

Using only those waterways surveyed in each of the years 1998–2002, the annual proportion of burns with fresh signs of occupation by water voles is shown in Figure 2. From the latter it can be seen that in both catchments, the proportion of positive burns declined during the period of study from 73–18% and from 78–16% for the Bynack and Geldie catchments respectively. By 2001 only 1 of 11 burns monitored throughout the study retained water voles in the Bynack, and 3 of 19 burns in the Geldie in 2002. The proportion of burns with water voles in the Bynack catchment (including the Allt an t-Seilich) increased to 2 of 11 burns in 2002, although the number of animals present is likely to be minimal (<5?).

The number of water vole colonies per kilometre of watercourse surveyed is presented in Table 2, which also shows data for previous years. A decline in colony abundance is evident over the period 1999-2002.

Table 2 The number of active water vole colonies per kilometre of watercourse surveyed, 1998-2002. The colony count for 1999, which is partly derived from Aars *et al.* (2001), is likely to be conservative. The number of colonies per kilometre of watercourse has declined.

		Number of extant colonies per kilometre (number of colonies)		
Year	Length of watercourse surveyed (km)	Bynack catchment	Geldie catchment	
1998		No data	No data	
1999	34 (Bynack);	0.35 (c.12)	No data	
2000	15.5 (Bynack); 46 (Geldie)	0.32 (5)	0.78 (36)	
2001	14.5 (Bynack); 28 (Geldie)	0.28 (4)	0.29 (8)	
2002	14 (Bynack); 21 (Geldie)	0.14 (2)	0.14 (3)	

Figure 3 shows that the percentage length of burn occupied by extant water vole colonies declined from 31–0.7% and from 26–5% in the Bynack and Geldie catchments respectively over the period 1997–2002.

Discussion

Whether considered in terms of the proportion of burns occupied, the number of water vole colonies per kilometre of water course, or the % length of burn occupied, it is clear that water vole populations in the Geldie and Bynack catchments continue to decline. With respect to these catchments, the species appears to be hovering on the brink of extinction.

Reassuringly it is known that water vole populations in upland habitats can fluctuate on a regional scale, even in the absence of mink, with synchrony within regions but not between them (Aars *et al.* 2001). Whether the population trends observed in the Geldie and Bynack catchments are a reflection of these apparent multi-annual fluctuations, or whether more sinister factors are exerting an influence remains to be seen.

It is possible to conceive three models of long-term water vole population dynamics in the Geldie/Bynack catchment. The population could continue its present downward spiral to extinction. Alternatively, the population could recover and continue to fluctuate about a long-term but relatively stable mean. The third model is a combination of the first two, in that the population may oscillate about a declining mean. As with the first model, this latter scenario ultimately results in extinction. Precisely which of these models prevails will only be determined by long-term monitoring.

Figure 1 Distribution of water vole colonies in the Geldie and Bynack catchments, 24th-28th June 2002. Red: occupied watercourses. Yellow: surveyed but unoccupied watercourses.



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Figure 2 The % of burns with fresh signs of occupation by water voles for each of the years 1998-2002 (Bynack catchment) and 2000-2002 (Geldie catchment). Only those burns surveyed in each of the respective years are included in the analysis. Sample size ranged from 11 burns (Bynack) to 23 burns (Geldie). Data labels show actual percentages. In both catchments, the proportion of burns with active vole signs declined over the period of study. By 2001, in the Bynack catchment, only one of the 11 burns surveyed in each year retained fresh signs of use by water voles, although by 2002 this had increased to two. Data for 1998 was derived from Aars et al. (2001).



Figure 3 The length of waterway with fresh water vole signs expressed as a percentage of the total length of waterway surveyed in the Bynack and Geldie catchments, 1997–2002. Data for 1997 from Lambin et al. (1998). 1998 and some 1999 data derived from Aars et al. (2001). Data labels show actual percentages. In both catchments the percentage of occupied waterway has declined. Lengths of waterway surveyed in the Bynack catchment: 14.4km (1997); 32.5km (1998); 34km (1999); 15.5km (2000); 14.5km (2001); 14km (2002). Lengths of waterway surveyed in the Geldie catchment: 46km (2000); 28km (2001); 21km (2002).



2 WATER VOLE HABITAT PREFERENCES

2.1 Introduction

Water vole populations in the uplands appear to be naturally fragmented comprising small, widely scattered colonies (eg Lambin *et al.* 1998; Aars *et al.* 2001; chapters 1 & 4, this study). Under these circumstances it would seem reasonable to speculate that such a distribution occurs in response, at least in part, to specific habitat requirements and the patchy occurrence of these preferred habitats within the wider upland environment. The extent to which water voles on Mar Lodge Estate exhibit habitat preferences is explored below.

2.2 Study area and methods

Data were collected from the Geldie sub-catchment, a headwater tributary of the River Dee, located in the Cairngorm Mountains, Scotland (Figures 2.1 & 2.17). For sampling purposes, this sub-catchment was stratified, the two strata comprising the main Geldie River stem and its tributaries respectively. For each stratum, the length of watercourse was measured from a 1:25,000 "Pathfinder" Ordnance Survey map. A total of eighty watercourse sample sites were then chosen at random, the number of sites per stratum being in proportion to stratum watercourse length. For example, the total length of watercourse in the Geldie catchment measured 76,900m, 14% of which comprised the Geldie River stem and 69 samples on the Geldie tributaries (Appendix 2, Table 1).

Sample sites were located on the ground using a 1:25,000 Ordnance Survey map, together with a handheld Garmin 45 Global Positioning System (GPS). Each sample site comprised 100m of burn side, within which the following variables were assessed:

- presence of water voles, as indicated by the occurrence of latrines, runs, burrows, feeding stations and sightings (1 = present; O = absent);
- number of latrines (piles of two or more faecal pellets);
- evidence for the presence of otter, mink, brown rat, stoat and weasel, in the form of tracks, faeces and sightings.
- physical burn and bank parameters, recorded in 5 replicates located at 20m intervals within the 100m sample site, alternating between banks wherever possible and comprising:
 - vegetation composition, cover and structure: a 5m chain, marked at intervals of 50, 75, 100, 200, 300, 400 and 500cm, was pegged at the top of the bank such that the chain assumed the bank profile while one end (0cm) was level with the water surface. A thin (3mm diameter) metal rod, marked at heights of 0–10, 10–30, 30–70 and >70cm was then placed at each of the 7 marked chain intervals and the number of contacts by each plant group in each of the 4 vertical intervals recorded. Plant groups comprised "rushes" (*Juncaceae*), "sedges" (*Cyperaceae*), "grasses" (*Gramineae*), "ericoids" (*Ericaceae*) and "other";

- bank angle (Ø): was calculated by standing canes vertically at the 50cm and 200cm chain intervals and measuring the horizontal distance (d) between the canes. Bank angle was subsequently determined by cos Ø = d/150. The same procedure was repeated for chain distances of 200cm and 500cm;
- bankfull width: measured at the point at which the burn spilled out of the channel;
- *water depth:* measured centre-channel;
- water velocity: assessed subjectively (1 = no perceptible flow; 2 = slow, with visible surface water flow but no surface disturbance; 3 = moderate flow with slight surface ripples; 4 = fast flow with surface disturbed by ripples and bubbles; 5 = extremely fast flow with white water and breaking waves);
- *bank penetration*: measured as the penetration depth of a 1m hollow aluminium rod (7mm external diameter) pushed into the soil by hand at five random points within 1m of the water edge;
- *deer pellet group density*²: measured as the number of pellet groups within a 2m wide transect centred on the chain used to assess vegetation cover and structure;
- poaching: assessed subjectively (1 = none; 2 = light, with localised hoof marks; 3 = moderate, with some exposed substrate but vegetation cover dominant; 4 = heavy, with exposed substrate and little vegetation cover).

The above variables were incorporated into subsequent analyses in the following forms:

- Plant Group Diversity Index (SI_D), calculated using Simpson's Index (Simpson 1949; Krebs 1994) by summing data for all five replicates within a sample site. The index is given by: $1 \cdot \text{sum}(p_i)^2$ where p_i is the proportion of contacts by the *i*th plant group at a site, irrespective of the layer in which the contact occurred. The index ranges in value from 0 (low diversity) to a maximum of (1-1/S), where "S" is the number of plant groups. With the 5 plant groups used in this study the maximum value of the index is therefore 0.8;
- Structural Diversity Index (Sl_l) , calculated using Simpson's Index by summing data for all five replicates within a sample site. The index is given by $1 \operatorname{sum}(p_i)^2$ where p_i is the proportion of contacts in the *i*th layer, irrespective of plant group;
- bank angle, bank full width, depth, velocity, pellet group count and poaching: mean values calculated for each sample site using the 5 replicate measurements;
- bank penetration: median value calculated for each sample site using the 25 replicate measurements;
- Percentage Grass Cover: mean value calculated by summing data for all five replicates within a sample site. % Grass given by 100 x (total contacts due to grass, irrespective of layer, divided by the total number of contacts for all plant groups in each sample site);

² Provides an indirect measure of grazing pressure.

- Percentage Sedge Cover: mean value calculated by summing data for all five replicates within a sample site. % Sedge given by 100 x (total contacts due to sedge, irrespective of layer, divided by the total number of contacts for all plant groups in each sample site);
- Percentage Rush Cover: mean value calculated by summing data for all five replicates within a sample site. % Rush given by 100 x (total contacts due to rush, irrespective of layer, divided by the total number of contacts for all plant groups in each sample site);
- Percentage Ericoid Cover: mean value calculated by summing data for all five replicates within a sample site. % Ericoids given by 100 x (total contacts due to ericoids, irrespective of layer, divided by the total number of contacts for all plant groups in each sample site).

Using the above data sets, the following analyses were undertaken:

- Principal Components Analysis, a multivariate statistical method that helps to reduce the number of factors needed to explain the variability in the data;
- Mann-Whitney U-Tests, a nonparametric univariate statistical procedure used to investigate differences between the median values of variables.

All the analyses were undertaken using Minitab (Release 13) Statistical Software.

Raw data were collected over a period of 21 days in 2000, distributed as follows: June (4 days); July (13 days); August (3 days); September (1 day). In order to minimise the possibility of falsely documenting vole absence, no data were collected following heavy or prolonged rain when burns were in spate. During flooding, latrines are washed away.

2.3 Results

Data used in the analyses are given in Appendix 2, Table 2. Habitat data were collected from 65 of the 80 randomly selected sites. Of these 65 sites, 23 (35%) were occupied by water voles and 42 (65%) were unoccupied. Fourteen variables were used in the first stage of the Principal Components Analysis (PCA):

- presence/absence of water voles (scored as "1" and "O" respectively);
- Plant Group Diversity Index;
- Structural Diversity Index;
- % Grass cover;
- % Sedge cover;
- % Rush cover;
- % Ericoid cover;
- mean bank angle (calculated for each sample site as the mean value for bank distances 50–200cm and 200–500cm combined);

- width;
- depth;
- velocity;
- bank penetrability;
- deer Pellet group density;
- poaching index.

The initial PCA resulted in the generation of fourteen principal components (PCs). The number of PCs to extract for subsequent analysis was determined by application of the Kaiser Criterion (Kaiser 1960), whereby only PCs with an eigenvalue greater than one were retained. Eigenvalues provide a measure of the amount of variance accounted for by each of the components. By selecting an eigenvalue greater than one, only those PCs or "factors" which explain at least as much of the data variability as the equivalent of one original variable were identified. Using the Kaiser Criterion, five PCs were selected for further analysis. Cumulatively, these accounted for 75% of the variation in the data. The PCA was then recomputed on the basis of these five PCs. The resulting correlation matrix and score plots for pairs of PCs were then interpreted by assessment of the coefficients for each component and examination of the graphed data points in order to identify the original values of the variable of interest. The results are shown in Tables 2.1–2.3 and Figures 2.2–2.16 and are interpreted below.

Plot of PC1 versus PC2 (Figure 2.2)

From the plot it can be seen that sites with voles are clustered in principal component space. PCs 1 and 2 account for 30% and 16% respectively of the total variance in the data (ie 46% cumulative). Increases in PC1 appear to reflect:

- decreasing grass cover;
- increasing plant group diversity;
- decreasing burn width;
- increasing ericoid cover; and
- increasing sedge cover.

PC1 can thus be thought of in terms a gradient of increasing vegetation diversity and decreasing burn width. At one extreme of this gradient are relatively wide burns with grass-dominated banks; while at the other are narrow burns with bank vegetation comprising habitat mosaics of grasses, sedges, rushes and ericoids. Occupied water vole sites are clustered towards the higher values of the PC1 axis.

Boxplots for each of the above variables for occupied and unoccupied sites are shown in Figures 2.3–2.7, and the results of Mann-Whitney Tests in which the median values of the variables are compared, are shown in Table 2.3. These plots are useful for showing the distribution characteristics of the data.

Increases in PC2 are associated with:

- decreasing average bank angle
- decreasing burn velocity
- increasing bank penetrability

PC2 can be interpreted as a gradient from high-energy fast flowing burns with steep impenetrable banks to relatively low-energy slow flowing burns with gently sloping and penetrable banks. Occupied water vole sites are clustered towards the higher values of the PC2 axis.

Boxplots for each of the above variables for occupied and unoccupied sites are shown in Figures 2.8–2.10, and the results of Mann-Whitney Tests are given in Table 2.3.

Plot of PC3 versus PC4 (Figure 2.11)

From the plot it can be seen that occupied water vole sites are loosely clustered in principal component space. PCs 3 and 4 account for 11% and 10% respectively of the variance in the data. Increases in Component 3 reflect increases in deer pellet group density, while increases in Component 4 are associated with increases in water depth. Occupied sites tend to be clustered in the region of moderate values for both PC3 and PC4 axes.

Boxplots for each of the above variables for occupied and unoccupied sites are shown in Figures 2.12 and 2.13, and the results of Mann-Whitney Tests are given in Table 2.3.

Plot of PC4 versus PC5 (Figure 2.14)

Occupied water vole sites are again loosely clustered in principal component space. PC 5 accounts for 8% of the total variance in the data. Increases in this component reflect increasing % Rush cover. Occupied sites tend to be associated with areas of relatively low to moderate Rush cover. A boxplot for this variable is shown in Figure 2.15, and the results of a Mann-Whitney Test are given in Table 2.3.

2.4 Discussion

From the results presented earlier in this report (vole distribution and abundance section) it is clear that water voles in the Geldie and Bynack catchments are not randomly distributed across the landscape. They exist as small, discrete and highly fragmented populations within the upland environment. The data collected in the present study confirm that this distribution is in part the consequence of habitat selection. In response to a specific combination of resource requirements, water voles appear to be selecting sites with a relatively tightly defined set of habitat conditions. The Principal Components Analysis, together with the results of the univariate analyses presented in Table 2.3, provides an insight into the nature of these habitat requirements and permits the characterisation of occupied water vole habitat. The data were collected in a catchment in which mink *Mustela vison* were absent. Water vole habitat selection is unlikely therefore to have been influenced by this introduced predator.

While mink did not influence the analysis of habitat selection, several other factors are likely to have compromised the isolation of good predictors of vole distribution. For example, water vole populations appear to exist as metapopulations, with frequent local extinctions. At any one time, a high proportion of potentially suitable habitat may therefore be temporarily vacant. The occurrence of unoccupied but favourable habitat is likely to have been inflated by the fact that water vole populations in the Geldie sub-catchment declined over the period of study. Both factors will have compromised the ability to establish statistically significant relationships between water vole distribution and habitat variables.

With these limitations in mind, what can we conclude from the data collected in the Geldie catchment in 2000? Relative to unoccupied sites, burns occupied by water voles were:

- significantly smaller (median width 52cm);
- significantly slower (median velocity 1.4).

They also tended (though differences not statistically significant) to be shallower (median depth 13.8cm).

Burn banks at occupied sites were significantly:

- more penetrable (median penetration 55cm);
- less steep (median bank angle between chain intervals 50cm and 500cm: 13.5°);

Bank side vegetation at occupied sites was characterised by:

- significantly greater sedge cover (median 28%);
- significantly less rush cover (median 0.9%);
- a tendency (though not statistically significant) for less grass cover;
- a tendency (though not statistically significant) for greater plant group diversity.

(See Figures 2.18–2.21 for photographs of favourable and unfavourable habitat).

How do these results compare with those obtained from previous studies both on the upper catchment of the River Dee and other parts of the UK?

Several such studies have found that water voles tend to occur on relatively narrow, slow-flowing and shallow watercourses (eg Strachan & Jefferies 1993; Strachan 1998; Lambin *et al.* 1998; Jones 1999; Aars *et al.* 2001; Telfer *et al.* 2001). Where quantified, these authorities cite preferred widths of less than 3m and depths of up to c.1m. Quite what the significance of burn width and water depth is to water voles is obscure. Voles may be at risk of being washed away in fast-flowing burns. Alternatively, it is possible that it is not burn width and depth that are being selected for, but correlated habitat variables eg vegetation or bank characteristics.

Given that water voles are burrowing animals, it is perhaps not surprising that both the present and previous studies (cited above) have found a preference for easily excavated bank substrates.

Consensus regarding bank-angle preference is more elusive. The present study found that relatively shallow bank angles are more likely to be colonised by water voles. This is consistent with the conclusions of Jones (1999) who found that sites with bank angles less than c.35° were more likely to be occupied. He collected data from the Bynack and Allt an t-Seilich catchments, which like the Geldie, are upper tributaries of the River Dee. In contrast, Lawton & Woodroffe (1991) concluded that steep bank angles were preferred, with occupied sites having a mean bank angle (measured between chain intervals of 25cm and 200cm) of 40°. This compares with a mean of 17° (measured between chain intervals 50cm and 200cm) in the present study. Strachan (1998) and Strachan & Jefferies (1993) also considered that stepped or steep bank profiles are important, such that animals can burrow and create nest chambers above the water table. Lambin *et al.* (1998) could find no evidence for a relationship between bank gradient and the presence or absence of voles.

The burns occupied by water voles in the Geldie catchment are regularly flooded, even during the summer months. Intuitively one would have expected water voles to select burns with steep banks, thereby conferring some protection from flooding. In their Yorkshire study area, Lawton & Woodroffe (1991) noted that when rivers were in spate, radio-tagged water voles moved to underground chambers further up the bank. Steep banks were thus advantageous, permitting water voles to construct extensive burrow systems at a number of levels. Despite regular and dramatic flooding, water voles in the Geldie catchment failed to preferentially select steep banks. This may be a function of hydraulic geometry and associated flow characteristics of burns where, for a given discharge, water will rise more quickly in steep-sided than shallow-sided channels. Perhaps in the context of upland catchments such as the Geldie, which are subject to flash flooding, selection for relatively shallow-sided channels and associated reduced rates of water level rise confers a selective advantage. Other factors associated with shallow bank angles may also play a role, such as vegetation type and potential food plants.

The role of grass cover as a factor influencing water vole habitat selection is also ambiguous. Lawton & Woodroffe (1991) found that breeding colonies were characterised by high grass cover of more than 66% (usually more than 70%). Aars *et al.* (2001) also concluded that occupied sites were associated with high grass cover. In contrast, grass-dominated areas appeared to be avoided in the present study (37% mean grass cover at occupied sites). Jones (1999) noted that while the probability of site occupancy by water voles was reduced with low grass cover, it was never zero. Although grasses have been recorded as a major food item in some studies (eg Stoddart 1977), this would not appear to be the case in the present study, at least during the summer months. Of 266 feeding stations examined, only 47 (17.7%) contained grass. Therefore, it is suggested that grass cover is likely to exert a positive influence on habitat selection by water voles in the Geldie catchment, but only where grasses constitute part of a mosaic with other plant groups (including sedges, rushes and ericaceous shrubs), and rarely where grasses comprise the dominant vegetation cover.

Within these habitat mosaics, sites with relatively high sedge cover, including *Carex* and *Eriophorum* spp. were more likely to be occupied by water voles. This is consistent with the finding that sedges appear to be of importance in the diet. Of 266 feeding stations examined during the summer months, 134 (50.4%) contained sedges, which in terms of frequency of occurrence, constituted the largest single food plant group (see Chapter 3). Other than Jones (1999), who found significantly greater sedge cover at occupied sites than unoccupied sites, the specific importance of sedges for upland water vole populations does not seem to have been previously documented.

Lambin *et al.* (1998) concluded that there was a very strong association between the presence of water voles and the availability of dense, tall "grassy" vegetation, particularly where it formed a wide strip along watercourses. The mean width of such strips was 20.4m and 10.3m at sites with and without water voles respectively. It is not clear what constitutes "grassy vegetation" in Lambin's report, but if it includes sedges, then the results are consistent with the results of the present study. In their Central Cairngorms surveys WildCRU (2004) concluded that water voles were "strongly associated with dense bankside vegetation comprising tall tussock-forming grasses, sedges, rushes and herbaceous plants".

With respect to vegetation structure, Lawton & Woodroffe (1991) found that water vole colonies tended to be associated with moderate to high layering of vegetation. Telfer (2000) also noted that in general water voles preferred structurally complex vegetation in her study area. No such relationship between site occupancy and vegetation structure was found in the present study (see Table 2.3). Rather than structural complexity, total vegetation cover, irrespective of the degree of layering, appears to have been of importance. Occupied sites were characterised by significantly greater total vegetation cover than unoccupied sites (Table 2.3, Figure 2.16). The importance of cover has also been highlighted by other studies (eg Strachan 1998; Strachan & Jefferies 1993; Telfer *et al.* 2001). Lambin *et al.* (1998) noted a strong association between the presence of voles and the availability of dense, tall, grassy vegetation.

Given the apparent importance of total vegetation cover, water voles are clearly potentially vulnerable to the effects of grazing, browsing and poaching by larger herbivores. Both red *Cervus elaphus* and roe deer *Capreolus capreolus* are present in the Geldie catchment, the former species being numerically dominant and the principal herbivore of open moorland habitats. Although not statistically significant, there was a tendency for occupied water vole sites to be associated with elevated deer pellet group density (Table 2.3, Figure 2.11). For whatever reason (but presumably feeding), red deer appear to favour the same grass, sedge, rush and ericoid habitat mosaics selected by water voles. However, within the Geldie catchment current levels of use by deer do not appear to be detrimental. If they were, a negative relationship between pellet group densities or poaching and the occurrence of voles would have been apparent. Within an adjacent catchment to the east of the Geldie (the Allt an t-Seilich burn), localised areas occur where grazing and poaching are probably sufficiently intense to prevent colonisation of otherwise suitable habitat by water voles. Vigilance is required to ensure that in relation to deer numbers, such localised effects do not become more widespread.

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Table 2.1The proportion of variance explained by the five Principal Components with
eigenvalues >1. The values were derived from the first phase of a Principal
Components Analysis using 14 environmental variables.

	PC1	PC2	PC3	PC4	PC5
Eigenvalue	4.12	2.16	1.57	1.33	1.11
Proportion	0.30	0.16	0.11	0.10	0.08
Cumulative	30%	46%	57%	67%	75%

Table 2.2 Results of a Principal Component Analysis using the five components with eigenvalues >1 indicated in Table 2.1. For each Principal Component the coefficients associated with the environmental variables are shown. (Pgdi = plant group diversity index; Sdi = structural diversity index).

VARIABLE	PC1	PC2	PC3	PC4	PC5
Voles	0.218	0.344	0.089	0.048	-0.144
Pgdi	0.371	-0.279	-0.104	0.062	0.030
Sdi	0.073	0.108	-0.615	-0.264	-0.000
% Grass	-0.408	0.266	-0.004	-0.229	-0.090
% Sedge	0.330	0.269	-0.081	-0.020	0.367
% Rush	-0.153	-0.130	0.108	-0.048	0.774
% Ericoids	0.339	-0.231	-0.080	0.283	-0.352
Average bank angle	-0.114	-0.463	-0.233	0.087	0.108
Burn width	-0.364	0.032	0.050	0.446	0.016
Water depth	-0.207	0.168	-0.111	0.695	0.021
Water velocity	-0.309	-0.360	-0.148	-0.099	-0.131
Bank penetrability	0.194	0.318	-0.240	0.249	0.203
Pellet group	0.091	0.022	0.631	-0.065	-0.070
Poaching index	0.256	-0.323	0.175	0.153	0.192

Table 2.3 Comparison of median values of habitat variables for sites occupied and unoccupied by water voles. Mann-Whitney Tests. NS = not significant, p>0.05; * = significant, p<0.05; ** = significant, p<0.01.

VARIABLE	OCCUPIED (n = 23)	UNOCCUPIED (n = 42)	SIGNIFICANCE
% Grass	34.8	41.6	ns
Plant Group Diversity Index	0.72	0.71	ns
Structural Diversity Index	0.48	0.48	ns
Burn width	52	101	**
% Ericoids	18.4	16.05	ns
% Sedge	27.2	20.5	*
Average bank angle	13.5	19.3	* *
Water velocity	1.4	2.7	* *
Bank penetrability	55	44	*
Pellet group density	1	0.6	ns
Water depth	13.8	17.5	ns
% Rush	0.9	3.0	*
% Total cover	83.3	77.9	*

Figure 2.1 Map showing the locations of the 65 random samples from which habitat data were collected. Enclosed area shows the extent of the Geldie catchment. Solid circles: occupied water vole sites (n = 23). Hatched circles: unoccupied water vole sites (n = 42).



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Figure 2.2 Principal Components Analysis: plot of Component 1 versus Component 2.

Figure 2.3 Boxplot comparing the statistical distribution of data (% grass cover) at sites with and without water voles. Horizontal lines across the box = medians; bottom line of box = first quartile; top line of box = third quartile; whiskers = lines extending from the top and bottom of the box to the adjacent values. Comparing occupied and unoccupied sites, the difference in median % grass cover did not differ significantly (Mann-Whitney U Test, p>0.05).



Figure 2.4 Boxplot comparing the statistical distribution of data (Plant Group Diversity Index) at sites with and without water voles. Horizontal lines across the box = medians; bottom line of box = first quartile; top line of box = third quartile; whiskers = lines extending from the top and bottom of the box to the adjacent values. Comparing occupied and unoccupied sites, the difference in median plant group diversity index did not differ significantly (Mann-Whitney U Test, p>0.05).



Figure 2.5 Boxplot comparing the statistical distribution of data (burn width) at sites with and without water voles. Horizontal lines across the box = medians; bottom line of box = first quartile; top line of box = third quartile; whiskers = lines extending from the top and bottom of the box to the adjacent values. Comparing median values, burn widths at occupied sites were significantly smaller than that at unoccupied sites (Mann-Whitney U Test, p<0.01).



Figure 2.6 Boxplot comparing the statistical distribution of data (% Ericoids) at sites with and without water voles. Horizontal lines across the box = medians; bottom line of box = first quartile; top line of box = third quartile; whiskers = lines extending from the top and bottom of the box to the adjacent values. Comparing occupied and unoccupied sites, the difference in median % Ericoids did not differ significantly (Mann-Whitney U Test, p>0.05).



Figure 2.7 Boxplot comparing the statistical distribution of data (% Sedge) at sites with and without water voles. Horizontal lines across the box = medians; bottom line of box = first quartile; top line of box = third quartile; whiskers = lines extending from the top and bottom of the box to the adjacent values. Comparing median values, the % Sedge cover at occupied sites was significantly greater than that at unoccupied sites (Mann-Whitney U Test, p<0.01).



Figure 2.8 Boxplot comparing the statistical distribution of data (average bank angle) at sites with and without water voles. Horizontal lines across the box = medians; bottom line of box = first quartile; top line of box = third quartile; whiskers = lines extending from the top and bottom of the box to the adjacent values. Comparing median values, the average bank angle at occupied sites was significantly less than that at unoccupied sites (Mann-Whitney U Test, p<0.01).



Figure 2.9 Boxplot comparing the statistical distribution of data (burn velocity) at sites with and without water voles. Horizontal lines across the box = medians; bottom line of box = first quartile; top line of box = third quartile; whiskers = lines extending from the top and bottom of the box to the adjacent values. Comparing median values, burn velocity at occupied sites was significantly less than that at unoccupied sites (Mann-Whitney U Test, p<0.01).



Figure 2.10 Boxplot comparing the statistical distribution of data (bank penetrability) at sites with and without water voles. Horizontal lines across the box = medians; bottom line of box = first quartile; top line of box = third quartile; whiskers = lines extending from the top and bottom of the box to the adjacent values. Comparing median values, bank penetrability at occupied sites was significantly greater than that at unoccupied sites (Mann-Whitney U Test, p<0.05).



Figure 2.11 Principal Components Analysis: plot of Component 3 versus Component 4.



Figure 2.12 Boxplot comparing the statistical distribution of data (Pellet Group Density) at sites with and without water voles. Horizontal lines across the box = medians; bottom line of box = first quartile; top line of box = third quartile; whiskers = lines extending from the top and bottom of the box to the adjacent values. Comparing occupied and unoccupied sites, the difference in median pellet group density did not differ significantly (Mann-Whitney U Test, p>0.05).



Figure 2.13 Boxplot comparing the statistical distribution of data (Water Depth) at sites with and without water voles. Horizontal lines across the box = medians; bottom line of box = first quartile; top line of box = third quartile; whiskers = lines extending from the top and bottom of the box to the adjacent values. Comparing occupied and unoccupied sites, the difference in median water depth did not differ significantly (Mann-Whitney U Test, p>0.05).





Figure 2.14 Principal Components Analysis: plot of Component 5 versus Component 4.

Figure 2.15 Boxplot comparing the statistical distribution of data (% Rush) at sites with and without water voles. Horizontal lines across the box = medians; bottom line of box = first quartile; top line of box = third quartile; whiskers = lines extending from the top and bottom of the box to the adjacent values. Comparing median values, the % Rush cover at occupied sites was significantly less than that at unoccupied sites (Mann-Whitney U Test, p<0.05).



Figure 2.16 Boxplot comparing the statistical distribution of data (% Total Cover) at sites with and without water voles. Horizontal lines across the box = medians; bottom line of box = first quartile; top line of box = third quartile; whiskers = lines extending from the top and bottom of the box to the adjacent values. Comparing median values, the % total cover at occupied sites was significantly greater than that at unoccupied sites (Mann-Whitney U Test, p<0.05).



Figure 2.17 Typical view over the Geldie catchment within which habitat data were collected, showing the main Geldie Burn.



Figure 2.18 Good upland water vole habitat. Slow flowing, narrow watercourse, with gently sloping penetrable banks, and bank side vegetation comprising a mixture of grasses, sedges, rushes and ericaceous shrubs.



Figure 2.19 Good upland water vole habitat, with the same features as per Figure 2.18. Note the surface water vole nest in the foreground. About the size of a rugby ball, it comprised woven grass and sedge stems. Only two such nests were found during the 3-year study.



Figure 2.20 Unfavourable water vole habitat, with fast flowing watercourse and impenetrable banks.



Figure 2.21 Potentially good water vole habitat adversely affected by localised heavy grazing and poaching by deer. Allt an t'Seilich catchment.



APPENDIX 2

Table 1Locations of the 65 random points within the Geldie catchment from which habitat
data were collected.

Sample No.	Grid Reference	Burn Type
1	NN95408705	Geldie Main
2	NN95658715	Geldie Main
3	NN95208715	Geldie Main
4	NN92658715	Geldie Main
5	NN97858750	Geldie Main
6	NN92808710	Geldie Main
7	NN95858710	Geldie Main
8	NN92408755	Geldie Tributary
9	NN94558860	Geldie Tributary
10	NN98558830	Geldie Tributary
11	NN95158730	Geldie Tributary
12	NN96608645	Geldie Tributary
13	NN97708925	Geldie Tributary
14	NN91708720	Geldie Tributary
15	NN94408545	Geldie Tributary
16	NN94708760	Geldie Tributary
17	NN94008835	Geldie Tributary
18	NN94958455	Geldie Tributary
19	NN92708705	Geldie Tributary
20	NN91808340	Geldie Tributary
21	NN97208705	Geldie Tributary
22	NN96858745	Geldie Tributary
23	NN98508820	Geldie Tributary
24	NN95158745	Geldie Tributary
25	NN94858495	Geldie Tributary
26	NN92308685	Geldie Tributary
27	NN92358585	Geldie Tributary
28	NN91658400	Geldie Tributary
29	NN91188498	Geldie Tributary
30	NN94058820	Geldie Tributary
31	NN97058690	Geldie Tributary
32	NN94758515	Geldie Tributary
33	NN92408545	Geldie Tributary
34	NN92058465	Geldie Tributary
35	NN97358715	Geldie Tributary
36	NN95458970	Geldie Tributary
37	NN92258490	Geldie Tributary

Table 1 (continued)

Sample No.	Grid Reference	Burn Type
38	NN92308615	Geldie Tributary
39	NN93708895	Geldie Tributary
40	NN91558445	Geldie Tributary
41	NN95658625	Geldie Tributary
42	NN91558340	Geldie Tributary
43	NN98408770	Geldie Tributary
44	NN92108405	Geldie Tributary
45	NN91658520	Geldie Tributary
46	NN91408525	Geldie Tributary
47	NN94608660	Geldie Tributary
48	NN96908740	Geldie Tributary
49	NN92458550	Geldie Tributary
50	NN96558605	Geldie Tributary
51	NN94858445	Geldie Tributary
52	NN97458940	Geldie Tributary
53	NN96658655	Geldie Tributary
54	NN95058685	Geldie Tributary
55	NN94308535	Geldie Tributary
56	NN91908720	Geldie Tributary
57	NN94808710	Geldie Tributary
58	NN97858920	Geldie Tributary
59	NN96658620	Geldie Tributary
60	NN94608420	Geldie Tributary
61	NN94358540	Geldie Tributary
62	NN93758885	Geldie Tributary
63	NN94358705	Geldie Tributary
64	NN92958715	Geldie Tributary
65	NN95258675	Geldie Tributary
66	NN96408785	Geldie Tributary

				_	_					_	_	_	_		_	_	_	_	_		_	_		_		-	
Mean %	Total Cover	74	79.6	81.3	75	86.4	86.5	97.8	77.9	73	75.7	79.8	81	96.3	84.4	75.3	71.8	68.5	67.1	77.8	79.2	81.5	64.3	91.7	78	68.5	75.3
Mean	poaching index	0	0.8	0	0	0.6	0	0	0	0.6	0.2	0.2	0	0	0.6	0.2	0.6	1.2	2	0.2	0.2	0	0.4	0.2	0.2	0.2	0.6
Mean	pellet group density	0.4	0.4	1.4	0.6	0.2	0.2	-	-	-	1.2	0.2	1.8	2.8	2.4	0.6	1.8	0.2	0.4	0	0	0.2	2.2	۲	2.6	0.6	0.4
Mean	bank penetration (cm)	46	39	70	55	56	44	28	14	43	50	46	45	76	40	49	42	29	23	63	59	64	22	55	28	52	61
Mean	Velocity	2.60	2.40	2.60	2.80	2.00	2.20	2.20	2.20	1.20	3.00	2.80	0.40	1.40	0.40	1.00	2.80	3.00	2.60	2.40	3.00	2.80	3.00	2.40	2.80	3.00	3.00
Mean	Depth (cm)	12.40	11.80	13.80	15.60	22.60	20.40	31.80	36.00	9.80	16.20	16.00	18.20	33.00	14.20	8.20	15.00	17.80	11.80	25.80	20.40	17.20	7.60	15.00	8.20	6.80	6.20
Mean	Width (cm)	330.00	58.00	186.00	77.00	74.00	57.00	61.00	1060.00	37.00	70.60	107.60	53.00	1120.00	42.00	52.00	94.80	102.00	152.00	79.00	80.00	87.00	32.00	133.00	63.00	93.00	25.00
Mean	bank angle 50-500cm	16.95	11.85	28.25	14.3	23.5	10.45	9.65	13.55	12.1	19.2	9.95	10.65	16.8	13.3	9.25	26.15	29.2	21.7	22.8	15.2	12.55	22.45	8.5	21.45	28	21.65
Mean	bank angle (200-500cm)	17.40	12.60	16.30	10.30	13.30	9.80	10.90	11.70	10.90	22.40	9.60	8.40	6.60	10.90	9.60	23.30	21.80	22.80	18.70	16.80	15.30	19.80	5.90	17.80	19.40	18.90
Mean	bank angle (50-200cm)	16.50	11.10	40.20	18.30	33.70	11.10	8.40	15.40	13.30	16.00	10.30	12.90	27.00	15.70	8.90	29.00	36.60	20.60	26.90	13.60	9.80	25.10	11.10	25.10	36.60	24.40
Mean	Gradient	-	-	-	2	-	-	0	-	2	2	-	-	-	-	-	m	с	m	2	2	-	m	۲	4	4	т
Mean %	Ericoids	1.50	18.40	00.0	00.00	30.50	24.70	35.90	3.50	23.60	6.50	7.70	33.00	2.40	20.80	36.00	11.70	19.60	21.90	27.30	16.80	16.70	0.00	00.00	0.00	0.00	12.40
Mean %	Rush	10.80	2.04	6.70	3.00	11.90	00.0	00.0	3.50	00.0	5.60	2.90	0.00	11.00	00.0	00.0	7.80	3.30	1.40	3.00	3.00	3.70	0.00	5.20	2.20	3.40	0.00
Mean %	Sedge	16.90	31.60	22.70	10.00	35.60	15.70	27.20	11.60	32.60	18.70	11.50	30.00	14.60	26.00	25.80	12.60	22.80	30.10	16.20	22.80	33.30	20.00	31.30	14.30	19.10	14.60
Mean %	Grass	44.60	27.60	52.00	62.00	8.50	46.10	34.80	59.30	16.90	44.90	57.70	18.00	68.30	37.70	13.50	39.80	22.80	13.70	31.30	36.60	27.80	44.00	55.20	61.50	46.10	48.30
Mean	structural diversity index	0.44	0.52	0.51	0.48	0.48	0.51	0.55	0.48	0.47	0.50	0.48	0.48	0.51	0.46	0.50	0.54	0.49	0.47	0.53	0.52	0.54	0.43	0.47	0.49	0.54	0.51
Mean	plant group diversity index	0.69	0.75	0.64	0.54	0.74	0.68	0.68	0.58	0.74	0.70	0.61	0.73	0.50	0.72	0.72	0.73	0.76	0.73	0.75	0.74	0.75	0.64	0.59	0.55	0.65	0.67
No.	Latrines	0	m	0	7	0	-	m	0	34	0	0	0	0	23	m	0	0	0	0	0	0	0	0	0	0	0
Occupied	(1) Unoccupied (0)	0	-	0	-	0	-	-	0	-	0	0	0	0	-	-	0	0	0	0	0	0	0	0	0	0	0
Site		<i>.</i> —	2	с	4	ы	6	7	ω	6	10	-	12	13	14	- 10	16	17	-00 -7	19	20	21	22	23	24	25	26

Table 2 Raw data used in the analysis of water vole habitat preference.

Site	Dccupied (1)	Latrines	Mean plant	Mean structural	Mean % Grass	Mean % Sedge	Mean % Rush	Mean % Ericoids	Mean Gradient	Mean bank	Mean bank	Mean bank	Mean Width	Mean Depth	Mean Velocity	Mean bank	Mean pellet	Mean poaching	Mean % Total
	Unoccupiec (0)	7	group diversity index	diversity index						angle (50-200cm)	angle (200-500cm)	angle 50-500cm	(cm)	(cm)		penetration (cm)	group density	index	Cover
27	0	0	0.71	0.47	36.80	34.70	9.50	3.20	0	10.70	8.40	9.55	160.00	13.00	0.80	32	1.4	0.2	84.2
28	0	0	0.67	0.43	48.20	24.70	8.20	2.40	0	13.90	13.40	13.65	470.00	22.00	2.40	28	0.6	0	83.5
29	0	0	0.68	0.48	44.60	8.10	1.40	17.60	с	22.90	15.60	19.25	1280.00	38.00	3.80	43	1.6	0	71.6
30	-	-	0.61	0.46	52.40	31.70	2.40	2.40	-	21.90	6.30	14.1	1040.00	94.00	1.00	100	0	0.2	89
31	1	2	0.77	0.50	16.30	16.30	9.80	29.30	3	20.80	13.30	17.05	34.00	10.20	1.40	47	2.6	-	71.7
32	-	15	0.72	0.55	14.70	16.50	0.90	35.80	2	21.50	20.20	20.85	52.00	8.00	1.20	56	1.6	0.6	67.9
33	0	0	0.72	0.52	7.40	34.70	2.10	29.50	с	17.10	16.50	16.8	90.00	18.20	1.00	100	2	~	73.7
34	-	ß	0.71	0.47	41.80	21.40	0.00	18.40	-	16.00	10.00	13	45.00	7.20	1.00	53	4	0	81.6
35	-	-	0.70	0.45	33.70	38.90	3.20	11.60	-	13.60	8.10	10.85	75.00	8.80	2.00	56	2	0	87.4
36	-	ы	0.71	0.43	39.20	30.90	8.20	4.10	-	8.40	11.50	9.95	40.00	13.80	1.40	56	1.4	0.2	82.5
37	0	0	0.73	0.43	13.80	33.30	2.30	31.00	0	16.50	20.20	18.35	46.00	15.20	1.00	52	1.8	1.4	80.5
38	-	0	0.73	0.51	31.70	25.60	0.00	28.00	-	19.90	16.30	18.1	42.00	9.60	0.60	61	1.4	0.6	85.4
39	0	0	0.72	0.15	15.80	7.90	7.90	26.30	-	22.30	18.20	20.25	99.00	15.00	2.40	50	e	0.6	57.9
40	0	0	0.57	0.28	57.10	2.90	2.90	5.70	-	13.60	12.40	13	1400.00	43.00	3.00	35	0.2	0	68.6
41	0	0	0.72	0.21	11.50	31.10	0.00	31.10	-	8.40	11.30	9.85	72.00	20.20	2.60	36	3.2	-	73.8
42	-	2	0.71	0.53	10.00	42.60	8.00	12.90	0	33.60	13.40	23.5	117.00	20.40	1.40	77	0.8	1.2	73.3
43	0	0	0.65	0.47	43.30	3.00	0.00	16.40	2	33.40	30.00	31.7	590.00	53.00	3.80	26	0.2	0	62.7
44	-	2	0.73	0.56	25.40	27.20	0.00	32.50	0	15.70	12.60	14.15	44.00	16.80	1.80	100	0.2	0.2	85.1
45	0	0	0.66	0.58	45.30	32.80	0.00	17.20	-	31.30	12.40	21.85	249.00	16.80	2.60	09	0	0	95.3
46	0	0	0.77	0.57	25.70	15.60	9.20	30.30	-	18.80	22.10	20.45	149.00	18.60	3.00	42	0.6	0.8	80.7
47	0	0	0.75	0.39	24.70	10.10	7.90	22.50	-	18.10	21.50	19.8	370.00	18.40	3.20	39	-	0.6	65.2
48	0	0	0.70	0.53	44.40	17.60	1.90	15.70	2	20.60	18.20	19.4	40.00	18.80	3.00	56	0.2	0	79.6
49	0	0	0.72	0.46	44.30	13.10	9.80	13.10	2	40.10	18.30	29.2	730.00	18.40	3.00	23	0.2	0	80.3
50	0	0	0.74	0.53	27.90	10.30	4.40	26.50	-	36.40	24.00	30.2	640.00	18.60	3.00	17	1	0.2	69.1
51	-	4	0.74	0.48	32.80	25.90	4.30	11.20	-	18.10	15.60	16.85	69.00	18.00	2.60	55	0.8	0.2	74.1
52	0	0	0.69	0.48	44.20	21.10	1.10	8.40	m	16.00	8.10	12.05	32.00	5.40	3.00	38	0.6	0.2	74.7

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Tab

3 WATER VOLE DIET

3.1 Introduction

Although water voles have on occasion been observed feeding on various species of freshwater mollusc and crayfish, the diet is generally exclusively vegetarian. Previous studies (eg Strachan & Jefferies 1993) have shown that over the country as a whole a wide range of plant species are consumed. However, within relatively impoverished upland riparian habitats potential food species are likely to be limited both in extent and quantity. Given that water voles may eat the equivalent of up to 80% of their body weight daily, the distribution of these food plants is likely to exert an important influence on habitat selection and, ultimately, the spatial and population dynamics of these animals in the uplands. In this chapter, data on water vole diet collected on Mar Lodge Estate is presented and assessed.

3.2 Study area and methods

Data were collected from the Geldie, Bynack and Allt an t-Seilich sub-catchments, headwater tributaries of the River Dee, located in the Cairngorm Mountains, Scotland (Figure 3.1).

Data were collected opportunistically from feeding stations, comprising piles of neatly chopped stems and leaves located in or at the end of vole runs, usually within c. 1–3m of water. At these points water voles harvest, collect and feed on plant material, some of which may subsequently be transferred to underground storage areas.

Upon locating a feeding station, plant remains were identified to generic and where possible specific level by matching plant fragments with uneaten plants growing in the vicinity. No attempt was made to quantify the amount of a particular plant species in a feeding station, presence only being documented. For the purpose of analysis, the proportion of feeding stations at which a particular plant species or plant group was found was calculated and expressed in terms of frequency of occurrence, ie number of feeding stations with species or plant group "x" / total number of feeding stations.

All data were collected within the following periods:

- 23/08/99 28/09/99
- 24/04/00 28/10/99
- 14/06/01 20/09/01

Information on diet was therefore restricted to the spring, summer and autumn months. No data were collected during the winter, when voles spend much time underground and surface signs of activity are scarce.

3.3 Results

Data were obtained from a total of 266 feeding stations. In terms of frequency of occurrence three plant families, sedges (*Cyperaceae*), rushes (*Juncaceae*) and grasses (*Graminae*) dominated, being found in 50%, 25% and 18% of the feeding stations respectively (see Figure 3.2a). Only one other family (*Liliaceae*) was represented in the form of bog asphodel *Narthecium ossifragum*, which occurred with a frequency of 7% (Figure 3.2a).

Considering each plant group separately, the sedges were dominated by *Carex* sp., although common cottongrass *Eriophorum angustifolium* also occurred (Figure 3.2b). Within the rushes, the most prevalent species were soft rush *Juncus effusus* and to a lesser extent heath rush *Juncus squarrosus* (Figure 3.2c). Grasses were dominated by purple moor-grass *Molinia caerulea* (Figure 3.2d).

3.4 Discussion

Feeding stations only provide information on the aboveground foliage eaten by water voles in the spring, summer and autumn. They do not provide information on the relative importance of underground plant structures such as roots and rhizomes which water voles are known to include in their diet, particularly during the winter months. The results of the present survey therefore only provide a snapshot of water vole diet at a particular time of year and specifically in relation to aboveground plant parts.

To what extent did the food remains found at feeding stations reflect water vole feeding preferences ie were voles feeding on different plant groups in proportion to their abundance, or were certain groups selectively exploited? This aspect was explored by comparing the frequency of occurrence of plant groups in the feeding stations with the frequency of such groups in the surrounding habitat. For this latter purpose, data from the habitat survey were utilised (see Chapter 2).

Using only habitat data for the 23 sites occupied by water voles, the overall frequency of the main plant groups was calculated as the percentage of point quadrats in which specific plant groups were present. Data were obtained from a total of 805 point quadrats (35 quadrats per site). Thus, if 64 quadrats contained the plant group of interest, frequency was calculated as $(64/805) \times (100) = 7.9\%$.

Feeding station data were collected opportunistically over the entire period of study, while habitat data were collected systematically over a smaller time period (June-September 2000) and not necessarily from the same sites. These inconsistencies are considered unlikely to have influenced the conclusions that follow, given that feeding station and habitat data were collected over similar seasons and that only habitat data for occupied vole sites were used.

The relationship between the availability of different plant groups within occupied vole sites and the representation of these groups in feeding stations was quantified by the calculation of a Preference Index based on that derived by Duncan (1983):

Pli = U/A, where:
Pli = preference index for plant group "i"
U = % frequency of plant group "i" in feeding stations
A = % frequency of plant group "i" in occupied water vole sites

Pli was log transformed to give a normalised index of preference, thus overcoming the potential problem of compressing values for plant groups that are not preferred relative to those which are. The modified index takes the form Pli = log(Pli + 1). With this index values of less than 0.3 indicate avoidance while values greater than 0.3 indicate selection. Parity, at which point the frequency of occurrence in feeding stations is in proportion to the frequency of occurrence of plant groups at occupied vole sites, is indicated by an index value of 0.3.

The raw data used in the calculation of preference indices are shown in Table 3.1 and the computed preference indices in Table 3.2.

Table 3.1 The frequency with which the main plant groups were found at occupied water vole sites and water vole feeding stations. Data derived from 805 point quadrats and 266 feeding stations respectively. These data were used to calculate preference indices. See Table 3.2.

		% Frequency Ma	in Plant Groups	
	Rushes	Sedges	Grasses	Ericoids
Occupied Vole Sites	6.5	55.4	60.4	34.3
Feeding Stations	25.2	50.4	17.7	0

Table 3.2Preference indices for main plant groups calculated from the % frequency in
feeding stations divided by the % frequency at occupied water vole sites.
The results were log transformed. Values of <0.3 indicate avoidance, while values
>0.3 indicate selection for a particular plant group. No ericaceous plants were
recorded at the feeding stations.

Plant Group	Preference Index
Rushes	0.69
Sedges	0.28
Grasses	0.11
Ericoids	n/a

From Tables 3.1 and 3.2 it would appear that rushes are positively selected as a dietary item in the frequency of this plant group in feeding stations exceeds the frequency of occurrence at occupied vole sites. In contrast, sedges appear to be eaten in proportion to availability, while the index for grasses is indicative of avoidance.

This apparent avoidance of grasses is consistent with the results of the habitat selection analysis presented in Chapter 2. Water vole colonies tend not to be located in grass-dominant habitats in the Geldie and Bynack catchments.

That grasses were not preferentially selected as a food item is at first surprising. Grass is said to be a major source of food, at least in lowland situations (eg Boyce 1991). In addition, Lawton & Woodroffe (1991) noted that water vole colonies tended to be associated with high percentage grass cover (usually >70%) in their upland study areas in Yorkshire.

The apparent avoidance of grass as a food item in the present study may reflect the dominance of purple moor-grass, a deciduous broad-leaved species of relatively little feeding value. While the spring growth of this grass can be quite digestible, this growth is late (eg late May/June) relative to other species and digestibility drops off quickly. This species starts to die off in August (Armstrong 1998). Presumably for similar reasons, purple moor-grass is little used by red deer *Cervus elaphus*, despite the abundance of this plant on many upland estates (Reynolds 1998).

The relationship between water voles and rushes is contradictory. While this plant group is clearly selected as a food item, at the habitat scale occupied water vole sites are characterised by significantly less rush cover than unoccupied sites (see Chapter 2). The reverse may have been expected. However, water vole habitat selection is likely to reflect a combination of sometimes-conflicting needs. For example, while rushes may be a preferred food item, other plants that cannot grow where rushes predominate may also be required. Rush-dominated areas may also be physically unsuitable in terms of associated bank profiles or substrate characteristics. This view of water vole sites having to satisfy conflicting demands is supported by the results presented in Chapter 2 in which water voles colonies appear to be located in habitat mosaics. What appears at first sight to be a contradiction, ie the preference for rushes in the diet but avoidance of rush-dominated habitats, is therefore perhaps a manifestation of the need to satisfy complex topographical, hydrological and nutritional demands.

3.5 References

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Figure 3.1 Map showing area within which the feeding station data were collected.

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Figure 3.2(a) Frequency of occurrence of plant groups found in water vole feeding stations. N = 266. Note that the Liliaceae were represented by one species, Narthecium ossifragum.

Figure 3.2(b) Frequency of occurrence of sedge species found in water vole feeding stations. N = 134.

Figure 3.2(c) Frequency of occurrence of rush species (Juncus spp.) found in water vole feeding stations. N = 67.

Figure 3.2(d) Frequency of occurrence of grass species found in water vole feeding stations. N = 47.

4 WATER VOLE POPULATION DYNAMICS

4.1 Introduction

Information on the demography of water voles living in upland environments is required if population viability models are to be developed. Such models are a potentially useful tool for conservation planning and management. To date, much of the demographic information for this species has been collected from lowland populations eg Stoddart (1971), Leuze (1976), Woodall (1977) and Efford (1985). In these environments factors such as birth, death, emigration and immigration rates may be very different from those that prevail in an upland situation. The purpose of this chapter therefore is to:

- assess individual colony size;
- describe population structure;
- describe changes in population size over time;
- quantify survival rates.

4.2 Study area and methods

Data were collected from sites within the Geldie, Bynack and Allt an t-Seilich sub-catchments, headwater tributaries of the River Dee, located in the Cairngorm Mountains, Scotland (Figure 4.1).

Live trapping was undertaken at various times at each of the sites shown in Figure 4.1. Single Sherman XLK 3 x 3.75 inch extra large folding aluminium traps were placed adjacent to active burrows or latrines and baited with apple. Between 1 and 20 traps were placed at each site (mean 10 traps).

A robust trapping design was used (Pollock 1982), comprising primary and secondary trapping sessions. The primary sessions were separated by a relatively long time interval (in this case monthly over the period August–October 1999, March–October 2000 and April–September 2002).

Each primary session consisted of secondary trap sessions of 1–6 consecutive or near consecutive days duration (mean 3 days), depending upon trapping success and weather conditions. Trapping was confined to daylight and traps remained open for a mean period of 6.5 hours per secondary trapping session (maximum 10 hours, minimum 2.2 hours). The decision to trap specific sites depended upon the presence of positive vole signs (active burrows, latrines, droppings or footprints), and logistical considerations (eg flooding and access constraints).

Trapped animals were sexed, reproductive state assessed and weight recorded to the nearest gram. Males were scored as having abdominal, scrotal or intermediate testes, depending on the extent to which these organs had descended into the scrotum. Females were noted as having a perforate or non-perforate vagina and were further classified as being parous (prominent areas of bare skin around the nipples) or nulliparous (no evidence of lactation).

All voles were individually marked. For animals weighing less than c.90g (juveniles), both ears were tagged using Michel wound clips (Nguyen-Boulenge & Boulenge 1986) serially engraved with unique numbers.

Animals larger than c.90g were tagged with individually coded 5mm Trovan Passive Internal Transponder (PIT) tags. These sterile tags were injected beneath the loose skin along the back. Satisfactory insertion was checked before release using a portable Trovan tag reader. The same equipment was used to assess the status (tagged or untagged) and identity (PIT tag code) of animals subsequently recaptured, by scanning along the back of the animal. For each animal, date, trap site, trap location, tag number and notes on condition were documented prior to release at the point of capture.

Programme CAPTURE (Otis *et al.* 1978) was used to calculate monthly estimates of population size for each site trapped. This programme uses closed models to estimate population size ie it is assumed that within a primary trapping session no mortality, recruitment, emigration or immigration take place. Programme CAPTURE comprises 8 models, each of which incorporates different assumptions regarding capture probability. Tests of these assumptions provide the basis for the selection of the most appropriate model. Each of the models, a brief description of which is given in Table 4.1, uses data from secondary trap sessions.

Table 4.1Model names and descriptions of the closed population models included in the
CAPTURE programme. Estimators of population size are available for all models
except M_{tbh}.

Model	Sources of variation in capture probability	Population estimator?
M _o	None. All individuals in all trap sessions have constant probability of capture.	Y
M _t	Probability of capture depends only on time (ie can vary between trap sessions).	Y
M _b	Behavioural response to trapping (ie different probabilities of initial capture and recapture).	Y
M _h	Capture probabilities vary between individuals (ie heterogeneity in capture rates).	Y
M _{th}	Time and heterogeneity.	Y
M _{tb}	Time and behaviour.	
M _{bh}	Behaviour and heterogeneity.	Y
M _{tbh}	Time, behaviour and heterogeneity.	None

While programme CAPTURE automatically selects the most appropriate model, the selection routine has low power, ie with small sample sizes the ability to detect real differences between population means or proportions is compromised. Use of an inappropriate model results in a population estimate of unknown bias ie systematic over or under estimation of a population parameter, and unrealistically small or unacceptably large variance (Otis *et al.* 1978). Under these circumstances the selection routine fails to reject model M_O in the absence of sufficient data. As sample sizes were generally small in the present study an initial exploration of the trapping results was undertaken using combined data from sites A & E. There was evidence of the movement of individual animals between these sites on a daily basis; therefore the two sites were treated as one colony. This colony was relatively large and persistent, with the largest number of animals and captures. Using the output from programme CAPTURE for the combined site A & E, the data were examined for evidence of time, heterogeneity, and behaviour as influences on capture probability and on this basis an appropriate model was manually selected. The results of this assessment are shown in Tables 4.2 and 4.3.

Table 4.2 Exploration of trapping parameters using combined data for primary trapping sessions from sites A & E. Programme CAPTURE assumes closure ie no mortality, recruitment, emigration or immigration within the period of the primary trapping session. Goodness of fit tests (χ^2 test statistic, p = 0.05) failed to reject the closure assumption in all cases. Also shown is "p" (the estimated mean probability of capture calculated under model M_o), "ip" (the estimated probability of initial capture under model M_b) and "c" (the estimated probability of recapture provides evidence for a behavioural response to trapping (predominantly trap aversion).

Trapping period	Test for closure	р	ір	С
24/04/00-28/04/00	p = 0.11	0.58	0.57	0.6
15/05/00-17/05/00	p = 0.89	0.53	0.62	0.43
12/06/00-15/06/00	p = 0.42	0.29	0.47	0.25
10/07/00-13/07/00	p = 0.15	0.46	0.64	0.35
07/08/00-11/08/00	p = 0.98	0.60	0.62	0.58
04/09/00-08/09/00	p = 0.92	0.61	0.51	0.71
26/10/00-28/10/00	p = 0.24	_	_	_
24/04/01	-	_	-	-
14/05/01-18/05/01	_	_	_	_
11/06/01-12/06/01	_	_	_	_
17/07/01-18/07/01	_	_	_	_
14/08/01-17/08/01	p = 1.0	0.99	0.99	1.0
17/09/01-21/09/01	p = 0.43	0.63	0.49	0.75

Table 4.3 Model selection criteria from programme CAPTURE. In most cases the programme selected model M_0 as being the most appropriate (value = 1). However, with small sample sizes, as here, the selection routine has low power and under these circumstances the selection routine fails to reject model M_0 . Closer examination of the data shows evidence for heterogeneity, with values for model M_h being consistently high relative to other models. Taken together with the data given in Table 4.2 it is concluded that both behavioural (different probabilities of initial and subsequent recapture) and individual variation in capture probabilities need to be taken into account. Accordingly model M_{bh} was used to estimate water vole population size at all trapping sites where there were sufficient data. Note that no estimator is available for the complex model $M_{tbh'}$ therefore it can not be used to estimate population size.

Trapping period	M _o	M _h	M _b	M _{bh}	M _t	M _{th}	M _{tb}	M _{tbh}
24/04/00-28/04/00	1.0	0.68	0.0	0.50	0.36	1.0	0.17	1.0
15/05/00-17/05/00	1.0	0.81	0.35	0.65	0.0	0.42	0.31	0.70
12/06/00-15/06/00	1.0	0.83	0.46	0.77	0.0	0.52	0.36	0.78
10/07/00-13/07/00	1.0	0.83	0.51	0.84	0.0	0.53	0.39	0.87
07/08/00-11/08/00	1.0	0.79	0.24	0.56	0.0	0.42	0.25	0.64
04/09/00-08/09/00	1.0	0.83	0.28	0.62	0.0	0.44	0.30	0.74
26/10/00-28/10/00	1.0	0.80	0.35	0.66	0.0	0.47	0.30	0.71
14/08/01-17/08/01	0.90	0.60	0.53	1.0	0.38	0.0	0.56	0.50
17/09/01-21/09/01	1.0	0.54	0.04	0.58	0.0	0.65	0.0	0.65

On the above basis model M_{bh} was selected since capture probability was clearly influenced by both behavioural and individual responses. This model was then used to estimate population size for all the trapped colonies. In those cases where sample size was too small I used the minimum number of animals alive (MNA) as the appropriate estimate of population size. This simply comprised a count of those animals caught during the primary trapping session.

Survival rate is an important parameter in demographic modelling. This variable was quantified using Programme MARK, which takes into account probability of capture in the estimation of survival rates. For the purposes of analysis, the effects of sex, cohort and age were not considered, and "apparent" survival was calculated ie the survival rates reflect the effects of both mortality and emigration.

Using Programme MARK an attempt was made to fit 4 models to the data for each trapping site (quantity of data permitting). These four models are described by the following notation:

- Φ(t), p(t)
- Φ(.), p(t)
- Φ(t), p(.)
- Φ(.), p(.)

Where " Φ " = survival rate, "p" = recapture rate and "t" indicates that the model is structured such that the estimate for a given parameter varies over time. The above models thus encompass scenarios in which either survival or recapture (or both) varies with time or in which survival or recapture (or both) are constant over time.

The objective of the above modelling approach was to find the best model, ie the model that is consistent with the data, while using the fewest number of parameters (the most parsimonious model). The initial model (Φ (t), p(t)) was tested for Goodness of Fit by the use of a parametric bootstrap routine incorporated within Programme MARK. This routine assesses the degree to which the data meet the expectations arising from the assumptions underlying the model. Where adjustments were required, these were accommodated using "c-hat" (quasi-likelihood parameter) to compensate for over dispersion. Following adjustment, the most parsimonious model was selected on the basis of the lowest Akaike Information Criterion.

4.3 Results and discussion

Trap site locations are shown in Figure 4.1. Details of trapping chronology, trap numbers and trap hours are given in Appendix 4, Table 1. Trapping was undertaken on 164 days over the period August 1999 to September 2001, involving over 10,000 trap hours. A total of 88 animals were tagged.

Population estimates for 11 water vole colonies trapped at various times during the above period are shown in Figure 4.2. Mean colony size was 4.6 animals (range 1–15, standard deviation. 3.84, 95% confidence interval 1.3, n = 36). Relative to 2000, mean/median colony size appeared to be lower in 2001 (Table 4.4), although the difference was not statistically significant.

Table 4.4Comparison of the estimated mean and median number of animals per water
vole colony in 2000 and 2001. The medians were not significantly different
(Mann-Whitney U-test, p>0.05).

Year	Mean (median) colony size	Range	Standard deviation	95% Confidence Interval	n
2000	5.1 (4)	1–13	3.67	1.77	22
2001	4.2 (2)	1–15	4.4	2.54	14

The ratio of sexually active males to fertilisable females (the "operational sex ratio" of Emlen & Oring 1977) is potentially useful for elucidating prevailing mating systems. In the present study, males with scrotal testes and perforate females were considered to be sexually active and fertilisable respectively. Using only data for those months in which *both* sexually active males and fertilisable females were recorded average sex ratios were calculated for 2000 and 2001, as shown in Table 4.5.

Table 4.5Numbers of sexually active males and fertilisable females in the 2000 and 2001
breeding seasons. The apparent surplus of females relative to males in 2000 was
not statistically significant (Mann-Whitney U-test, p>0.05).

	Year 2000			
Site	Month	Males	Females	
Geldie A & E	May	1	2	
Geldie A & E	June	3	5	
Geldie A & E	July	3	3	
Geldie A & E	August	2	4	
Geldie J	June	1	1	
Bynack 4	May	1	1	
Total		11	16	
Mean ratio (m/f)		1	1.46	
		Year 2001		
Month	Males	Females		
Geldie A & E	August	1	1	
Geldie H	June	1	1	
Geldie H	July	1	1	
Geldie Q	June	1	1	
Allt an t'Seilich	July	1	1	
Allt an t'Seilich	September	1	1	
Total		6	6	
Mean ratio (m/f)		1	1	

Although the data for 2000 suggests that on average there were more fertilisable females than sexually active males at colonies, the difference was not statistically significant (Mann-Whitney U-test, p >0.05; median number of males 1.5; median number of females 2.5). The mean operational sex ratio of 1 male to 1.46 females is identical to that recorded by Sharul (1998) in his lowland study areas near Aberdeen (mean derived from Sharul's Table 5.3, omitting September data for Nether Kirkton because no breeding females were recorded during this month). In 2001 the mean operational sex ratio in the present study was unity.

The degree to which inter and intra-sexual range overlap occurred is shown in Table 4.6, using data from site Geldie A & E for the year 2000 breeding season. This site was selected for the analysis because of relative continuity of occupation and, although still small, relatively large sample size. Range overlap was considered to occur if voles were captured in the same traps during a monthly trapping session. Only sexually active males and fertilisable females were used in the analysis.

Table 4.6Frequency of inter and intra sexual range overlap at site Geldie A & E for the
year 2000 breeding season (May-August inclusive). Range overlap was
considered to occur if voles were captured in one or more of the same traps
during a monthly trapping session. Four categories of home range overlap were
considered: male-male; female-female; male-female (male overlapping a female
home range); and female-male (female overlapping a male home range).

Category of overlap	n	Number of range overlaps	Frequency of range overlaps	
Male-Male	9	0	6 (67%)	
		1	2 (22%)	
		2	1 (11%)	
Female-Female	14 0		10 (71%)	
		1	4 (29%)	
Male-Female	e-Female 9 O		6 (67%)	
		1	2 (22%)	
		2	0	
		3	1 (11%)	
Female-Male 14 O		0	10 (71%)	
		1	3 (21%)	
		2	1 (7%)	

From Table 4.6 it can be seen that within both males and females, the levels of inter and intra sexual range overlap are similar. This is consistent with a promiscuous mating system (Emlen & Oring 1977; Davies 1991) in which males tend to be mobile and non-territorial; prolonged pair bonding before and after copulation is absent; and both males and females mate with several different individuals. On average, as determined by trapping, a male's home range overlapped with 0.55 females (sd = 1.01, n = 9), while females overlapped with 0.36 (sd = 0.63, n = 14) males. The corresponding figures for Sharul's study area in Aberdeenshire were 2.36 and 1.18 respectively (Sharul 1998).

In the 2001 breeding season, when in any one month colonies comprised just one sexually active male and one fertilisable female (Table 4.5), monogamy is presumed to have prevailed, in which males were able to monopolise single females for the duration of at least one oestrus period.

The duration of the 2000 and 2001 breeding seasons, as defined by the first and last occurrence of perforate females and scrotal males, is shown in Figure 4.3. The 2000 breeding season was both earlier and longer than that recorded in 2001, perforate females being recorded over a period of 134 days and 65 days respectively. The first perforate females were captured on the 27th April 2000 and not until the 13th June 2001. Corresponding dates for the first capture of juvenile animals, defined as those weighing less than 80g, were the 16th May 2000 and the 16th July 2001.

In her lowland Aberdeenshire study area, Telfer (1996) noted that the breeding season began at the end of April, as assessed by the occurrence of scrotal males and perforate females.

In addition to information on the numbers of sexually active animals in a population and the length of breeding season, population dynamics models also require data on fecundity, ie the numbers of offspring produced over a period of time. It was not possible to document pre-weaning mortality in this study; consequently the number of young entering the trappable population was used as a measure of fecundity.

Given that dispersal can occur at an early age in water voles (eg Leuze 1976), fecundity may be underestimated using this approach. Consequently, for the purpose of quantifying fecundity, trapped young of the year >120g in weight were assumed to be immigrants. Young of the year were distinguished from overwintered adults on the basis of weight and condition (particularly the coat and feet). Animals weighing 120g or less were considered to be pre-dispersal young of the year. These juvenile animals were classified as litter mates if they were of similar weight and were caught in the same or adjacent traps within a primary trapping period. Their age was estimated using the standard growth curve of Stoddart (1968).

Using this approach it was possible to calculate aspects of water vole fecundity, in addition to refining details of the breeding season in terms of conception and birth dates. Summarised data are presented in Table 4.7, which has been compiled from the raw data given in Appendix 4, Table 2.

Table 4.7 Summary of fecundity parameters derived from the analysis of combined data for all sites for 2000 and 2001. Birth and conception dates were extrapolated from estimates of age derived from Stoddart's (1968) growth curve and an assumed gestation period of 22 days (Leuze 1976). It was not possible to estimate preweaning mortality; consequently fecundity was assessed using the numbers of young 120g or less in weight entering the trappable population. Such animals are likely to be pre-dispersal young of the year. Juvenile animals were classified as litter mates if they were of similar weight and were caught in the same or adjacent traps during primary trapping sessions. The raw data from which this summary table has been derived are given in Appendix 4, Table 2.

	Mean	Standard Deviation	Min	Мах	Range	n
Weight when first trapped (for animals <120g)	79.4g	27.80	30	115	85	50
Estimated age from birth when first trapped	35.5 days	11.08	19	48	29	50
Estimated conception date	6th June	37.0 days	3rd April	25th August	144 days	50
Estimated birth date	28th June	37.0 days	25th April	16th September	144 days	50
Estimated litter size	2.08	1.56	1	6	_	24
Litters per perforate female per site	1.07	1.03	0	3	-	13
Young of year <120g per perforate female per site	2.22	2.61	0	8	-	13

Reproductive females can produce a new group of weanlings every 34–37 days, comprising 22 days gestation; an 11–13 day transition from pup to weanling; and a post-partum oestrus 1–2 days after parturition (Leuze 1976). From Table 4.7 it can be seen that the maximum duration of the breeding season (from first to last conception date) was 144 days. It was possible therefore for each reproductive female within the study areas to have produced 4.1 litters during the breeding season (assuming weanlings were produced every 35 days; and that females survived throughout the breeding period). That this potential was not achieved is evident from Table 4.7: on average only 1.07 litters per perforate female were produced, with a maximum of 3 being recorded.

How do these measures of breeding ecology compare with previous studies? Telfer (1996) concluded that adult females could theoretically produce up to 4 litters during a single breeding season in her lowland Aberdeenshire study area. She estimated the first conceptions to have occurred on the 14th April. In a similar lowland study area in Aberdeenshire, Stoddart (1968) estimated first conception dates of 16th April 1966 and 15th April 1967. This compares with a first conception date of the 3rd April during the present study. Both Telfer (1996) and Stoddart (1968) concur with the results of the present study in concluding that the breeding season generally ends in August, with a latest conception date of 25th August being recorded at Mar Lodge.

Telfer (1996) estimated that, when first trapped, most juvenile animals were between 30 and 40 days of age. Mean litter size, calculated at the stage when animals first entered this trappable population, was 3.0 (se = 0.62, n = 7). Using the same criteria, a mean litter size of 2.08 was found in the present study (se = 0.32, n = 24). Comparing medians, these differences were not statistically significant (p>0.05, Mann-Whitney test).

Maturation rates were considered in terms of the proportion of females of the year with perforate vaginas. Young of the year were defined as those animals weighing less than 175g (overwintered animals weighed 175g or more). Combining data for all sites, the maturation rate for 2000 and 2001 was 52.2% (n = 23) and 22.2% (n = 9) respectively, or 43.2% for both years combined (n = 32). The observed difference in maturation rate between years was not statistically significant (χ^2 = 2.358, p>0.05). Depending on site, Telfer (1996) recorded female maturation rates of 13%, 17% and 50%.

Apparent survival rates, calculated using Programme MARK, for those sites with sufficient data are presented in Table 4.8.

Table 4.8	Apparent survival rates, calculated using Programme MARK, for those sites w				
	sufficient data. These survival rates reflect the effects of both mortality and				
	losses due to emigration. Pooled data for both overwintered and young of year				
	animals.				

SITE	MODEL SELECTED	STANDARD ERROR	SURVIVAL ESTIMATE	95% CONFIDENCE INTERVAL
Geldie A&E, April-October 2000	Φ (.)p(.)	0.121	0.42	0.21-0.66
Geldie H, June-September 2001	Φ (.)p(.)	0.411	0.69	0.05–0.99
Geldie Q, June-September 2001	Φ (.)p(.)	0.153	0.25	0.06-0.62

Telfer (1996) reviewed data for 7 sites in the UK and concluded that most summer monthly survival rates were greater than 0.7 (data for June-September, and pooled overwintered and young of year animals). She recorded a summer survival rate of 0.54 at her Nether Tulloch study site in 1995 and considered this to be lower than most summer populations previously studied.

For her lowland Aberdeenshire study sites, Telfer (2000) subsequently provided the following summer survival estimates (summer defined as period April-September):

- estimated monthly summer survival of overwintered animals: 0.69 (0.62–0.75 confidence interval)
- estimated monthly summer survival of young of year older than 2 months: 0.80 (0.67-0.88 confidence interval).

On this basis, the summer survival rates documented in the present study appear to be relatively low.

It would appear then that relative to other studies, water voles in the Geldie sub-catchment were not achieving their full reproductive potential over the period of study as a consequence of:

- reduced length of breeding season (2001)
- low fecundity in terms of:
 - fewer litters per reproductive female
 - smaller litter size
- low maturation rate (2001)
- low apparent survival rate

Why this should be is a matter for conjecture. For example, the reproductive potential of water voles living in upland habitats may be consistently lower than populations living in lowland situations. In the former areas food quantity and quality may be poorer and climatic conditions (eg the incidence and severity of flooding) more extreme. If this is the case, then limited fecundity is likely to restrict the potential of individual colonies to provide the source of colonising animals so vital for the maintenance of metapopulations. If relatively low fecundity and low survival rate is a regular feature of upland water voles it follows that the overall fragility of metapopulations in such environments is likely to be increased. Relative to lowland situations, isolation thresholds, beyond which metapopulations collapse, may be lower in such situations. That is, upland water vole populations may more sensitive and less able to withstand factors that decrease fecundity and/or survival.

Alternatively the relatively low measures of reproductive output obtained in the present study may be a normal manifestation of multi-annual population fluctuations. It is known for example that cyclic vole populations undergo changes in demographic traits depending on cycle stage. Thus, the length of the breeding season becomes successively shorter as the cycle progresses; litter production per reproductive female declines, as do maturation rates; and survival rates fluctuate (Löfgren 1995). Monitoring will be required to establish if the observed reproductive data are a reflection of multi-annual fluctuations or, alternatively, are a manifestation of a metapopulation in terminal decline.

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Figure 4.1 Map showing the locations of sites at which live trapping was undertaken.

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Figure 4.2 Water vole population estimates (red line) for each of the 11 sites trapped on Mar Lodge Estate. Where sample size is sufficient, 95% confidence intervals are shown (vertical lines). These intervals are indicative of the precision of the population estimate: we can be 95% certain that the true population size falls within the upper and lower 95% confidence intervals calculated from the samples of trapped animals. Where available, latrine counts are also shown (columns).





Figure 4.3 The length of breeding season recorded in years 2000 and 2001, as determined by the occurrence of perforate females and scrotal males in live-trapped animals. Relative to 2001, the breeding season in 2000 was both earlier and longer, perforate females being recorded from the 27th April over a period of 134 days and the first juveniles being trapped on 16th May. In contrast, in 2001 perforate females were recorded over a period of 65 days starting on the 13th June and the first juveniles were not trapped until the 17th July. Juvenile animals were defined as those weighing <80g at first capture.



APPENDIX 4

TRAP SITE	TRAPPING SESSION	DAYS TRAPPING	NUMBER OF TRAPS	TRAP HOURS
Bynack 9(a)	26/08/99-27/08/99	2	20	328.4
NN971841	28/09/99-01/10/99	3	20	319
Dupock 4	21/03/00-22/03/00	2	14-10	201.34
Bynack 4 NNI976853	30/09/99-01/10/99	2		90.96
1117700000	18/05/00-19/05/00	2	9	136.26
	15/06/00-16/06/00	2	9	134.73
Geldie A	24/04/00-28/04/00	4	15	451.75
NN976889	15/05/00-17/05/00	3	15	302.4
	12/06/00-14/06/00	3	13	301.99
		4	10-12	291.82
	04/09/00-08/09/00	3	14-17	290.99
	26/10/00-28/10/00	3	13–14	213.27
	24/04/01-	1	15	103.5
	14/05/01-18/05/01	5	9	314.64
		2	5	65.6
	14/08/01-17/08/01	Δ 2	6-7	170.97
	17/09/01-21/09/01	4	9–10	245.03
Geldie B	24/04/00-28/04/00	4	1	25.18
Coldio E	27/04/00 28/04/00		10	161.00
NN977893	15/05/00-17/05/00	2	17	347 31
	12/06/00-15/06/00	4	17	499.97
	10/07/00-13/07/00	4	17-20	508.09
	07/08/00-11/08/00	4	14	332.22
	04/09/00-08/09/00	3	12-14	222.78
	26/10/00-28/10/00	1	15	224.77
	14/05/01-18/05/01	5	9	293.76
	11/06/01-12/06/01	2	5	61.85
Geldie H	12/06/01-15/06/01	4	12	353.4
NN960871	16/07/01-19/07/01	4	10-12	304.82
		5	10-12	381.6
	22/10/01-25/10/01	3	10–11	115.5
Geldie I	16/05/00-17/05/00	2	8–13	152.95
NN953869	13/06/00-15/06/00	3	9–10	324.91
	12/07/00-27/07/00	5	5-10	255.5
	05/09/00-08/09/00	2	5	64.35
Geldie J	20/06/00-23/06/00	2		157.86
1010902072	07/08/00-08/08/00	2	6	61.2
Geldie L	03/07/00-07/07/00	4	10	258.8
NN956865	12/07/00-13/07/00	2	10-12	150.76
	25/07/00-27/07/00	3	4-5	105
	05/09/00-08/09/00	2	4	52.28
Geldie O NN985880	17/05/01-18/05/01 11/06/01-12/06/01	2	8 6	112.8 86.46
Geldie Q	13/06/01-15/06/01	3	9	198.54
NN958875	16/07/01-19/07/01	4	6-8	193.84
	13/08/01-17/08/01	5	7	208.53
	22/10/01-25/10/01	4	9	333.74 178.38
Geldie R	14/06/01-15/06/01	2	5	61.35
NN952875	16/07/01-19/07/01	4	4	103.36
	13/08/01-17/08/01	3	4	69.64
TOTAL		164		10818.66

Table 1Chronology and other details of water vole trapping sessions.

Table 2The raw data used in the assessment of fecundity parameters. Assumed litter-
mates indicated by subscript numbers.

Site	Date first trapped	Weight when first trapped	Trap No.	Estimated age from birth when first trapped	Birth date (conception date)	Sex & reproductive status (perforate, imperforate, scrotal, ascrotal)
Geldie A&E	14/06/00	801	1a (E)	c.35 days	c.10/05/00 c.(18/04/00)	F(I)
Geldie A&E	07/08/00	65 ₂	3a (A)	c.30 days	c.08/07/00 c.(16/06/00)	F (I)
Geldie A&E	13/06/00	851	4 (E)	c.35 days	c.09/05/00 c.(17/04/00)	M (S)
Geldie A&E	11/07/00	115 ₃	1 (E)	c.48 days	c.24/05/00 c.(02/05/00)	F (P)
Geldie A&E	13/06/00	1104	9 (A)	c.48 days	c.26/04/00 c.(04/04/00)	F (P)
Geldie A&E	08/08/00	110 ₆	1 (E)	c.48 days	c.21/06/00 c.(30/05/00)	M (S)
Geldie A&E	12/06/00	901	15 (E)	c.40 days	c.03/05/00 c.(11/04/00)	F (P)
Geldie A&E	12/06/00	1154	13 (A)	c.48 days	c.25/04/00 c.(03/04/00)	F (P)
Geldie A&E	16/05/00	307	1 (E)	c.19 days	c.27/04/00 c.(05/04/00)	M (A)
Geldie A&E	12/06/00	801	8 (E)	c.35 days	c.08/05/00 c.(16/04/00)	M (A)
Geldie A&E	13/06/00	1107	15 (E)	c.48 days	c.26/04/00 c.(04/04/00)	F (I)
Geldie A&E	28/10/00	100 ₈	8 (A)	c.42 days	c.16/09/00 c.(25/08/00)	F (I)
Geldie A&E	08/08/00	502	11 (A)	c.23 days	c.16/07/00 c.(24/06/00)	F (I)
Geldie A&E	08/08/00	502	3 (A)	c.23 days	c.16/07/00 c.(24/06/00)	F (I)
Geldie A&E	08/09/00	85 ₅	3a (A)	c.35 days	c.04/08/00 c.(13/07/00)	F (I)
Geldie A&E	08/09/00	50 ₅	6 (A)	c.23 days	c.16/08/00 c.(25/07/00)	M (A)
Geldie A&E	10/07/00	1053	1 (E)	c.47 days	c.24/05/00 c.(02/05/00)	M (A)
Geldie A&E	10/08/00	452	3 (A)	c.21 days	c.20/07/00 c.(28/06/00)	F (I)
Geldie A&E	10/08/00	452	4 (A)	c.21 days	c.20/07/00 c.(28/06/00)	F (I)

Table 2(continued)

Site	Date first trapped	Weight when first trapped	Trap No.	Estimated age from birth when first trapped	Birth date (conception date)	Sex & reproductive status (perforate, imperforate, scrotal, ascrotal)
Geldie I	27/07/00	110,9	4	c.48 days	c.09/06/00 c.(18/05/00)	F (I)
Geldie L	13/07/00	105 ₁₀	3	c.47 days	c.27/05/00 c.(05/05/00)	F (P)
Geldie J	20/06/00	40 ₁₁	8	c.20 days	c.31/05/00 c.(09/05/00)	M (A)
Geldie J	12/07/00	90 ₁₁	8	c.40 days	c.02/06/00 c.(11/05/00)	F (I)
Geldie J	23/06/00	55 ₁₁	10	c.24 days	c.30/05/00 c.(08/05/00)	M (A)
Geldie J	20/06/00	45 ₁₁	9	c.21 days	c.02/06/00 c.(11/05/00)	M (A)
Geldie J	12/07/00	35 ₁₂	7	c.19 days	c.23/06/00 c.(01/06/00)	F (I)
Geldie J	12/07/00	105 ₁₁	5	c.47 days	c.26/05/00 c.(04/05/00)	F (I)
Geldie Allt Dhaidh Beag	12/07/00	110 ₁₃	2	c.48 days	c.25/05/00 c.(03/05/00)	M (S)
Geldie Allt Dhaidh Beag	08/08/00	75 ₁₄	1	c.33 days	c.06/07/00 c.(14/06/00)	F (I)
Geldie Allt Dhaidh Beag	08/08/00	70 ₁₄	2	c.32 days	c.07/07/00 c.(15/06/00)	?
Geldie Allt Dhaidh Beag	04/09/00	115 ₁₅	2	c.48 days	c.18/07/00 c.(26/06/00)	F (P)
Geldie Allt Dhaidh Beag	10/08/00	70 ₁₄	2	c.32 days	c.09/07/00 c.(17/06/00)	F (I)
Geldie Allt Dhaidh Beag	08/09/00	85 ₁₆	4	c.35 days	c.04/08/00 c.(13/07/00)	F (I)
Bynack 9 (a)	27/08/99	65 ₁₇	13	c.30 days	c.28/07/99 c.(06/07/99)	F (I)
Bynack 9 (a)	01/10/99	115 ₁₈	14	c.48 days	c.14/08/99 c.(23/07/99)	F (I)
Geldie H	16/07/01	35 ₁₉	4	c.19 days	c.27/06/01 c.(05/06/01)	M (A)
Geldie H	18/07/01	35 ₁₉	4	c.19 days	c.29/06/01 c.(07/06/01)	M (A)
Geldie H	19/07/01	35 ₁₉	4	c.19 days	c.30/06/01 c.(08/06/01)	M (A)
Geldie H	19/07/01	35 ₁₉	6	c.19 days	c.30/06/01 c.(08/06/01)	M (A)

Table 2(continued)

Site	Date first trapped	Weight when first trapped	Trap No.	Estimated age from birth when first trapped	Birth date (conception date)	Sex & reproductive status (perforate, imperforate, scrotal, ascrotal)
Geldie H	17/09/01	100 ₂₀	6	c.46 days	c.02/08/01 c.(11/07/01)	M (A)
Geldie Q	16/08/01	80 ₂₁	6	c.35 days	c.12/07/01 c.(20/06/01)	M (A)
Geldie Q	17/08/01	55 ₂₂	6	c.24 days	c.24/07/01 c.(02/07/01)	M (A)
Geldie Q	19/09/01	100 ₂₃	10	c.46 days	c.04/08/01 c.(13/07/01)	M (A)
Geldie Q	18/09/01	100 ₂₃	10	c.46 days	c.03/08/01) c.(12/07/01)	F (I)
Geldie Q	18/09/01	85 ₂₃	6	c.35 days	c.14/08/01 c.(23/07/01)	F (I)
Geldie Q	21/09/01	105 ₂₃	9	c.47 days	c.05/08/01 c.(14/07/01)	F (I)
Geldie Q	17/09/01	95 ₂₃	9	c.43 days	c.05/08/01 c.(14/07/01)	F (I)
Geldie Q	18/09/01	90 ₂₃	7	c.40 days	c.09/08/01 c.(18/07/01)	F (I)
Allt an t-Seilich	20/09/01	105 ₂₄	1	c.47 days	c.04/08/01 c.(13/07/01)	F (I)
Allt an t-Seilich	21/09/01	10524	3	c.47 days	c.05/08/01 c.(14/07/01)	F (I)

5 ESTIMATING WATER VOLE POPULATION DENSITY FROM LATRINE COUNTS

5.1 Introduction

During the breeding season, water voles regularly defecate and scent mark at specific locations. The resulting accumulation of droppings, known as latrines, probably communicate information regarding range occupancy and individual home range extent (Stoddart 1970; Leuze 1976; Woodroffe *et al.* 1990).

A relationship between the number of latrines found and the number of voles trapped was originally described by Woodroffe *et al.* (1990), based on data collected in upland river systems in the North Yorkshire Moors National Park. The precise nature of the relationship was refined by Morris *et al.* (1998) following the discovery of typographical errors in the original publication.

Latrine counts thus provide a potentially useful indirect measure of water vole population size. However, the precise nature of the relationship may change between sites depending on factors such as population density, season, the availability of suitable latrine sites and variable habitat-related latrine detection rates.

Given these variables, it was considered prudent to establish the specific nature of the relationship between latrine numbers and water vole population density for an upland catchment in Scotland. The means by which this was achieved, together with an assessment of the potential value of latrine counts as indirect measures of population size, are the subject of this chapter.

5.2 Study area and methods

Data for the present study were collected from two of 10 live-trapping sites (Sites A&E) in the Geldie sub-catchment, a headwater tributary of the River Dee, located in the Cairngorm Mountains, Scotland (Figure 5.1). Sites A & E were trapped monthly during the period April-October 2000 and April-September 2001. Monthly trapping sessions were on average of 3 days duration and all trapped animals were individually marked. Full details of trapping and marking procedures will be found in Chapter 4. Although located on separate burns, some animals were shown to regularly move between sites A & E on a daily basis. In consequence this composite site was considered to constitute a single discrete colony. Site A&E was selected for study in view of the relative persistence of the colony (and thus continuous data sets) and the relatively high number of animals captured (larger sample size for the purpose of population modelling).

Programme CAPTURE (Otis *et al.* 1978) was used to provide monthly estimates of population size. Programme CAPTURE comprises 8 models, each of which incorporates different assumptions regarding capture probability. Tests of these assumptions provide the basis for the selection of the most appropriate model. Analysis of the live-trapping data for Site A&E dictated the selection of model M_{bh} since capture probability was clearly influenced by both behavioural and individual responses. See Chapter 4 for further details.

Latrine counts were made at the start of each monthly live-trapping session, or at the end if heavy rain and thus high water levels had occurred within the period 48 hours prior to the first day's trapping. A latrine was defined as an accumulation of two or more droppings deposited at a discrete location. In searching for latrines vegetation was parted such that both bank sides and burn bed were exposed.

Simple linear regression was used to examine the relationship between the response variable y (water voles/100m) and the predictor variable x (latrines/100m). Regression provides the line of best fit to data of this type and was used to:

- determine if a statistically significant relationship exists between vole density and latrine density;
- define the nature of such a relationship in quantitative terms; and using this equation, to
- predict water vole density for any given value of latrine density.

All data were analysed using *Minitab* (*Release 13*) Statistical Software.

5.3 Results

Data used in the simple linear regression are shown in Table 5.1.

Table 5.1Raw data from live-trapping Site A&E used to explore the relationship between
latrine density and water vole population density. Vole population estimates were
derived using programme CAPTURE. Data for May and June 2001 (*italicised*) were
omitted from the linear regression analysis as no voles were trapped.

Month	Extent of field signs (m)	Estimated number of voles	Voles/100m	Number of latrines	Latrines/100m
Apr 2000	770	4	0.52	29	3.77
May 2000	770	7	0.91	44	5.71
Jun 2000	770	13	1.69	43	5.58
Jul 2000	770	7	0.91	44	5.71
Aug 2000	770	13	1.69	50	6.49
Sep 2000	770	10	1.30	49	6.36
Oct 2000	770	5	0.65	12	1.56
Apr 2001	770	0	0	0	0
May 2001	770	0	0	14	1.82
Jun 2001	770	0	0	4	0.52
Jul 2001	770	0	0	0	0
Aug 2001	770	2	0.26	9	1.17
Sep 2001	770	2	0.26	5	0.65

The results of the linear regression are shown in Figure 5.2. The relationship between water vole density and latrine density is described by y = 0.055 + 0.0205x where y = number of voles per 100m (estimated using model M_{bh} of programme CAPTURE) and x = number of latrines per 100m. The regression was significant (t = 6.20, 20 df, p<0.01) ie there is a true linear relationship between these two variables.

5.4 Discussion

Previous mark-recapture studies have attempted to calibrate the relationship between numbers of water voles captured and latrine counts. The study areas used and resulting regression equations describing the relationship are summarised in Table 5.2.

Source	Study Area	Regression Equation
Morris <i>et al.</i> (1998)	North York Moors National Park (upland study site)	y = 1.48 + (0.683x), where $x =$ latrines counted per 100m and $y =$ water voles per 100m based on actual number of voles trapped.
Telfer 1996; Lambin <i>et al.</i> 1996	Ythan tributaries (inland lowland study sites) Aberdeenshire	y = 2.96 + (0.07x) where $x =$ latrines counted per km and $y =$ water voles per km based on actual number of voles trapped.
Telfer 1996; Lambin <i>et al.</i> 1996	Coastal burns flowing into sea north of Newburgh, northeast Scotland (lowland study sites)	y = -1.12 + (0.34x) where $x =$ latrines counted per km and $y =$ water voles per km based on actual numbers trapped.
Sharul 1998	Ythan tributaries & coastal burns flowing into sea north of Newburgh, northeast Scotland. High-density water vole population sites (lowland study areas)	y = (0.390x) + 21.41 where $y =$ water voles per km based on estimated vole populations using model M _{bh} of programme CAPTURE and $x =$ latrines counted per km.
Sharul 1998	Ythan tributaries & coastal burns flowing into sea north of Newburgh, northeast Scotland. Low-density water vole population sites (lowland study areas)	y = (0.2692x) + 1.848, where $y =$ voles per km based on estimated vole populations using model M _{bh} of programme CAPTURE and $x =$ latrines per km.

Table 5.2 Regression equations derived from previous studies that describe the relationship between water vole density and latrine density.

Using the equations given in Table 5.2 and the results of the present study it is possible to compare the estimates of water vole population density based on a hypothetical site in which latrine density is 3.77/100m and field signs extend over a distance of 500m. The results of this comparison are given in Table 5.3.

Table 5.3Estimates of water vole population density produced using 6 regression equations
describing the relationship between vole density and latrine density.
The relationships were derived from 6 different study areas. For the purposes of
comparison, latrine density was assumed to be 3.77/100m with field signs
extending over a distance of 500m in each case.

	Regression Equation					
	Present study	Morris <i>et al.</i> (1998)	Ythan equation. Telfer (1996); Lambin <i>et al.</i> (1996).	Coastal equation. Telfer (1996); Lambin <i>et al.</i> (1996)	High population equation, Sharul (1998)	Low population equation, Sharul (1998)
Voles/100m	4	20	3	6	18	6

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The data presented in Table 5.3 confirm that the specific form of the relationship between latrine and water vole density varies from study area to study area. The nature of the relationship could be affected by factors such as season, population density and population structure. For example, Woodroffe *et al.* (1990) showed that latrine production increased progressively from early spring to mid/late summer, declining thereafter. Sharul (1998) found that although latrine density and water vole density were positively related, the nature of this relationship was significantly different in high and low-density populations. Differences in habitat, and associated variation in the ability to detect latrines, could also influence the precise form of the relationship. Therefore, wherever latrine counts are to be used for the purpose of quantifying water vole density it would be wise to establish the precise form of the relationship afresh. For example, had the regression equation of Morris *et al.* (1998) been used to quantify water vole populations on Mar Lodge estate, densities would have been over-estimated by a factor of 5.

Estimates of water vole density calculated using the regression equation obtained in the present study are similar to those produced by the Ythan and Coastal equations of Lambin *et al.* (1996), and the low population equation of Sharul (1998) (see Table 5.2).

In order to assess just how good the estimates of water vole population density are using the above regression equations there is a need to quantify two sources of error in the estimates. Firstly, variation in the regression line itself has to be taken into account. This line is based on sample data and therefore subject to the same sort of sampling error that occurs in the estimation of a mean. This variation is addressed by attaching a 95% confidence zone around the regression line. The second source of error concerns the scatter of estimates about the regression line. This variation is addressed by defining a second, wider, 95% prediction zone about the regression line that encloses variation of an estimate made from a particular latrine count. Morris *et al.* (1998) did not provide any such measures of uncertainty and this limits the predictive value of the regression equation. The 95% confidence and prediction bands for the regression equation derived from the present study are shown in Figure 5.2.

For the regression equation derived from the present study some examples of predicted water vole densities and associated 95% prediction intervals are given in Table 5.4.

Table 5.4 Predicted water vole densities (voles/km) estimated from specific latrine counts, together with upper and lower prediction intervals for the estimates. Data derived from the regression equation describing the relationship between vole and latrine density obtained during the present study. For a count of 5 latrines/100m we can be 95% confident that corresponding vole densities will be between 4 and 18 voles per km.

Latrines/100m	Predicted water voles/km	Lower 95% Prediction Interval	Upper 95% Prediction Interval
3	7	0	13
4	9	2	15
5	11	4	18
6	13	6	20
7	15	8	22

Given the relatively large prediction intervals evident in Figure 5.2 and Table 5.4 it can be seen that latrine counts, when used to predict water vole densities, are relatively imprecise. This is likely to reflect:

- the less than perfect relationship between vole and latrine densities;
- measurement errors in assessing the numbers of voles and counting the number of latrines; and
- systematic bias caused by factors such as habitat and substrate variables between sites.

When used in this way, latrine counts will provide an estimate of population size for a specific area. However, for monitoring purposes, because of the imprecision of such estimates, these are likely to be relatively insensitive to the detection of statistically significant changes in population size over time. Taking this into account, monitoring would be best achieved by undertaking latrine counts in combination with assessments of percentage site occupancy. Latrine counts would provide an index of vole population abundance, while measures of site occupancy (eg percentage burns occupied) would permit changes in distribution to be monitored. Both parameters are easily measured and, taking into account water vole metapopulation dynamics, should be monitored at the catchment scale.

5.5 References

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Figure 5.1 Map showing the locations of the Geldie catchment and live-trapping site A&E where data on the relationship between water vole and latrine density were collected.



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Figure 5.2 Linear regression showing the relationship between water vole and latrine density. Data from Table 5.1. For a given latrine density we can be 95% confident that the population mean for vole density lies between the upper and lower confidence intervals. The prediction bands (PI) illustrate the range of likely values for new observations. Thus, for a given new observation of latrine density we can be 95% confident that the actual value for vole density lies between the upper and lower prediction intervals. The R-Sq value describes the amount of variation in the observed response values (water vole density) that is explained by the predictor (latrine density).



6 THE CONSERVATION OF UPLAND WATER VOLE POPULATIONS: CONSIDERATIONS AND RECOMMENDATIONS

6.1 Introduction

Although formerly common and widespread, the British water vole population has undergone a long-term decline during the 20th century. The Vincent Wildlife Trust (VWT) has undertaken two national surveys in 1989–1990 and 1996–1998. The first survey (Strachan & Jefferies 1993) showed that since 1900 a minimum of 68% of occupied sites had been lost. By 1996–1998 this loss had increased to 89% and is considered to have been "one of the most rapid and serious declines of any British wild mammal resulting from 20th century change" (Strachan *et al.* 2000).

A number of probably interacting factors are implicated in the decline of the water vole, including habitat loss and fragmentation, agricultural intensification, water pollution and, more recently, predation by introduced American mink *Mustela vison* (Strachan & Jefferies 1993). Scottish water vole populations have not been immune to decline, with the estimated population on Mainland Scotland having decreased from over 2 million in 1989–1990 to a mere 354,000 in 1996–1998. Nevertheless, this latter figure is believed to comprise c.40% of the British population (Table 2 of Strachan *et al.* 2000).

In this context the populations of water voles that frequent the upland habitats of Scotland are a key resource. It is appropriate therefore, to consider how best these populations should be managed if the uplands are to continue to function as a refuge for a species that is hovering on the verge of extinction. The purpose of this chapter is to explore conservation options based on existing knowledge of water vole ecology in the uplands.

6.2 Considerations

Populations of water voles in the uplands appear to function as metapopulations ie they comprise clusters of discrete smaller sub-populations with frequent dispersal amongst them (Harrison 1994; Aars *et al.* 2001). Although individual sub-populations may go extinct (through risks associated with small population size) they are subsequently replaced by colonisation from other sub-populations. While population turnover at the sub-population level can therefore be considerable, the overall population may remain relatively stable. An appropriate analogy is a constellation of twinkling stars: although the brightness of individual stars fluctuates, the form of the constellation remains visible as different stars temporarily dim and brighten.

The metapopulation structure appears to be a fundamental feature of water voles in the uplands of Scotland (Aars *et al.* 2001), Yorkshire (Lawton & Woodroffe, 1991) and lowland farmland in north-east Scotland (Telfer *et al.* 2001). The fragmented structure does not necessarily result from the erosion of a formerly continuous population as a consequence of habitat loss or predation by mink. For example, water vole distribution in the Assynt area of northwest Sutherland conforms to the metapopulation model, despite being beyond the present known range of mink (Aars *et al.* 2001). Similarly, in the present study the Geldie catchment also exhibits the characteristics of a metapopulation, despite the absence of mink. In these cases the metapopulation structure is a reflection of specific habitat preference and the naturally fragmented and patchy distribution of such habitat (see Chapter 2).

Fahrig & Merriam (1994) identified four characteristics of landscape spatial structure of importance for the survival of regional metapopulations:

- size, shape and quality of habitat patches;
- presence of dispersal routes;
- quality of dispersal routes;
- spatial configuration of component patches.

All but habitat patch shape is likely to be of importance for the conservation of water vole populations.

Telfer (2000) and Telfer *et al.* (2001) showed that local population persistence is predominantly influenced by population size, with large populations being more resistant to adverse stochastic demographic and environmental change. In addition, recolonisation rates are influenced by the degree of isolation from other colonies and habitat quality. Dispersing voles are more likely to colonise/recolonise sites that are closer in geographical space and, given the same level of isolation, are more likely to occupy relatively good habitat. Good quality habitats are likely to confer enhanced fecundity and survival and in consequence will provide a source of dispersing animals for the potential colonisation or recolonisation of sites with low survival rates (due for example to poor habitat quality or predation).

These "good" and "poor" sites can be thought of as "source" and "sink" populations respectively (Pulliam 1988). The spatial configuration of source and sink populations could be important for the persistence of a metapopulation. For example, the loss of key source populations or increasing isolation between colonies such that dispersal processes are effectively disrupted, could lead to the eventual loss of regional metapopulations if an isolation threshold is exceeded.

Current evidence suggests, at least for lowland areas, that water voles are able to recolonise sites within a 1–2km radius of source populations. Dispersal is fundamental to the functioning of regional populations of water voles; therefore the quality of dispersal routes is likely to be of importance. There is some evidence that when dispersing, water voles may not necessarily follow watercourses but are capable of travelling overland (Telfer 2000; Telfer *et al.* 2001). While most water voles appear to disperse only a short distance, exceptional movements in excess of 8km have been recorded (Lambin, *pers. comm., Aars et al.* 2001).

The fact that the fate of constituent colonies appears to be independent is conducive to metapopulation persistence. Under such conditions local colony extinctions are not spatially correlated and, overall, extinction rates and colonisation rates balance such that the metapopulation is maintained.

This stability can be disrupted in one of two ways. The arrival of mink in a metapopulation can be catastrophic. By systematically predating adjacent water vole colonies, spatially correlated extinctions can occur. Under these circumstances recolonisation becomes less likely as the availability of source populations in close proximity declines. Thus, the Bynack sub-catchment was colonised by mink in 1999 and resulted in the extinction of 11 adjacent colonies over a very short period (Aars *et al.* 2001, and this study). Water vole populations in this sub-catchment have still not recovered, despite the fact that mink are no longer present.

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Natural synchronous fluctuations in water vole numbers at a regional scale over a period of years can also disrupt metapopulation stability. Thus, in the Grampian mountains, within which the current studies were undertaken, colony extinction rates have exceeded colonisation rates since 1998, and the metapopulation is in decline. In contrast, in the Assynt area in northwest Scotland over the same period colonisation rates have exceeded extinction rates and the metapopulation is increasing (Aars *et al.* 2001 and this study). The key point here is that what appear to be natural processes can clearly reduce the density of water vole colonies to very low levels.

Current predictions of likely global warming effects on the climate suggests that precipitation in Scotland could increase by 8% by 2050 (Hill *et al.* 1999). There is also some evidence that flood frequencies may already have increased in Scottish rivers (Black & Burns 2002) although distinguishing genuine trends from stochastic variation is difficult (Gibbins, *pers. comm.*) Although adapted to riparian habitats and able to withstand occasional moderate flooding, increasing flood frequency and severity could conceivably cause spatially correlated losses of clusters of water vole colonies under some circumstances. Burns within the Bynack and Geldie catchments used in the present study are "flashy" in character ie burn levels can rise extraordinarily quickly, transforming slow flowing burns into raging torrents within minutes. Burrow systems are quickly flooded and in the context of upland habitats it is difficult to comprehend where the voles take refuge at such times and in situations where suitable burrowing habitat above the water table is scarce.

Although some tagged voles were subsequently retrapped in the same sites following such flood events in the Geldie catchment, sample size is too small to permit analysis of the effects of flooding on recapture rates. One tagged and apparently healthy animal was found dead on the surface amongst flood debris following a flood in the Bynack catchment. The role of flooding in water vole metapopulation dynamics is thus unclear but its is conceivable that if flood frequency and intensity increase the persistence of at least some water vole metapopulations could be threatened.

6.3 Recommendations

In attempting to conserve populations of water voles in upland habitats it is important to know where best to direct scarce resources. On a country scale there is a need to identify, by means of surveys, where water voles occur in the uplands. That is, there is a requirement for a basic inventory of sites. Within areas of potentially suitable habitat and in the absence of mink, negative or poor survey results should be treated with caution. In such areas the paucity of signs may reflect multi-annual fluctuations in water vole numbers. Such areas should not therefore be discounted but should be resurveyed after say a three-year interval (we currently have little idea regarding the period of multi-annual fluctuations, this figure being based on information from the Grampian and Assynt areas (Aars *et al.* 2001).

At a more local level there is a need to decide if conservation effort should be focussed on individual core colonies or at the larger regional metapopulation scale. Core colonies are likely to be relatively large and to occupy optimum water vole habitat. Their large size confers a degree of stability in terms of resistance to stochastic demographic and environmental change. In consequence such colonies can produce relatively large numbers of dispersing animals that "rescue" smaller adjacent declining colonies, or recolonise those which have undergone local extinction. However, within the Geldie/Bynack sub-catchments, and possibly many other upland catchments, the small size of the colonies is unlikely to confer immunity to local extinction due to stochastic changes in demographic or environmental parameters. In the present study, colonies

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comprised a mean of 4.6 animals (range 1–15). Therefore, core populations, as defined above, probably don't exist. Aars et al (2001) draw similar conclusions based on their wider studies in upland areas in northeast and northwest Scotland. The largest colony known to them was estimated to contain only 12 breeding females.

Most colonies therefore are likely to have a limited persistence, even in the absence of mink. Telfer *et al.* (2001) recorded population turnover rates of 25% per year even before mink invaded her study area in northeast Scotland. In consequence, the protection of individual colonies is likely to be ineffective. *It follows that in the absence of obvious core colonies, conservation effort should be directed at extensive catchment or multi-catchment scale areas. At any one time such extensive areas will contain suitable but unoccupied water vole habitat. It is essential that such areas be protected, as their loss may threaten the persistence of the metapopulation. It is also essential that conservation areas include a sufficiently large number of colonies to buffer the high rates of colony turnover.*

Within such conservation areas it will be necessary to maintain colony density above an isolation threshold for metapopulation persistence. The probability that a site will be reached by dispersers declines exponentially with distance from the source colony ie most voles move relatively short distances from the natal colony, with a steeply decreasing proportion undertaking longer movements (Telfer 2000). In a lowland study area in northeast Scotland Telfer *et al.* (2001) found that the mean overland distance between occupied colonies ranged from 0.62–0.70km and that no site further than 1.1km overland from its nearest neighbour was recolonised. Within their study area in Assynt, northwest Scotland, Aars *et al.* (2001) measured median overland distances between occupied colonies of between 0.2 and 1.6km. This area is devoid of mink and the figures are therefore indicative of the levels of isolation found in pristine water vole metapopulations. Collectively the studies cited above provide a crude indication of the point at which an isolation threshold may apply, and beyond which metapopulation decline may occur. *Based on existing information, conservation management should endeavour to achieve mean levels of colony isolation not exceeding c.1.5km, ie on average, adjacent occupied colonies should be within a 1.5km radius of one another.*

Within the Bynack/Allt an t-Seilich sub-catchment on Mar Lodge Estate, the arrival of mink in 1999 led to the extinction of 11 adjacent colonies over a period of less than 4 months (Aars *et al.* 2001). Sources of colonising animals were thus lost simultaneously ie colony extinctions were spatially correlated. The persistence of metapopulations depends on the fate of constituent colonies being independent, with no spatial correlation between extinction events. Sources of potential dispersing animals were thus lost from a wide area and the distance between adjacent occupied colonies increased. As of summer 2002 recolonisation had still not occurred, despite the fact that no further signs of mink have been found since May 2000.

Failure to recolonise could reflect the influence of two factors. A critical isolation threshold for metapopulation persistence could have been exceeded such that dispersal and colonisation are impeded. In addition, the whole of the Geldie/Bynack catchment appears to be undergoing a spatially correlated decline in water vole colony occupancy, perhaps reflecting a regionally synchronised multi-annual fluctuation (Aars *et al.* 2001). If the population in the Bynack/Allt an t-Seilich catchment fails to recover within the next two years, and there is no evidence for the presence of mink, then it is reasonable to assume that an isolation threshold has been exceeded. *Under these circumstances consideration should be given to the "seeding" of captive bred animals at a number of sites within the catchment with a view to establishing colonies as sources of dispersers, reducing inter-colony distance and rejuvenating metapopulation establishment and persistence.*

Mink are highly mobile generalist predators, and are likely to recolonise areas from which they have previously been removed (Dunstone 1993). They tend to systematically exploit adjacent water vole colonies, resulting in spatially correlated extinctions. As a consequence sites from which water vole colonies are lost become isolated from sources of colonists, delaying or preventing recolonisation even after mink have disappeared. *Constant vigilance will be required to prevent mink colonisation of upland sub-catchments.* This could be achieved by targeted and co-ordinated trapping effort concentrated at critical times and at critical sites eg during the months of January to April inclusive at the mouths of upland sub-catchments. With respect to the upper Dee catchment potential mink trapping locations are shown in Figure 6.1. These sites have been selected with a view to intercepting the upstream movement of dispersing mink into sub-catchments known to be of importance for water voles. A co-ordinated system for monitoring trapping effort, trapping results and mink distribution will also be required.

Rabbits may be a key alternative food resource for mink. In addition, female mink use rabbit warrens as breeding dens. Rabbits may therefore encourage the spread and establishment of mink by providing potential breeding sites and facilitating permanent rather than transitory colonisation. Rabbits do occur in upland habitats. For example, they were occasionally seen from the track between Linn of Dee and White Bridge on Mar Lodge Estate during the three years of the present study. On the same estate rabbits have also previously been recorded near the mouth of the Geldie Burn (in the vicinity of the abandoned dwelling at NO003869) and Bynack Lodge near the mouth of the Bynack Burn at NO000855 (personal communication with stalking staff, Mar Lodge). *Given their possible pivotal role in facilitating permanent colonisation by mink, every effort should be made to prevent the spread of rabbits into upland subcatchments where mink colonisation is considered possible, and where rabbits are already established, colonies should be destroyed, subject to there being no other overriding conservation concerns.*

Given the same degree of isolation, areas of better quality habitat are more likely to be colonised by dispersing voles. These colonies are also likely to be more productive in terms of fecundity and survival. *It follows therefore that such areas should be protected and where possible enhanced.* Good quality water vole habitat comprises sedge-rich habitat mosaics, including grasses, rushes and ericaceous vegetation adjacent to slow flowing, shallow burns with moderate bank angles and penetrable substrate. In terms of vegetation composition these riparian habitats are precisely those likely to be favoured by grazing deer and sheep and are in consequence potentially vulnerable to both excessive grazing and poaching (Figure 6.2). *Other than in exceptional circumstances, fencing to exclude grazing in upland habitats is unlikely to be a realistic approach to the protection of water vole habitat. It would be better to adopt a more holistic approach to range management by reducing grazing levels at a catchment or multi-catchment scale, through stock reduction where necessary. Other than in highly localised situations, there was little evidence of excessive grazing and poaching in relation to water vole habitat within the Geldie and Bynack sub-catchments on Mar Lodge Estate.*

The retention of open riparian corridors through new woodland plantations, or the creation of such corridors where plantation woodland already exists, would benefit water voles, in terms of the creation of potential breeding habitat and/or the provision of corridors for dispersal. Where they include areas of suitable water vole habitat new native woodland schemes will need to make provision for suitable riparian corridors as an integral part of their design. In addition, known water vole colonies or potentially suitable habitat should not be subjected to muirburn.

Other than global action to counter the effects of climate change it is difficult to see how specific measures could be taken to reduce the presumed adverse effects of flash flooding, the occurrence of which may increase. *In certain areas, and subject to no overriding conservation constraints, it may be possible to create habitat refuges away from regularly flooding burns.* For example, in otherwise uniform areas of open hill, pool systems could be excavated, and sedges, rushes and grasses encouraged to colonise. In addition, such refuges could act as ecological stepping-stones, enhancing overland dispersal at a time when it is assumed that voles are particularly vulnerable to predation. Further, in reducing colony isolation these refuge sites could conceivably enhance metapopulation persistence.

Within the Geldie/Bynack sub-catchments annual latrine surveys should continue in order to monitor changes in the distribution and population of water voles. Data already exist for the years 1998–2002 and the collection of further data will identify whether the observed decline is merely a reflection of multi-annual fluctuations or is the consequence of a mink-induced isolation threshold having been exceeded, leading to metapopulation collapse. *Simultaneously, signs of mink invasion should also be monitored.*

6.4 References

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Addendum - flow regimes and water quality

From the outset of the studies at Mar Lodge the need for more data on flow regimes and water quality was recognised. To this end discussions were undertaken with Roger Owen, Mike Davidson and Drew Aitkin of the Scottish Environment Protection Agency (SEPA), and with Chris Gibbins of the University of Aberdeen Geography Department. The main points arising from these discussions are summarized below.

- no monitoring of organophospates/heavy metal loads takes place on the Upper Dee.
- acidification data is available for sites downstream of the Linn of Dee.
- there is a continuous flow monitoring station at Mar Lodge.
- a computer model (Micro-Low-Flow) has been developed by SEPA to predict flow regimes based on physical parameters of specific watercourses. However, the model appears to be unreliable in its predictive ability and is therefore unlikely to be useful for desk-based assessments of the potential of specific burns to support water voles.
- while flow data are available for the Mar Lodge monitoring station the interpretation of such data is a specialist field. In addition, what happens at this monitoring station may bear little resemblance to flow regimes on individual burns higher up the catchment.

Predation

Other than mink, the only other potential mammalian predators seen in the study area were stoat *Mustela erminea*, weasel *Mustela nivalis*, otter *Lutra lutra* and fox *Vulpes vulpes*. A total of 39 otter spraints, 4 stoat/weasel droppings and 12 mink droppings were collected and sent to Dr Xavier Lambin at the University of Aberdeen for analysis. No results are available at the time of writing, but a previous study (Easter 2001) concluded that:

- water vole occurred with a frequency of occurrence of 64% in a sample of 17 mink scats from northeast Scotland, 11 of which were obtained on Mar Lodge from the Allt an t-Seilich and Bynack catchments in a three year period up to 2001;
- four otter spraints were analysed, two from north-east and two from north-west Scotland. All four spraints contained water vole;
- five fox scats were analysed, all from north-west Scotland. None contained water vole.

The above study did not analyse stoat/weasel scats. Weasels were caught in water vole live traps on two occasions in the present study. Given the above, it would seem highly likely that otters, stoats and weasels will also predate water voles at Mar Lodge and other upland areas. Foxes are considered less likely to be significant predators: unlike otters they cannot pursue prey in water; and unlike stoats and weasels they cannot penetrate water vole burrows. Water voles dispersing overland may however be vulnerable to fox predation. Unlike mink, all these mammalian predators are native and it would be surprising if, in view of what must be a long evolutionary association, water vole populations could not tolerate predation from these indigenous sources in the absence of mink.

Golden eagle and grey heron were the only avian predators seen at Mar Lodge potentially capable of predating water voles, although no predation attempts were witnessed.

Figure 6.1 Map of the upper Dee catchment showing the approximate locations (kite symbols) of potential mink trapping sites (precise positions will depend on physical and logistical constraints). Traps located at these sites are intended to intercept and prevent mink dispersing upstream into sub-catchments known to support water vole colonies. Trapping sites (left to right) are: junction of Geldie and Bynack burns; White Bridge; Lui-Dee junction; Ey-Dee junction; Dubh Ghleann-Dee junction; Clunie-Dee junction.



Figure 6.2 Heavy grazing and poaching of riparian habitat, as here, results in the loss of otherwise suitable water vole habitat. Cover is reduced, potential food plants removed and burrow systems destroyed.

