

Report on the work carried out on Skomer voles between 2001 - 2013

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1.1 Introduction

The Skomer vole (*Myodes glareolus skomerensis*) is a distinct island race that has recently evolved after probably accidental introduction to the island (Corbet 1964, Hare 2009). Despite being geographically isolated from the mainland it is not genetically isolated and is able to interbreed with the bank vole producing fertile hybrids (cited in Fullagar *et al.* 1962). It is larger than the mainland bank vole (*Myodes glareolus*), has a distinct pelage and the shape of the nasal passages are unique (Corbet 1964).

Skomer voles have a shorter breeding season generally lasting from May to September and voles born early in the season may reach sexual maturity in the same year (Coutts and Rowland 1969). Bank voles usually start breeding in April and continue through to October but in some years may continue over the winter depending on the abundance of the seed crop. Higher population densities have been recorded on Skomer that may be up to four times higher than the UK mainland populations (Healing 1984) and these are much higher than would be predicted by geographic range (Blackburn *et al.* 1997). In the UK, *M. glareolus* generally exhibit an annual cycle of abundance (Alibhai and Gipps 1985, Gipps *et al.* 1985) with a spring decline and then increasing numbers over the summer and autumn. Skomer populations also appear to exhibit an annual cycle with minimum densities occurring in late spring prior to breeding and increase during the summer and autumn but also exhibit irregular year to year fluctuations in peak densities (Healing 1984). The dynamics of Skomer populations are unclear and there appear to be irregular fluctuations in peak populations but as yet there are no long-term data to establish the population dynamics. Skomer has no ground predators and avian predators, which include barn owls, short-eared owls, kestrels pose the main predation risk. On the mainland mammalian predators such as weasels, cats and foxes may also be important in local population dynamics. On Skomer, voles are most numerous in areas that provide good cover such as bracken (*Pteridium aquilinum*) and brambles (*Rubus fruticosus*). However, the habitat extends below the surface and includes use of the numerous rabbit and Manx Shearwater burrows but interactions with

these species are unclear. Mainland bank voles are able to utilise a number of habitats including mixed woodland, hedgerows and grasslands.

The higher population densities found on Skomer have implications for social organisation with respect to spacing behaviour. Wolff (1997) proposed that females have evolved territoriality in response to resource competition by other females for safe breeding space and that pup defence is key to breeding females exhibiting territorial behaviour. This will limit space, which will influence density and dispersal. However, the degree of relatedness or possibly familiarity may also mediate space sharing among females (Bekoff 1981). Wolff (1997) also proposed that dispersal should be density independent in non-territorial species but inversely density dependent in territorial species limiting its potential to regulate at high density. Reproductive suppression also has the potential to regulate population growth by limiting the number of breeding females. Wolff (1993) suggested this could be adaptive under two conditions of threat of infanticide or to prevent inbreeding. Higher densities would predict a higher rate of breeding suppression, which in turn will affect space utilisation and dispersal dynamics. As densities increase, breeding space declines which may decrease dispersal of young animals. The cost of emigration may be prohibitive at this time due to social fence effects with aggressive males and territorial females thus reducing dispersal rates (Hestbeck 1982). Reduction in dispersal rates will increase density thus acting in an inverse density dependent way.

Ostfeld (1985, 1990) suggests that availability of food resources will dictate social organisation. If resources are limited either temporally or spatially and are slowly renewed then breeding females should defend resources to ensure successful reproduction, which will lead to territoriality. If resources are abundant and quickly renewed, then a non-territorial social organisation would be expected. Both the Skomer vole and bank vole are herbivorous. Skomer voles feed on bracken, bluebells (*Endymion non-scriptus*), ground ivy (*Glechoma hederacea*) and other vegetation, whilst bank voles feed on hard and soft mast, fungi, moss leaves and herbs. During the breeding season forage is abundant which would predict a non-territorial social organisation. However, plant

secondary compounds may influence the quality of forage and may also be an important factor in inhibiting reproduction (Berger *et al.* 1977).

If females are defending pups against resource competition infanticide, they would be expected to be territorial unless related or familiar. Alternatively, if food is abundant and quickly renewed, this would predict non-territoriality social organisation among breeding females. Trap revealed home ranges indicate a degree of overlap among males and females (Healing 1984) but the social organisation remains unclear.

The current work has focused on monitoring population dynamics and demography of Skomer voles and has investigated the social organisation and associated changes through the breeding season of female Skomer voles using intensive trapping and radiotracking.

2.1 Methods

The study grid was situated in an area approximately 300 m. south of North Pond (GR094724). Dominant vegetation consisted of bluebells, bracken, grass and wood sage and was situated in a medium density habitat (Healing 1984). The study grid was 32 x 32 m. with an inter-trap station distance of 4 m. and a single trap at each point (81 traps in total). Traps were not a permanent feature of the environment and were removed between each trapping session. Each trapping period consisted of 5 days with two trap checks per day. They were baited with whole oats and contained non-absorbent cotton wool bedding. Each animal was individually marked using ear tags in both ears (Le Boulenge-Nguyen and Boulenge 1986). For each capture the following data were recorded: tag number, trap station, weight, sex, and breeding condition. Density estimation included a boundary strip of 4 m. around the study grid and used Minimum Number Alive.

Trapping and radiotracking were carried out for one week during May, July and August/September in 2001, 2003 and 2004. Radiocollars (Biotrack Ltd, Wareham, Dorset) weighed approximately 2.5 g and had a battery life of approximately 14 days. Collars may interfere with movement and behaviour (Ostfeld, 1986; Varty, 1987, White & Garrett ,1990; Mendonça, 1999 and references therein). It was not possible to use dummy collars (see Loughran 1999) to offset these effects and the collars had the potential to influence movement. The weight of the collar may also have energetic considerations and the general rule is that collars should not exceed 10 % of body mass (White & Garrett, 1990) but see Berteaux *et al.* (1996). This did not present any problems in selecting subjects with most breeding males and females attaining weights greater than 25 g. The application of collars did not cause any serious wounds or injury. From 2004 onwards, trapping was carried out 2 to 3 times a year in the spring (April/May), summer (July/August) and autumn (September).

In spring trappability was low and voles were radiotracked over a period a longer period of 6 to 7 days. In the middle to late summer it was possible to track two waves of voles for approximately three days, collars being removed from the first subjects and applied to the next. Fixes were recorded at minimum time intervals of 30 minutes (discontinuously), with a minimum of 30 fixes being recorded

for each animal (Kenward & Hodder 1995) with a maximum of seven animals being tracked at anyone time.

The position of an animal may not be independent of its previous location, i.e. fixes may be autocorrelated, which may underestimate range size. White & Garrett (1990) describes a general rule of thumb to determine statistical independence of observations and considers locations to be independent if enough time has elapsed for the animal to move from one end of its range to the other. Rooney *et al.* (1998) suggest that as short a time interval as possible between fixes should be used over an extended period of time for best estimation of range size. Fixes were taken at minimum time intervals of 30 minutes during the day, (between 06.30 – 19.30) (no tracking was carried out at night) and would satisfy both the above criteria. Each animal was located to an area 4 m² using paths between trap points and its location recorded as the centre of this square.

Range areas were calculated using two methods. Kernel and Minimum Convex Polygon (MCP) analyses were carried out for each animal using the ranges V program (Kenward and Hodder, 1995). Kernel analyses were calculated using fix density and a 40 x 40 grid with a smoothing factor of 1 because this gave the most accurate picture of the fix data (Worton, 1989). In this study core area is defined as the proportion of the home range, which is most heavily utilised, determined from utilisation distributions. Core areas were estimated from distributions being considered to represent the peripheral areas of the ranges, which generally fell between 75% and 85% of the total range areas.

3.1 Results

3.2 Population Process

The overwinter survival of the marked population varied from 0% to 30% but was difficult to estimate accurately as trappability was reduced due to poor cover early in the season. Generally, overwinter survival was greater for females than males but numbers were low.

In 2001 the overwinter survival of the marked population was 30% (males 28%, females 42%) all of which had been born in the previous year and tagged as juveniles or sub-adults. Breeding commenced in May and was asynchronous with 2 of 14 females recorded as pregnant. The population increased over the summer (Figure 1). The proportion of adult males remained the same during May and July but there was a 50% change in composition. The number of adult males continued to increase in August but the composition again changed with only 40% of the males present in July being trapped at this time. Female residency on the study area was more stable during May and July but only 43% of females captured in July were recorded in August although it was not possible to distinguish mortality from emigration.

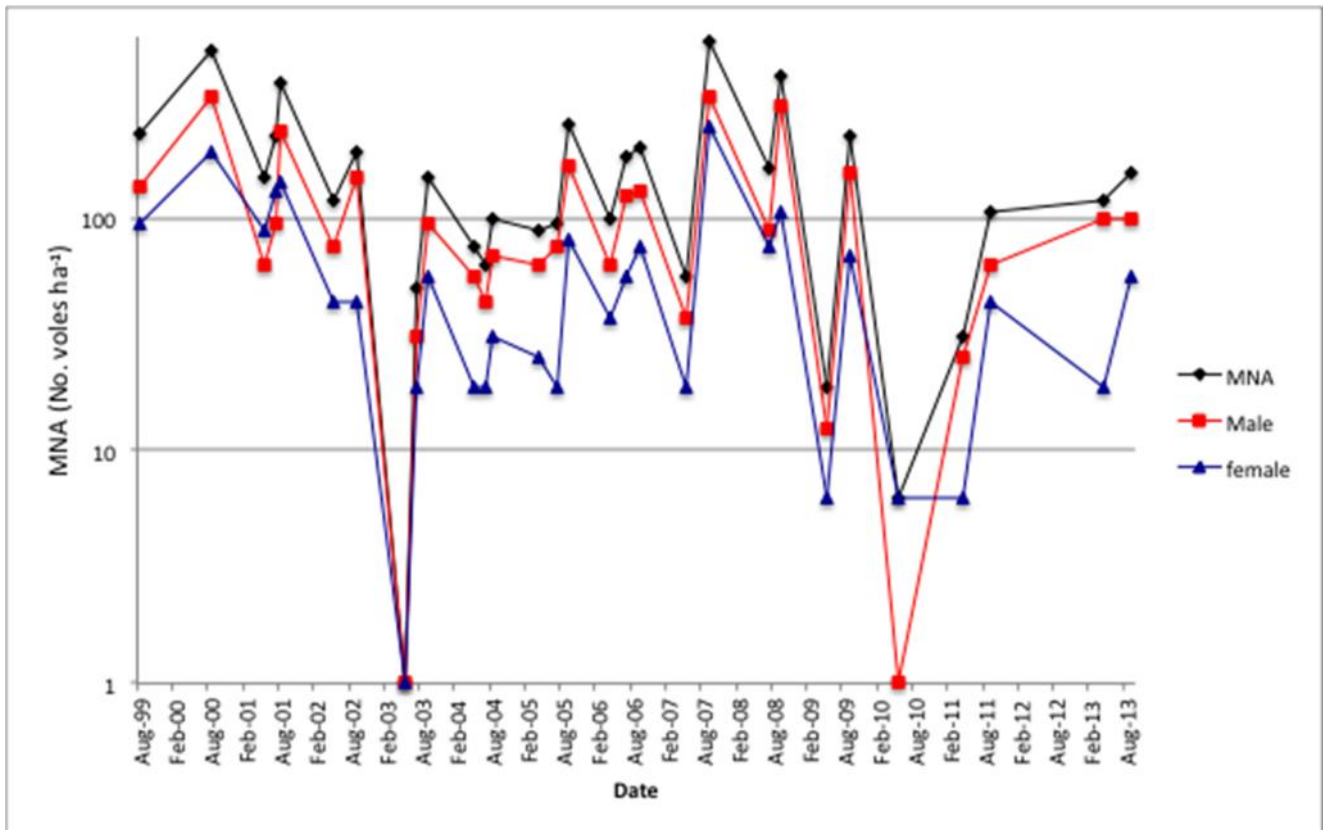
In 2002, the population declined over the winter and early spring by 69% to 19 voles (MNA 119 ha⁻¹) and the overwinter survival of the marked population was 10% (males 10.5%, females 8.7%). Onset of breeding in May was again asynchronous with 2 of 7 females being recorded as pregnant (Figure 5). In September 2002 the population had increased to 31 voles (MNA 194 ha⁻¹). From September 2002 to May 2003 the population declined to zero on the study area. There was some immigration of adults in July 2003 but no captures of previously marked voles. The population increased by September and all females were breeding being pregnant and/or lactating. The reasons for the crash in vole numbers in 2003 are unclear but the population had been declining from a peak in 2001. During the breeding season of 2003 predation may have been higher with 3 pairs of short-eared owls (*Asio flammeus*) and at least two pairs of little owls (*Athene noctua*), of which one pair had nested within 100 m of the study area.

The population declined over the winter and early spring by 50% to 12 voles with only 3 voles (2 males and a female) being recaptured from the previous year (overwinter survival of 12.5% of the marked population). There was a slight decline in the population in July 2004 that was due to a reduction in adult males with numbers of females remaining stable. The number of breeding females was low in May at three adults, all of which were pregnant but only one of these was recaptured in July. There was little recruitment to the population with one sub-adult male being recorded by July. In August the number of adult females had increased to five but only one was breeding; the remainder appeared to be young adults that had probably been born earlier in the year. There was again little recruitment with only one juvenile and three sub-adult males being recorded in August. A number of factors are likely to have contributed to the low numbers observed in 2004. The growth of bracken (*Pteridium aquilinum*) was poor which reduced field cover and increased vulnerability to predation. Owl predation was probably high with a breeding pair of barn owls (*Tyto alba*) nesting at the farm.

In 2005, there was a slight decline over the winter with overwinter survival for marked population rates of 18% for males and 20% for females. The population increased over the breeding season and was recorded at 250 voles ha⁻¹ (MNA). The population declined overwinter with survival rates of 15% male and 30% female for marked population in April 2006. The population increased to 200 voles ha⁻¹ by September and then declined by 75% over the winter of 2007 with no marked animals being recaptured. Pregnancies were observed early in 2007 with reproduction occurring in April and may have contributed to high population numbers recorded in this year (575 voles ha⁻¹). In the following year the September population density was again high reaching 406 voles ha⁻¹ but thereafter lower densities between 106 – 225 voles ha⁻¹ were recorded in autumn. No monitoring was carried out in 2012. There is a five-fold variation in peak population densities over the late summer and autumn but no consistent pattern in population fluctuations. There are occasional years when spring population numbers are very low but autumn densities are in the lower range. There are likely to be a number of factors operating that may influence population numbers that include field cover that is likely to influence predation rates. Other factors such as disease may account for mortality but are unknown

factors. Food quantity and quality may also play a significant role in population dynamics, during the breeding season bluebells provide the first flush of protein that is supplemented by bracken, ground ivy and other vegetation. However, dietary composition and availability of forage is poorly understood over the winter period and has the potential to influence mortality rates.

Figure 1 Density estimates based on MNA that include a boundary strip of 4 m.



3.3 Sex Ratios

The operational sex ratio was only female biased in 2001 and in subsequent years the operational sex ratio was male biased apart from July 08 when there was a slight female bias (Figures 2 & 3). The operational sex ratio generally ‘hovered’ around the 2 :1 mark but on occasions was recorded higher early in the breeding season when the numbers of breeding adults was low. The sex ratio was predominately male biased with a short period early in the study when a female bias was recorded until July 2001. There was no consistent pattern in both operational sex ratios and sex ratios between

years apart from a predominant male bias with ratio both increasing and decreasing over the breeding season.

Figure 2 Sex ratio and operational sex ratio of Skomer voles

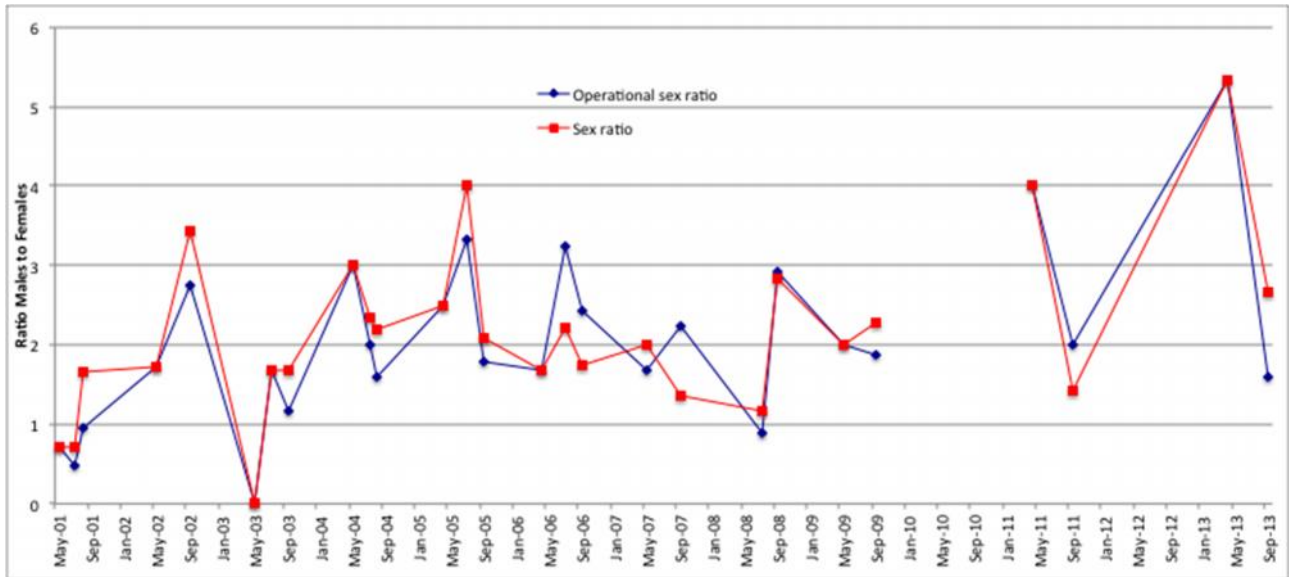
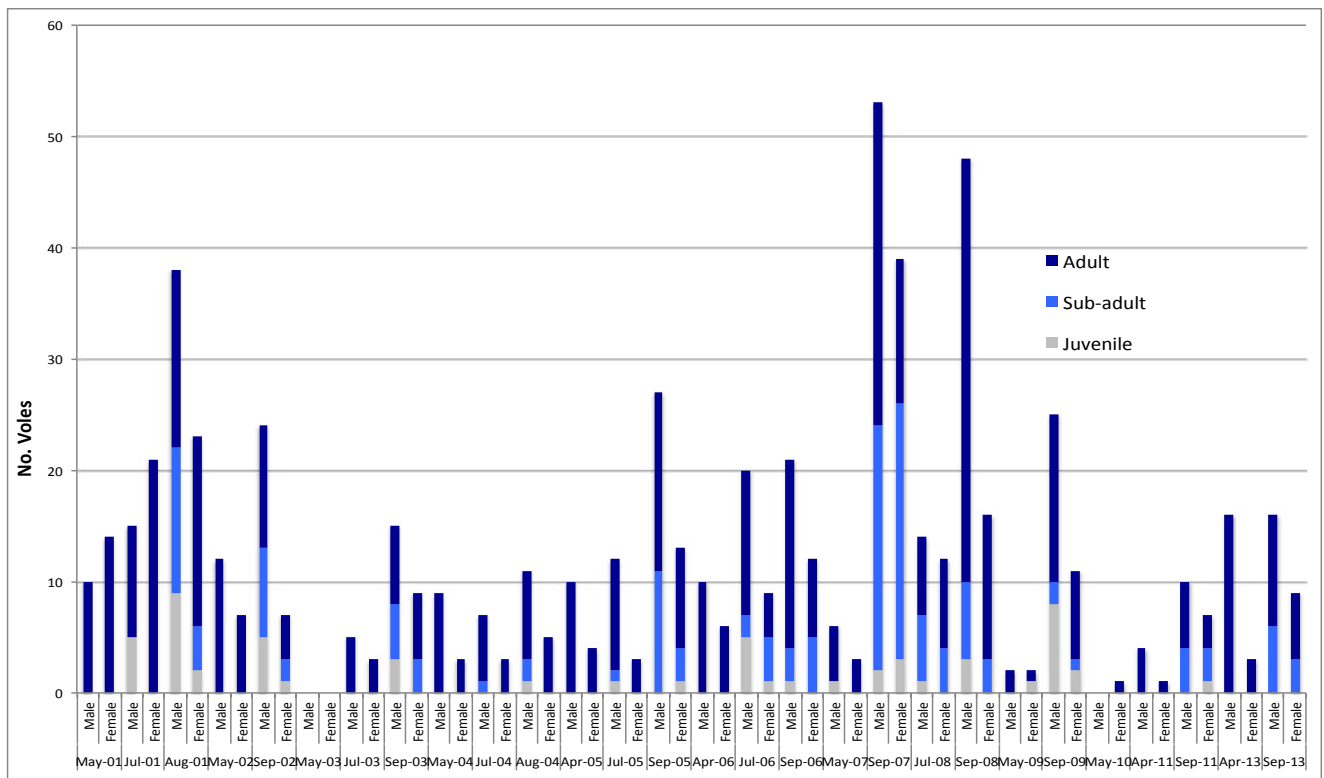


Figure 3 Age classes for each sex by trapping session



3.4 Breeding condition

Male breeding condition was determined by whether testes were scrotal or abdominal and if scrotal was considered to be capable of breeding. All males had attained breeding condition by May in all years apart from 2003 when densities declined to zero but there is currently little data on when overwintered males start to attain breeding condition and the underlying processes (Figure 4).

Figure 4 Breeding condition of male voles by trapping period.

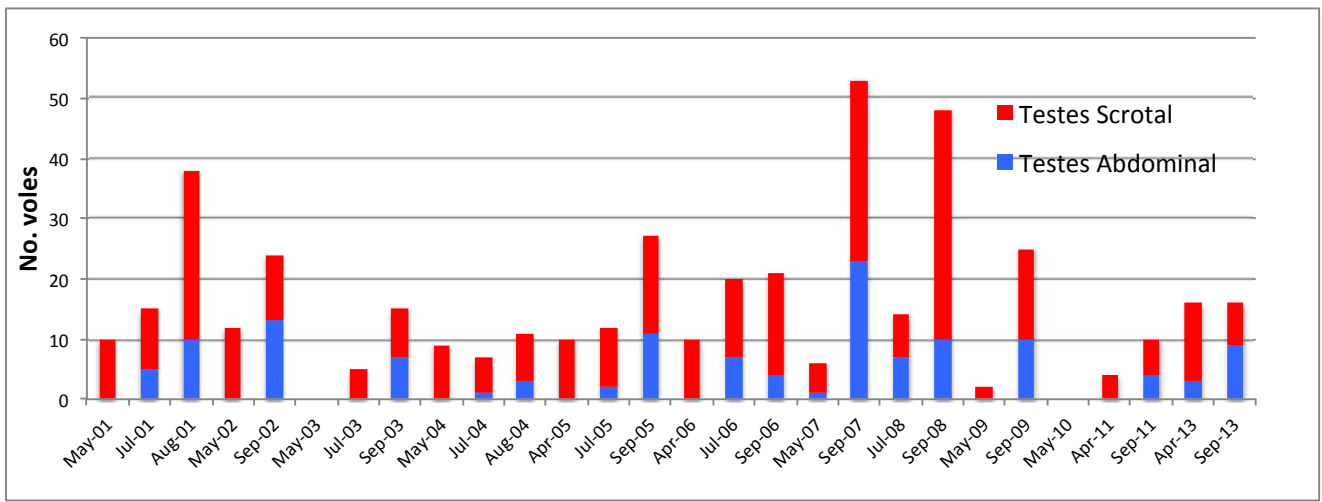
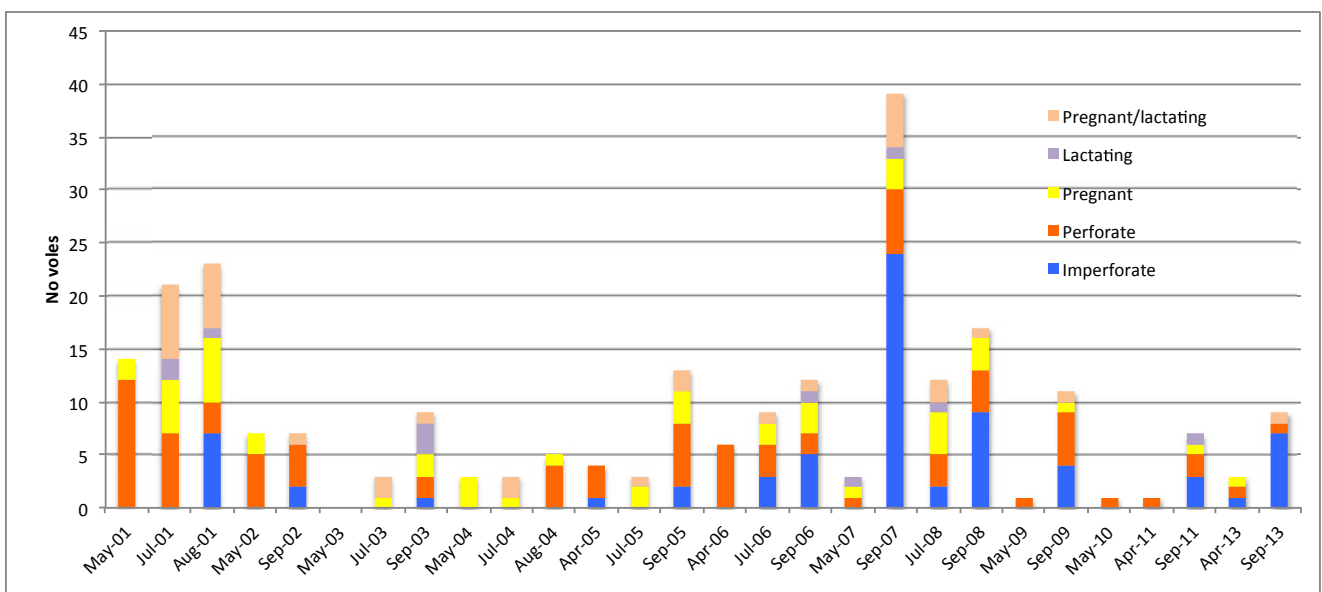


Figure 5 Breeding condition of female voles by trapping period. Skomer voles experience post partum oestrus and lactating females may also be pregnant.



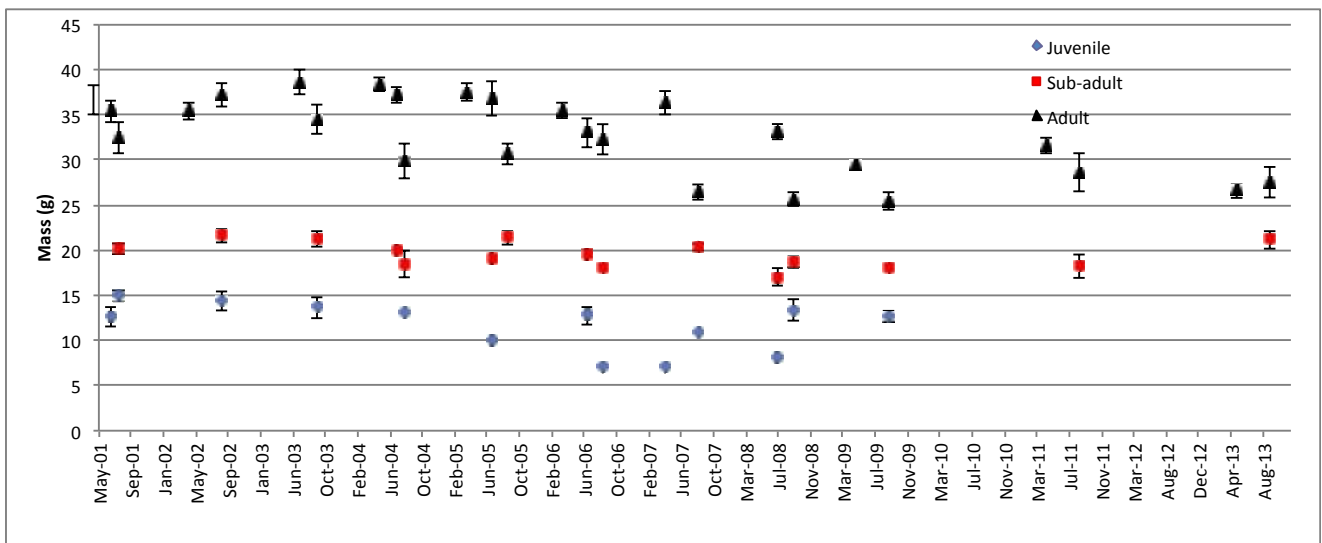
Females usually commenced breeding in May with the occurrence of first pregnancies but this was earlier in 2013 with first pregnancies in April (Figure 5). Onset of breeding was asynchronous in all

years but there was consistency in the onset of breeding as defined by the first detected pregnancy. The proportion of females that were breeding generally increased in July and August/September but in 2004 the number of adult females that were recorded as breeding declined in August with only one animal being recorded as pregnant.

3.5 Body mass

Male adult mass generally declined as the breeding season progressed and is likely to be associated with maturation of young males into the adult population. However, male mass increased from May to September in 2002 and the reason for the change in dynamics remains unclear but may reflect reduced recruitment of younger males (Figure 6).

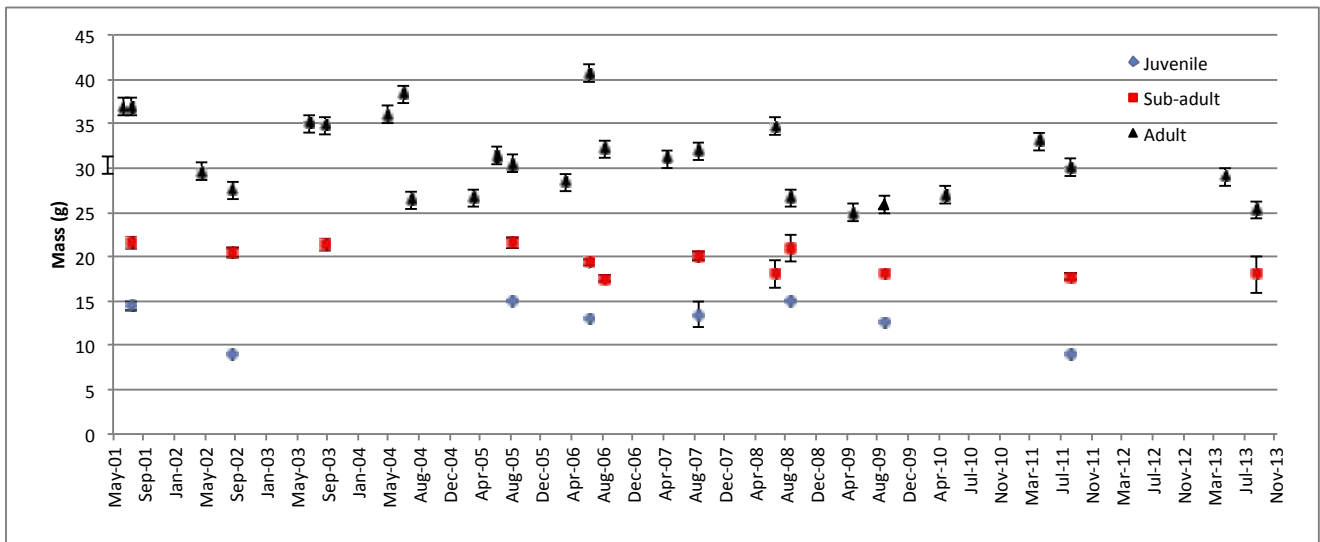
Figure 6 Mean male mass for different age classes in the trappable population. Error bars show +/- 1 standard error of the mean.



Female body mass will vary according to reproductive state and thus data needs to be viewed with caution. There were no clear trends in body mass over the breeding season with increase in some years and decrease in others. There are a number of factors that may affect these results including recruitment of younger females, breeding state and death of older animals and effects of social organisation such reproductive suppression. In some years there were higher numbers of female voles

that were both pregnant and lactating whereas in other years, breeding events were distinct. There reasons for these changes are not understood.

Figure 7 Mean female mass for different age categories. Error bars show +/- 1 standard error of the mean.



4.0 Social organisation

4.1 Home range and core area size

The RangesV programme was used to estimate home range size by the kernel method using fix density with a smoothing factor of 1 (Worton 1989). Core areas were estimated from utilisation distributions with the beginning of the last steep increment of these distributions being considered to represent the peripheral areas of the ranges, which generally fell between 75% and 85% of the total range areas. In this study core areas were standardised at the 80% isopleth whereas home ranges were estimated using the 95% isopleth (Tables 1 - 3). These studies of social organisation occur against a background of declining population numbers from 2001. In 2003 and 2004 a small number of males were tracked due to the low number of adult females available.

Core areas and home range areas were log transformed to achieve a normal distribution (core area: Kolmogorov-Smirnov $Z = 0.569$, $P > 0.05$, Home range area: Kolmogorov-Smirnov $Z = 0.703$, $P > 0.05$). There was no significant difference in female core area between years $F_{0.05, 2, 39} = 0.929$, $P > 0.05$ (log transformed data, observed power = 0.199) or home range areas between years

Table 1 Individual, mean, standard error (s.e.) and coefficient of variation (CV %) of range sizes in m² calculated for 95% and 80% range area for kernel and Minimum Convex Polygon 100% (MCP) analyses using RangesV programme in 2001. Breeding condition given in parentheses; Perf - vagina perforate, Preg - pregnant, Lact - lactating.

Females	<i>May</i>				Females	<i>July</i>				Females	<i>August</i>			
	Mass	80%	95%	MCP		Mass	80%	95%	MCP		Mass	80%	95%	MCP
F1 (Perf)	29	15	42	61	F1 (Preg)	43	45	81	102	F19 (Preg)	44	107	114	42
F2 (Perf)	27			87	F2 (Preg)	38	19	33	53	F18 (Lact)	35	85	126	97
F3 (Perf)	27	41	61	46	F4 (Perf)	35	38	60	87	F11 (Preg)	39	6	19	115
F4 (Preg)	31	8	22	41	F7 (Preg)	43	40	74	109	F17 (Perf)	33	57	67	29
F5 (Perf)	34	24	51	69	F8 (Lact)	31	23	50	61	F16 (Preg)	42	40	53	74
F6 (Perf)	30	29	63	91	F9 (Lact)	38	29	40	44	F7 (Lact)	39	58	119	259
		45	90		F10 (Lact)	41	72	93	95	F15 (Perf)	33	248	351	148
					F11 (Lact)	36	22	42	59	F5 (Lact)	37	27	36	121
					F12 (Lact)	32	17	31	56	F1 (Lact)	37	17	30	236
					F13 (Preg)	40	426	672	439	F14 (Lact)	39	52	82	96
										F20 (Perf)	27	154	198	239
Mean		27	55	66	Mean		73	118	102	Mean		77	109	132
s.e.		5.9	9.4	8.4	s.e.		39.6	62.0	53.0	s.e.		21.3	29.0	24.1
CV		53%	42%	31%	CV		171%	167%	87%	CV		91%	86%	60%
No. breeding females present = 14					No. breeding females present = 21					No. breeding females present = 17				

Table 2 Individual, mean, standard error (s.e.) and coefficient of variation (CV %) of range sizes in m² calculated for 95% and 80% range area for kernel analyses and Minimum Convex Polygon 100% (MCP) using RangesV programme in 2003. Breeding condition given in parentheses; Perf - vagina perforate, Preg - pregnant, Lact – lactating, T.S. – testes scrotal.

Females	Mass	<i>May</i>			Females	<i>July</i>				Females	<i>September</i>			
		80%	95%	MCP		Mass	80%	95%	MCP		Mass	80%	95%	MCP
					F1 (Lact)	32	25	38	47	F3 (Lact)	32	28	53	62
					F2 (Preg)	39	114	198	233	F4 (Lact)	34	64	154	223
										F5 (Preg)	31	80	146	213
										F6 (Preg)	35	18	42	37
					Mean		69	118	140	Mean		47	99	134
					s.e.		44.5	80.0	93.0	s.e.		14.6	29.7	48.9
					CV		91%	96%	94%	CV		62%	60%	73%
No. breeding females present = 0					No. breeding females present = 3					No. breeding females present = 6				
					Males	Mass	80%	95%	MCP					
					M1 (T.S.)	36	132	278	263					
					M2 (T.S.)	42	140	261	263					
					M3 (T.S.)	35	62	94	141					
					Mean		112	211	216					
					s.e.		24.9	58.9	38.0					
					CV		39%	48%	30%					

Table 3 Individual, mean, standard error (s.e.) and coefficient of variation (CV %) of range sizes in m² calculated for 95% and 80% range area for kernel analyses and Minimum Convex Polygon 100% (MCP) using RangesV programme in 2004. Breeding condition given in parentheses; Perf - vagina perforate, Preg - pregnant, Lact – lactating, T.S. – testes scrotal.

Females	<i>May</i>				Females	<i>July</i>				Females	<i>August</i>			
	Mass	80%	95%	MCP		Mass	80%	95%	MCP		Mass	80%	95%	MCP
F1 (Preg)	33	15	48	53	F3 (Lact)	38	54	139	183	F5 (Perf)	22	205	407	462
F2 (Preg)	31	104	178	178	F4 (Lact)	38	34	68	78	F6 (Perf)	23	116	220	219
										F7 (Perf)	27	217	423	423
										F8 (Perf)	23	63	122	295
										F9 (Preg)	37	19	34	51
Mean		59	113	114	Mean		44	103	131	Mean		124	241	305
s.e.		44.6	65.0	60.5	s.e.		10.1	35.8	52.5	s.e.		38.8	76.9	71.9
CV		106%	81%	75%	CV		33%	49%	57%	CV		70%	71%	53%
No. breeding females present = 3					No. breeding females present = 3					No. breeding females present = 5				
Males	Mass	80%	95%	MCP										
M1 (T.S.)	41	153	341	526										
M2 (T.S.)	39	49	71	119										
M3 (T.S.)	38	83	125	124										
Mean		95	179	261										
s.e.		30.7	82.4	132.7										
CV		56%	80%	88%										

Table 4 Mean home range and core area estimates for male and female voles (s.e. = standard error of mean, CV = coefficient of variation). Data pooled for months within years.

Year		Males				Females			
		n	Mean range size (m ²)	s. e.	CV (%)	n	Mean range size (m ²)	s. e.	CV (%)
2001	Core	-	-	-	-	27	65	17.0	137
	Range	-	-	-	-	27	100	25.5	132
2003	Core	3	112	25.0	39	6	55	15.5	69
	Range	3	211	58.9	48	6	105	28.2	66
2004	Core	3	95	30.7	56	9	92	25.4	83
	Range	3	179	82.5	80	9	182	48.4	80
All years	Core	6	103	18.1	43	42	69	12.3	116
	Range	6	195	45.9	58	42	118	20.1	110

Table 5 Breeding female home range and core area estimates (s.e. = standard error of mean, CV = coefficient of variation).

	Core Area				Home Range		
	n	Mean range size (m ²)	s. e.	CV (%)	Mean range size (m ²)	s. e.	CV (%)
Perforate	13	95	23.2	88	164	39.9	88
Pregnant	14	75	28.7	142	125	44.7	134
Lactating	15	40	5.6	54	73	11.0	58

$F_{0.05, 2, 39} = 2.385$, $P > 0.05$ (log transformed data, observed power = 0.453). There was also no significant difference in female core areas between months $F_{0.05, 3, 38} = 1.636$, $P > 0.05$ (log transformed data, observed power = 0.394) or home range areas $F_{0.05, 3, 38} = 0.811$, $P > 0.05$ (log transformed data, observed power = 0.208)(Table 4). There was no significant difference between male and female core areas $F_{0.05, 1, 46} = 3.846$, $P > 0.05$ (log transformed data, observed power = 0.484) but there was a significant difference between male and female home range areas $F_{0.05, 1, 46} = 4.079$, $P = 0.049$ (log transformed data, observed power = 0.507). There was no significant

differences in core area between female breeding states $F_{0.05, 2, 39} = 1.355$, $P > 0.05$ (log transformed data, observed power = 0.274) or home range areas $F_{0.05, 2, 39} = 1.749$, $P > 0.05$ (log transformed data, observed power = 0.344) (Table 5). There was no significant correlation between female core areas and density ($n = 42$, Spearman's $r = 0.015$, $P > 0.05$) and female home range areas and density ($n = 42$, Spearman's $r = -0.147$, $P > 0.05$).

4.2 Female social organisation

In 2001, six females were radiotracked in May. Of these females, two had distinct core areas whereas two pairs of females overlapped (Figure 8). One female (F5) was pregnant and the others were perforce and this distribution would suggest a non-territorial social organisation. In July 10 females were radiotracked. Most female core areas were distinct suggesting a change to a territorial system (Figure 9). However, there were two females that had overlapping home ranges and core areas. These appeared to be part of a small cluster of females that had stable associations over the breeding season that showed varying degrees of home range overlap through the breeding season. Females F4 and F5 overlapped in May but also shared space with F7 who was captured within their home range. In July females F4 and F7 had overlapping core areas. One female had a large home range which appeared to be biased by an exploratory movement away from her core area that lasted a day. In August F4 was not captured but females F5 and F7 continued to overlap. There were overlaps among five females at the core area level, the remaining female core areas were distinct again suggesting territoriality (Figure 10). The mean percentage overlap of core areas decreased with the onset of breeding (Table 6). As breeding commenced there appeared to be a change in social organisation from a non-territorial system to a territorial system, although some females appeared to form stable clusters and shared space. The relationships among these females were not known but they could be mediated by either genetic or familiar mechanisms. It was possible to determine home range shifts for a number of females between months. Generally, the range shifts recorded were small and all incorporated at least part of their previously recorded home range

(Table 7). No radiotracking was carried out in 2002. In May 2003 the population had declined and no voles were captured on the study area. Densities remained low over the rest of 2003 and 2004 and there was no overlaps of adult females at the core area level suggesting that social organisation was territorial (Figures 11 and 12, Table 6).

Figure 8 Female core areas (80% isopleth) and home ranges (95% isopleth) for May 2001.
Core areas (80%) Home Range (95%)

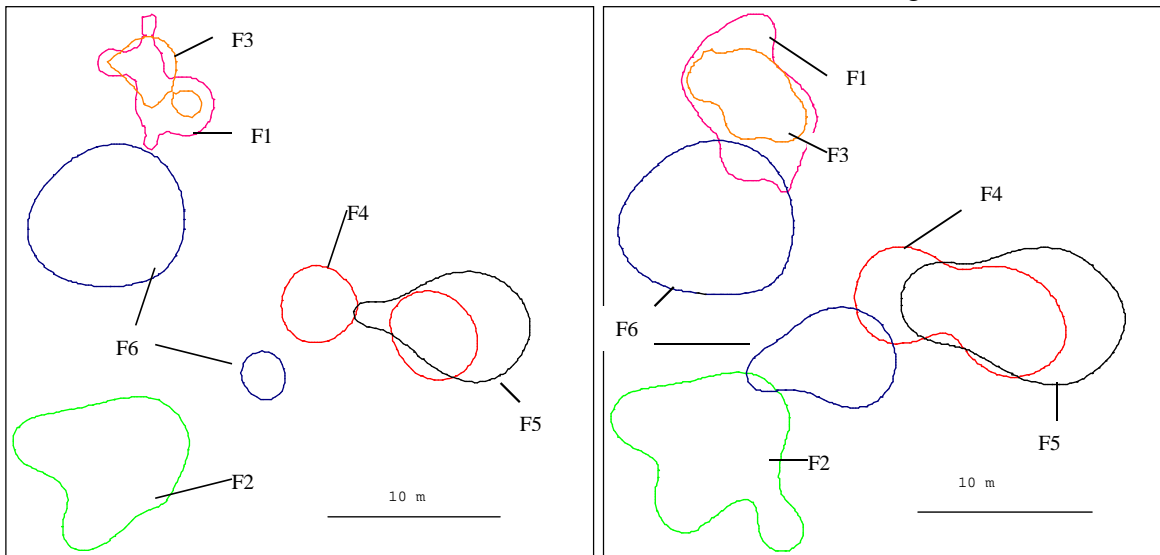


Figure 9 Female core areas (80% isopleth) and home ranges (95% isopleth) for July 2001.
Core areas (80%) Home Range (95%)

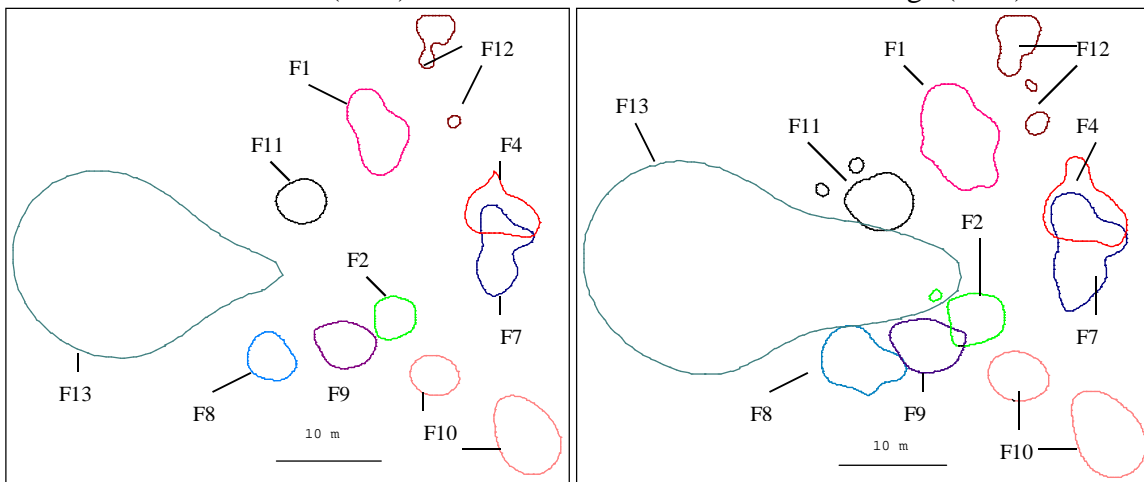


Figure 10 Female core areas (80% isopleth) and home ranges (95% isopleth) for August 2001.
Core areas (80%) Home Range (95%)

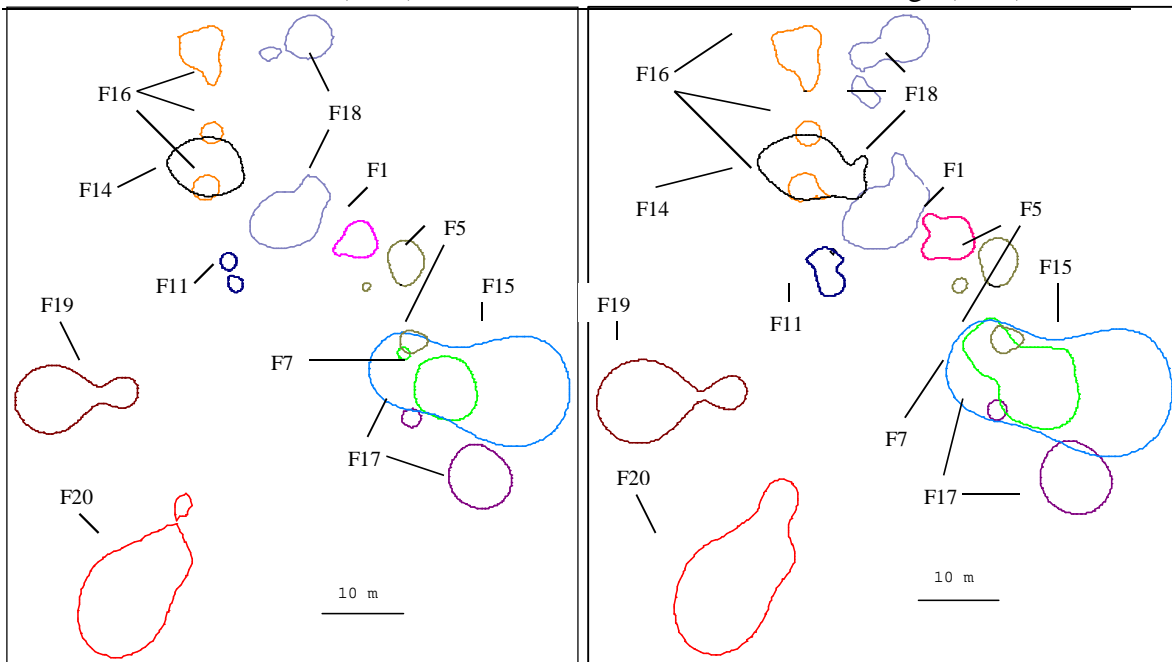


Figure 11 Female core areas (80% isopleth) and home ranges (95% isopleth) for September 2003
Core areas (80%) Home Range (95%)

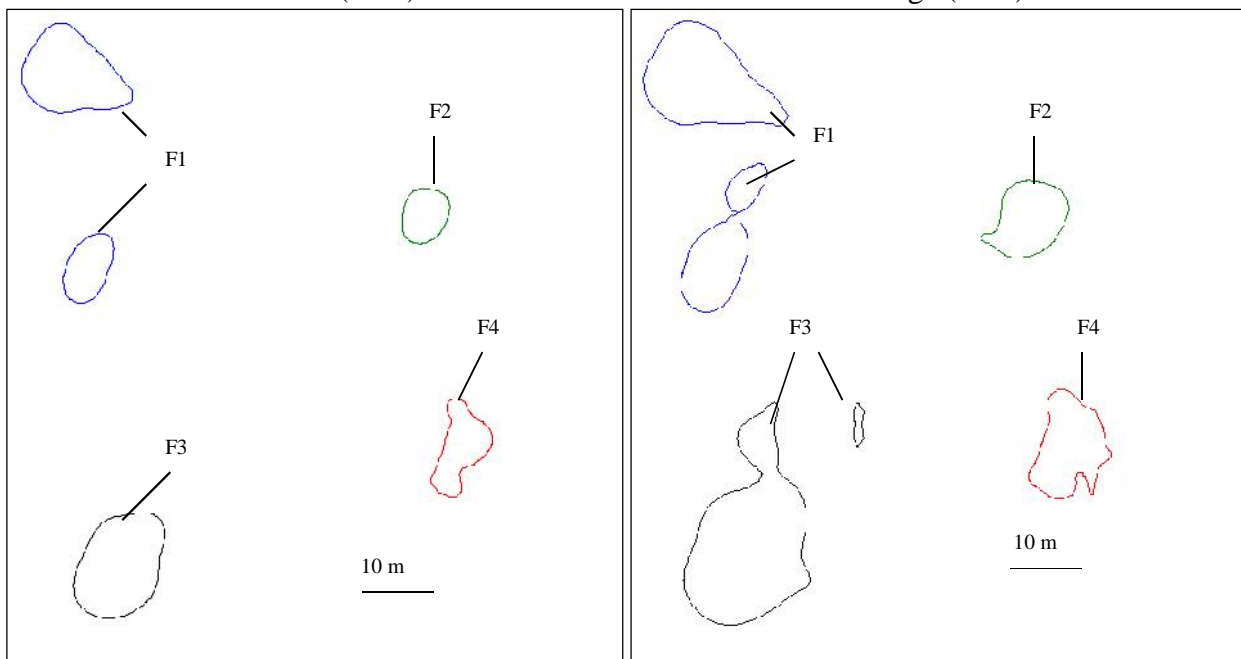


Figure 12 Female core areas (80% isopleth) and home ranges (95% isopleth) for August 2004

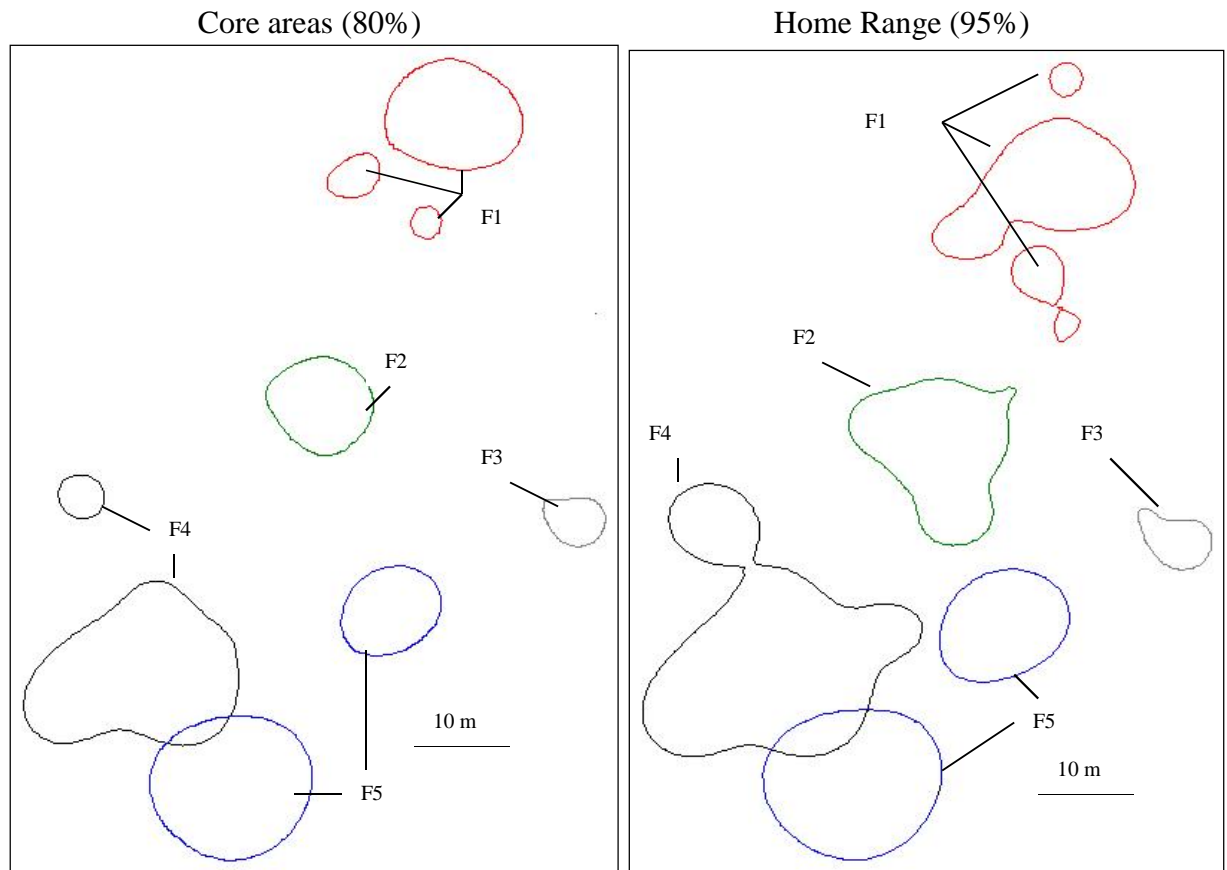


Table 6 Number of pairs of overlapping adult females and mean percentage overlap among females for core areas and home ranges.

	n	No. females with exclusive core areas (80%)	No. pairs females overlapping	Mean % overlap of overlapping female core areas (80%)	No. pairs females overlapping	Mean % overlap of overlapping female home ranges (95%)
May 2001	6	2	2	55.2	6	25.5
July 2001	10	9	1	30.4	3	19.5
August 2001	11	6	3	27.8	7	18.2
May 2003	0	-	-	-	-	-
July 2003	2	2	0	0	0	0
Sept. 2003	4	4	0	0	0	0
May 2004	2	2	0	0	0	0
July 2004	2	2	0	0	0	0
August 2004	5	3	1	3.5	1	9.4

Table 7 Home range shifts between months in 2001, distance between home range centres and percentage overlap of range area on previous range area.

Female	Period	Distance (m)	% Overlap of range area
1	May - July	3.1	99.6
2	May - July	5.1	55.3
3	May - July	6.1	21.5
5	May - Aug	5.1	28.2
4	July - August	3.2	35.1
1	July - August	8.7	7.6
6	July - August	10.7	24.2
Mean		5.9	38.8
Std dev		2.8	30.5

Table 8 Nearest neighbour analyses showing mean distance, expected distance, aggregation indices and minimum and maximum distances for female voles. Standard error of mean distance and t values shown. R = Index of aggregation. If the spatial pattern is random then R = 1. If animals are clumped in distribution then R approaches zero and in a regular spatial pattern R approaches an upper limit of approximately 2.15. There were no distributions significantly deviating from a random distribution.

	n	Mean distance (m.)	Expected distance (m.)	s.e.	Index of aggregation R	Max. & Min distances	t
May 2001	6	6.48	4.7	1.21	1.38	2.83 – 10.0	1.47
July 2001	10	11.54	8.37	1.95	1.38	6.32 – 23.32	1.63
Aug 2001	11	13.97	10.81	2.32	1.29	6.32 – 28.64	1.63
Sep 2003	4	27.93	18.73	4.38	1.49	20.4 – 36.77	2.10
Aug 2004	5	20.44	14.53	3.97	1.41	10.77 – 28.64	1.49

4.3 Nearest neighbour analyses

In 2001, Mean female nearest neighbour distances increased during the breeding season, which is consistent with increasing territoriality observed during July and August (Table 8). In 2003 (September) and 2004 (August) there were sufficient numbers of females to carry out nearest neighbour analyses although densities were low. As might be expected, mean nearest neighbour distances were greater at lower densities. All aggregation indices did not significantly differ from random distributions

5.0 Discussion

5.1 Population processes

Trappability was lowest in spring when field cover was poor and mainly provided by bluebells. This may contribute to underestimation of population numbers at these times due to voles primarily using runways and burrows. As field cover increased with the appearance of bracken, movement on the surface increased thus increasing trappability. It is thought that in the summer most adults were captured. Juvenile trappability was higher and their use of traps was generally localised to a small area, although captures were male biased suggesting different movement patterns or propensity to enter traps. Trappability is complex with a number of factors influencing trap use. Social behaviour and dominance may influence trap use, which is likely to be associated with odour (Viitala and Hoffmeyer 1985). Little and Gurnell (1992) also showed that trap odour may affect trap use and this may well extend to odour marks around the trap, as they were permanent features of the environment.

The population has declined since 2001 and is likely to be associated with the intensity of predation. In both 2003 and 2004 predation by owls was heavy and this was further enhanced by poor field cover in 2004. In 2003 and 2004, intense predation coincided with the first wave of reproduction suppressing population growth. Erlinge *et al.* (1983) reported similar effects of predation early in the season, curtailing and delaying population growth. Rainfall in 2004 was also low over the spring and summer and this affected the growth of bracken which was patchy and low that would have increased vulnerability to predation. The island wide survey of 2004 also confirmed the decline in vole numbers in this study (Healing & Loughran unpublished).

There is a clear population decline over the winter and early spring but it is not clear whether this population experiences a spring decline which is part of the typical dynamics of mainland populations that exhibit annual cycles (Alibhai and Gipps 1985, Bujalska 1991, Yl nen *et al.* 1995). Breeding females were generally born in the previous year and this was their first

breeding event. The genetic relationships were not known but overwintered animals may be familiar, having longer spatial and temporal associations. Familiarity reduce antagonism among breeding females at the start of the breeding season (Lambin and Krebs 1991) and Ylönen *et al.* (1997) have shown that familiarity also reduces infanticidal behaviour. This would reduce the spring decline and contribute to breeding success and increase population growth. There were associations between a number of individual females that continued through the breeding season. Space sharing may have positive effects on defence and pup survival increasing population growth but reproductive suppression may operate in limiting numbers of breeding adults (Wolff 1997). In most years the population increased over the late spring and early summer apart from 2004 when the number of breeding adults declined due to predation. In 2001 there was generally a decline in the number of overlapping adults as the breeding season progressed suggesting increasing territoriality although in other years of the study this may be an artefact of low densities. Predation is likely to reduce relatedness and familiarity among adults that may also lead to an increase in territoriality among residents (Korpimäki 1985). The first juveniles and sub-adults were caught in July. Post-partum oestrus occurs in Skomer voles but in all years breeding was discontinuous and the reasons for this are unclear but may be associated with physical condition and possibly nutritional limitations due to seasonal changes in vegetation. Few female animals matured into the breeding population in the year of their birth. A number of mechanisms may be operating in constraining maturation. Limited dispersal opportunities due to social fence effects (Hestbeck 1982) and patchy nature of habitat may constrain habitat availability and thus limit dispersal. This could lead to differential dynamics and densities depending on patch size, vegetation characteristics and vulnerability to predation. Other factors that may affect maturation may be associated with food quality and this may be important later on in the season as forage quality declines (Oksanen *et al.* 2000).

Maximum densities showed five-fold variation in peak population densities in late summer/autumn but there was no consistent pattern in population fluctuations, e.g multi-annual cycles. There are occasional years when spring population numbers are very low and autumn densities are in the lower range. The factors influencing population numbers are likely to be due to a combination of first order effects such as functional response of generalist avian predators such as owls and intraspecific competition as well as secondary effects associated with food resources (Sundell 2006, Lima *et al.* 2006) that may be influenced directly or indirectly by weather and vegetation cover (Gorini *et al.* 2012). Predation usually exhibit numerical response to prey density and is unlikely to account for the decline to zero on the study area in May 2003 (Anderson and Erlinge 1977, Korpimaki 1985, Sundell 2003). Combinations of extrinsic factors are still poorly understood but include disease processes/parasitism and competition for resources may also contribute to population fluctuations. Food quantity and quality may also play a significant role in population dynamics, during the breeding season bluebells provide the first flush of protein that is supplemented by bracken, ground ivy and other vegetation. However, dietary composition and availability of forage is poorly understood over the winter period and has the potential to influence mortality rates (Haapakoski *et al.* 2012). Low rainfall may have affected the quality of food resources in some years and a number of studies have demonstrated demographic effects of food quality on survival and reproduction that may be important in the Skomer population (Crespin *et al.* 2002, Oksanen *et al.* 2000, Desy and Batzli 1989, Taitt and Krebs 1983, Cole and Batzli 1979). Food resources and their quality are patchy in their distribution, varying temporally in their abundance and renewability but these dynamics are poorly understood in relation to Skomer voles and require further study. For example, breeding commences in late spring that coincides with the first flush of new plant growth (bluebells). Female reproduction may be triggered by the increased protein availability and possibly response to other factors such as plant oestrogens (Orton 2000). After the

bluebells had flowered, bluebell seeds become available to voles, which along with bracken may be important in diet breadth. Over the winter it is unclear what food resources voles are utilising but it is suspected that bluebell bulbs may constitute an important food source. The population dynamics of Skomer voles remains unclear and further long term work is required to elucidate these dynamics.

Generally, sex ratios and operational sex ratios were male biased. Operational sex ratio bias may be related to a promiscuous breeding system but other factors such as female territoriality and fence effects may limit the number of female home ranges in relation to adult males.

5.2 Home range and core area size

The sizes of home range revealed by radiotracking and trapping were similar but radiotracking was more representative of space use and relationships between different animals. The mean home range areas reported for Skomer voles are considerably smaller than those reported for bank voles (Koskela et al. 1997, Karlsson and Potapov 1998, Ylönen et al. 1995, Oksanen 2000). Food resources have been reported to be important in territoriality in voles and increases in food resources have resulted in decreased home range and increasing overlap with neighbouring females (Taitt and Krebs 1981, Ostfeld 1986). A number of studies have also demonstrated demographic effects of food quality on survival and reproduction (Desy and Batzli 1989, Taitt and Krebs 1983, Cole and Batzli 1979). Food availability and quality will vary through space and time, which in turn may influence female social organisation. Food resources and particularly quality are variable over the breeding season on Skomer but could be considered as abundant and widely distributed. This may be a contributing factor to the smaller home ranges observed on Skomer. Also the structure of the habitat is more three dimensional if the rabbit and Manx Shearwater burrows are considered and this may be important in access to food resources such as bluebell bulbs. However, the resource dynamics

may radically change over the winter period with little green plant material available and poor field cover to support movement on the surface.

There was no difference in home range areas of females between different breeding states. Although female home ranges and core areas showed some reduction during lactation this was not significant, range areas were small and it may not have been necessary to restrict their core area for effective pup defence. Range contraction during lactation has been found in other studies and would support a pup defence hypothesis (Loughran 1999, Koskela *et al.* 1997). However, these dynamics are complex and there is some evidence to suggest that they are related to parental investment (see Koskela *et al.* 2000). There are no data on infanticide in Skomer vole populations but it has been reported in bank vole populations (Ylönen *et al.* 1997). Female core areas and home ranges were not correlated with density suggesting that other factors influenced space use in Skomer voles.

5.3 Female social organisation

At higher densities in 2001, overlap among females varied seasonally. At the beginning of the breeding season female core area overlaps varied with some overlapping whilst others were distinct. This could reflect some females being territorial, whilst others were non-territorial. As the breeding season progressed, spacing patterns suggested that territoriality was again more prevalent with most core areas being distinct although there appeared to be stable associations between some females who shared space which may be due to genetic relationships or possibly familiarity (e.g. Wolff 1997, Lambin and Krebs 1991, Bekoff 1981). In bank voles mature females have been observed to be territorial (Bujalska 1991, Ylönen *et al.* 1995, Koskela *et al.* 1997, Bujalska and Saitoh 2000). In 2003 and 2004 female core areas were distinct suggesting territoriality but these results may be an artefact of low densities recorded during these years.

Densities were lower at the beginning of the breeding season and space was not limiting. Food resources were considered to be abundant although food quality is likely to have varied through the year. The onset of reproduction coincided with the first flush of new plant growth as the bluebells flower, after which bracken becomes the most dominant vegetation providing both food and cover. Ostfelds (1985) hypothesis would predict a non-territorial social organisation but as breeding commenced most breeding females were territorial.

At the level of the core area, the observed pattern of female social organisation suggested that territoriality was prevalent in breeding females throughout the breeding season. Some breeding females did show overlap of home ranges and core areas and appeared to be stable lasting over a number of months and breeding events. Core area sizes were small during lactation when nutritional demands were highest suggesting that they were independent of food resource. The small core areas recorded for lactating females were not consistent with food resource defence, which again suggested that this aspect was unimportant in determining female social organisation.

In relation to Wolff's (1997) pup defence hypothesis there was a change in social organisation at the start of the breeding season from a non-territorial to a territorial system which could be considered consistent with pup defence. Core areas of lactating females were small which would facilitate defence of the nest site. Also core area size did not vary greatly over the breeding season despite varying densities and food resources. The recorded range shifts through the breeding season suggest that home ranges are relatively stable which over a short breeding season may be important in establishing female kin groups that overwinter and form the next breeding cohort.

The main features of *Clethrionomys* social systems are aggregation in the winter, territoriality in the spring and summers but this appears to be mediated by both kin and possibly familiar relationship at the beginning of the breeding season (Bujalska 1991, Ylönen *et al.* 1995,

Bujalska and Saitoh 2000). The social organisation observed in Skomer voles appears to be similar to that of other *Clethrionomys* species and there is increasing evidence that pup defence may mediate spacing behaviour among adult females. At higher densities, as the breeding season progresses, the degree of home range and core area overlap decreases as densities increase suggesting increasing territoriality. This is similar to the bank vole *C. glareolus* where home range overlaps have been reported to decrease with increasing density (Ylönen *et al.* 1988, Bujalska 1991, Bujalska and Saitoh 2000).

6.0 References

- Alibhai, S. K. and Gipps, J. H. W. (1985) The population ecology of bank voles. *Symp. Zool. Soc. Lond.* 55; 277 – 305.
- Anderson, M. and Erlinge, S. (1977) Influence of predation on rodent populations. *Oikos* 29; 591 - 597.
- Bekoff, M. (1981) Vole population cycles: kin selection or familiarity. *Oecologia* 48; 131.
- Berger, J.P., Saunders, E.H., Gardiner, P.D. and Negus, N.C. (1977) Phenolic plant compounds functioning as reproductive inhibitors in *Microtus montanus*. *Science* 195; 575 - 577.
- Berteaux, D., Masseboeuf, F., Bonzom, J., Bergeron, J., Thomas, D. W. & Lapierre, H. (1996). Effect of carrying a radiocollar on expenditure of energy by meadow voles. *Journal of Mammology* 77: 359 - 363.
- Blackburn, T.M., Gaston, K.J., Quinn, R.M., Arnold, H. & Gregory, R.D. 1997. Of mice and wrens: the relation between abundance and geographic range size in British mammals and birds. *Philosophical Transactions of the Royal Society of London B* 352: 419 - 427.
- Bujalska, G. (1991) The ecology of territoriality in the bank vole. *Trends in Ecology and Evolution* 6: 300 – 301.
- Bujalska, G. and Saitoh, T. (2000) Territoriality and its consequences. *Polish Journal of Ecology* 48 (Suppl.): 37 – 49.
- Cole, F.R. and Batzli, G.O. (1979) Nutrition and population dynamics of the prairie vole *Microtus ochrogaster* in Central Illinois. *Journal of Animal Ecology* 48; 455 - 470.
- Corbet, G. B. (1964) Regional variation in the bank vole *Clethrionomys glareolus* in the British Isles. *Proc. Zool. Soc. Lond.* 143; 191 – 219.
- Coutts, R. R. and Rowlands, I. W. (1969) The reproductive cycle of the Skomer vole (*Clethrionomys glareolus skomerensis*). *Journal of Zoology* 158; 1 – 25.

- Crespin, L., Verhagen, R., Stenseth, N.C., Yoccoz, N.G., Prévot-Julliard, A., and Leberon, J. (2002) Survival in fluctuating bank vole populations: seasonal and yearly variations. *Oikos* 98: 467 – 479.
- Desy, E.A. and Batzli, G.O. (1989) Effects of food availability and predation on prairie vole demography: A field experiment. *Ecology* 70(2); 411 - 421.
- Erlinge, S., Goransson, G., Hansson, L., Hogstedt, G., Liberg, O., Nilsson, I.N., Nilsson, T., von Schantz, T. and Sylven, M. (1983) Predation as a regulating factor on rodent populations in southern Sweden. *Oikos* 40; 36 - 52.
- Fullagar, P.J., Jewell, P.A., Lockley, R.M. and Rowlands, I.W. (1963) The Skomer vole (*Clethrionomys glareolus skomerensis*) and long tailed field mouse (*Apodemus sylvaticus*) on Skomer Island, Pembrokeshire in 1960. *Proc. Zool. Soc. Lond.* 140: 295 – 314.
- Gipps, J.H.W., Flynn, M.P, Gurnell, J. and Healing T.D. 1985. The spring decline in populations of the bank vole *Clethrionomys glareolus* and the role of female density. *Journal of Animal Ecology* 54: 351 - 358.
- Gorini, L., Linnell, J.D.C., May, R., Panzacchi, M., Boitani, L., Odden, M. and Nilsen, E.B. (2012) Habitat heterogeneity and mammalian predator–prey interactions. *Mammal Review* 42, No. 1, 55–77.
- Haapakoski, M., Sundell, J. and Ylönen, H. (2012) Predation risk and food: opposite effects on overwintering survival and onset of breeding in a boreal rodent. *Journal of Animal Ecology*, 81, Issue 6, pages 1183–1192.
- Hare, E.J. (2009) Island syndrome in rodents; a comparative study on island forms of the bank vole, *Myodes glareolus*. Unpublished PhD thesis. London University.
- Healing, T.D. (1984) Factors affecting the population dynamics of the Skomer vole (*Clethrionomys glareolus skomerensis*). Unpublished Phd thesis, University of London.

- Hestbeck, J.B. (1982) Population regulation of cyclic mammals: the social fence hypothesis. *Oikos* 39; 147 - 163.
- Karlsson, F. and Potapov, E.R. (1998) Consistency and change in bank vole (*Clethrionomys glareolus*) home ranges across a decade. *Canadian Journal of Zoology* 76: 1329 – 1334.
- Kenward, R.E. & Hodder, K.H. (1995). *Ranges V : an analysis system for biological location data*. Institute for Terrestrial Ecology. Dorset, UK. pp. 75.
- Korpimäki, E. (1985) Rapid tracking of microtine populations by their avian predators: possible evidence for stabilising predation. *Oikos* 45; 281 - 284.
- Koskela, E., Mappes, T. and Ylönen, H. (1997) Territorial behaviour and reproductive success of bank vole *Clethrionomys glareolus* females. *Journal of Animal Ecology* 66: 341 – 349.
- Koskela, E., Juutistenaho, P., Mappes, T. and Oksanen, T. A. (2000) Offspring defence in relation to litter size and age: experiment in the bank vole *Clethrionomys glareolus*. *Evolutionary Ecology* 14: 99 – 109.
- Lambin, X. and Krebs, C. J. (1991) Can changes in female relatedness influence microtine population dynamics. *Oikos* 61: 136 - 132.
- Le Boulenger-Nguyen, P. Y. & Le Boulenger, E. (1986) A new ear-tag for small mammals. *Journal of Zoology, London* 209: 302-304.
- Lima, M., Berryman, A. A. and Stenseth, N. C. (2006) Feedback structures of northern small rodent populations. *Oikos* 112: 555_/564.
- Little, J. and Gurnell, J. (1989) Shrew capture and rodent field studies. *Journal of Zoology (London)* 218; 329 - 331.
- Loughran, M.F.E. (1999). A Study of the demography and social organisation of the field vole, (*Microtus agrestis* L), in relation to food resources. Unpublished PhD thesis. London University.

- Mendonça, P.G. de (1999) Impacts of radio collars on yellow neck mice (*Apodemus flavicornus*). *Mammal Review* 29: 129 – 134.
- Oksanen, T., Oksanen, L., J drzejewski, W., J drzejewska, B., Korpimaki, E. and Norrdahl, K. (2000) Predation and the dynamics of the bank vole *Clethrionomys glareolus*. *Polish Journal of Ecology* 48 (Suppl.): 197 – 217.
- Orton, F. (2001) The effect of diet on the behaviour, physiology and reproduction of the female field vole (*Microtus agrestis*). Unpublished MPhil thesis. London University.
- Ostfeld, R.S. (1985) Limiting resources and territoriality in microtine rodents. *American Naturalist* 126; 1 - 15.
- Ostfeld, R.S. (1986) Territoriality and mating system of Californian voles. *Journal of Animal Ecology* 55: 691 - 706.
- Ostfeld, R. S. (1990) The ecology of territoriality in small mammals. *Trends in Evolution and Ecology* 5(12): 411 - 415.
- Rooney, S.M., Wolfe, A. and Hayden, T.J. (1988) Autocorrelated data in telemetry studies: time to independence and the problem of behavioural effects. *Mammal Review* 28; 89 - 98.
- Sundell, J. (2003) Population dynamics of microtine rodents: an experimental test of the predation hypothesis. *Oikos* 101: 416 – 427.
- Sundell, J. (2006) Experimental tests of the role of predation in the population dynamics of voles and lemmings. *Mammal Review* 36, No. 2, 107–141.
- Taitt, M.J. and Krebs, C.J. (1983) Predation, cover and food manipulations during the spring decline of *Microtus townsendii*. *Journal of Zoology* 52; 1593 - 1599.
- Taitt, M.J. and Krebs, C.J. (1981) The effect of extra food on small rodent populations: 2 Voles (*Microtus townsendii*). *Journal of Animal Ecology* 50; 125 - 137.
- Varty, N. (1987). A study of range and activity in the short tailed vole (*Microtus agrestis*) by live trapping and telemetry. Unpublished PhD thesis, Kings College, London University.

- Viitala, J. and Hoffmeyer, I. (1985) Social organisation in *Clethrionomys* compared with *Microtus* and *Apodemus*: Social odours, chemistry and biological effects. *Ann. Zool. Fennici* 22: 359 – 371.
- White, G. C. and Garrott, R. A. (1990) Analysis of wildlife radiotracking data. Academic Press, Inc., San Diego, California.
- Wolff, J.O. (1993) Why are female mammals territorial? *Oikos* 68(2); 364 - 370.
- Wolff, J.O. (1997). Population regulation in mammals: An evolutionary perspective. *Journal of Animal Ecology* 66: 1 - 13.
- Worton B. J. (1989) Kernel methods for estimating the utilisation distribution in home range studies. *Ecology* 70; 164 - 168.
- Ylönen, H., Kojola, T. and Viitala, J (1988) Changing female spacing behaviour and demography in an enclosed breeding population of *Clethrionomys glareolus*. *Holarctic Ecology* 11: 286 – 292.
- Ylönen, H., Pusenius, J. and Viitala, J (1995) Impact of kinship and familiarity on the annual social organisation and population dynamics of *Clethrionomys* and *Microtus* voles. *Ann. Zool. Fennici* 32; 225 - 232.
- Ylönen, H., Koskela, E. and Mappes, T. (1997) Infanticide in the bank vole (*clethrionomys glareolus*): occurrence and the effect of familiarity on female infanticide. *Ann. Zool. Fennici* 34; 259 – 266.