Demography and social structure of water vole populations: implications for restoration

A thesis submitted for the degree of

Doctor of Philosophy

Tom Moorhouse

Lady Margaret Hall, University of Oxford

Michaelmas Term, 2003

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ABSTRACT

Water voles (*Arvicola terrestris*) are semi-aquatic rodents which mainly inhabit linear ranges bordering water-courses and are an endangered species in the United Kingdom. Habitat loss and predation from American mink have resulted in lowland populations that are increasingly becoming fragmented and spatially isolated. Conservation measures for water voles may therefore include habitat restoration and re-introduction.

The main objective of this thesis was to study the interactions between habitat quality, population demography, social structure and dispersal biology of water voles in extant populations, providing information with which to produce practical guidelines for habitat restoration and re-introduction.

Higher population densities were associated with larger quantities of available forage, larger growth rates, heavier individuals and smaller range-lengths of both males and females. Population densities apparently responded to increased food resources. Increasing widths of riparian habitat may, therefore, increase numbers of individuals within water vole populations.

Males were apparently non-territorial at all population densities studied, and their range sizes limited by a maximum number of females they could overlap, possibly resulting from aggressive interactions with other males and females. The geographical location of females' territories and males' ranges constantly drifted. The degree to which female territories drifted was smaller at a high population density site than at a low density site. At even higher densities, female territories may potentially reach a minimum size and cease drifting. Female territory sizes apparently reached a maximum size at low population densities. Ideal spacing of release pens for re-introducing females should lie between these minimum and maximum range sizes.

A decline in numbers of females at one study site during radio-tracking was associated with male-biased birth sex ratios. Stress caused by radio-collars could have resulted in maternal sex ratio adjustment. Radio-tracking of water vole populations may, therefore, be inappropriate in some cases.

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Chapter 1

Introduction

OVERVIEW

This thesis examines extant populations of water voles (*Arvicola terrestris*) in order to derive guidelines for habitat restoration and re-introduction for their conservation. The correct habitat in the correct quantities is necessary for the continued persistence of any species (Gilpin & Soulé, 1986) and without high habitat quality, re-introductions have low chances of success (Balmford et al., 1996; Griffith et al., 1989). The quantity and quality of habitat is likely to determine the size of the populations inhabiting it (Ostfeld, 1985), and the size of a population may influence the length of time that it will remain in existence (Caughly, 1994).

In this introduction I argue that understanding the interactions between habitat quality, population demography, social structure and dispersal biology of water voles is fundamental to our ability to restore sufficient habitat of sufficient quality, and to restore sufficient numbers of water voles to that habitat to enhance the conservation-status of the species.

THE NATIONAL DECLINE OF WATER VOLES

Water voles are a semi-aquatic, endangered small mammal, have been declining in the United Kingdom since at least 1900 (Jefferies et al., 1989; Macdonald & Strachan, 1999; Strachan et al., 2000; Strachan & Jefferies, 1993) and have undergone the greatest decline of any British mammal in the last century (Telfer et al., 2003). This decline results mainly from a combination of habitat loss and predation by American mink (Barreto & Macdonald, 2000; Barreto et al., 1998a; Barreto et al., 1998b; Bonesi et al., 2002; Macdonald & Strachan, 1999; Woodroffe et al., 1990).

In most UK habitats, water voles live in colonies arranged along the length of water courses in a series of home-ranges (Pelikan & Holisova, 1969; Stoddart, 1970; Woodroffe et al., 1990). Instances of riparian habitat degradation and fragmentation in the UK are legion, with riparian maintenance works and unsympathetic agricultural management practises being frequently implicated in the loss of water vole colonies (Barreto et al., 1998a; Macdonald & Strachan, 1999; Strachan, 1998; Strachan et al., 2003), usually leaving highly dispersed patches of suitable, occupied habitat.

Predation upon water voles by American mink (*Mustela vison*) can lead to rapid extirpation of populations (Barreto & Macdonald, 2000; Strachan et al., 1998; Woodroffe et al., 1990). Barreto et al. (1998a) hypothesised that the impacts of mink were exacerbated since the majority of populations of water voles inhabit linear habitats, and also that in the presence of greater quantities of occupied habitat, water voles and American mink may be able to co-exist. Some evidence supports this (Carter & Bright, 2003; Macdonald & Strachan, 1999); nevertheless, since many water vole populations occupy linear habitats, they are likely to be vulnerable to mink predation.

Water vole populations in the UK can be roughly divided into two types. Upland populations tend to be arrayed along waterways and are typically subdivided into colonies consisting of a small number of individuals (Aars et al., 2001; Lawton & Woodroffe, 1991; Stoddart, 1970; Telfer et al., 2001; Telfer et al., 2003). In these habitats the water voles form a metapopulation in which extinction and recolonisation of habitat patches are at least partially determined by dispersal of individuals (Aars et al., 2001; Stewart et al., 1999; Telfer et al., 2001). Lowland populations can be much larger than some upland populations, contain many more individuals, and are often more spatially separate (Barreto & Macdonald, 2000; Barreto et al., 1998b; Carter &

Bright, 2003; Woodall, 1993). This thesis specifically examines populations occurring in lowland habitats in the UK, in which the numbers of individuals living in close proximity can be sufficient to examine the population demography, social structure and habitat requirements of large numbers of males and females at different population densities.

Occupation of habitats in lowland ecosystems can be determined by the spatial arrangement of water vole colonies. Studies by Barreto et al. (1998b), Bonesi et al. (2002) and Macdonald & Strachan (1999) show that occupancy of a location is generally determined by three factors: 1) the presence of suitable habitat; 2) the absence of American mink; 3) the degree of isolation from other water vole colonies. Bonesi et al. (2002) found that water voles could be absent from optimal habitat if conspecifics were absent from the immediate neighbourhood, but that if neighbouring colonies were present, then water voles could persist in sub-optimal habitat. Similar results were found by Telfer et al. (2001) in highland populations: persisting populations were clustered together and the degree of isolation influenced distribution patterns. This implies that the dispersal ability of water voles partially determines habitat occupation. If suitable habitat is beyond the dispersal distance of individuals from an extant colony, it is likely to remain unoccupied.

The above factors affecting site occupancy suggest that water vole conservation in the UK is likely to require 1) habitat management and restoration to maintain or increase the size of extant populations; 2) existing populations to be safe-guarded via control of American mink; 3) management to increase linkage between isolated populations, and the re-introduction of water voles to areas too remote to be reached by natural dispersal. These actions constitute restoration ecology.

RESTORATION ECOLOGY

Restoration may be appropriate as a conservation action, either to reverse a process of deterioration and loss, or to reinstate a species which has been lost. It is restoration to repair, or even recreate, the habitat that a particular species or community requires (Macdonald et al., 2002a). Less obviously, restoration may involve not only the fostering of beneficial factors, but the removal of inimical ones (Macdonald et al., 2002a). Thus, control of American mink may constitute restoration for water voles.

The principle of restoration is so broad that it scarcely differs from conservation, the distinction being that the goal of conservation is to prevent deterioration, while that of restoration is to reverse it. Since most ecosystems are deteriorated, most conservation is restoration (Macdonald et al., 2002a).

Whatever the restoration measures, they need to have clearly defined objectives, the attainment of which allow the restoration to be considered a "success" (Macdonald et al., 2002a; Macdonald et al., 2002b). This will generally involve an endpoint which incorporates the particular species or community to be restored within a fully functioning ecosystem. Wheeler (1995) offers the generalisation, derived from consideration of plant community restoration, that a suitable end-point is that restoration "must result in the development of a self-sustaining semi-natural habitat (under a given management regime)". This is also applicable to restoring animal communities, a criterion for success being a viable, self-sustaining population in the wild (Ebenhard, 1995; Griffith et al., 1989; IUCN, 1998; Nolet & Baveco, 1996; Saltz & Rubenstein, 1995; Sarrazin & Barbault, 1996). This can be applied to both extant and re-introduced populations of water voles.

The success of actions to preserve extant populations and establish re-introduced populations are likely to relate to two factors: the degree of isolation of the population and the population size. Completely isolated populations cannot be "rescued" from extinction by immigration of dispersing individuals from larger populations (Brown & Kodric - Brown, 1977; Pulliam & Danielson, 1991), and cannot be recolonised after extinction (Hanski, 2001; Kareiva & Wennergren, 1995). Therefore for isolated water vole populations, in the absence of American mink, persistence will ultimately relate to the number of individuals they contain (Caughly, 1994).

Small populations are vulnerable to extinction through demographic and environmental stochasticity (for a review, see Caughly, 1994). Demographic stochasticity results from random variations in birth and death rates among individuals in a population. The smaller the population, the greater the impact on the average rate due to variability in each individual's contribution (Bevlovsky et al., 1994), and therefore the more likely it is that the population may go extinct (Caughly, 1994).

Environmental stochasticity is the effect of environmental fluctuations upon a population's demographic parameters (Caughly, 1994). Water voles are known to be vulnerable to flooding over winter and therefore subject to environmental stochasticity (Macdonald & Strachan, 1999). The environmental impact may be direct (via catastrophes such as flooding or fire) or indirect (e.g. annual variations in weather affecting the primary production). Environmental stochasticity increases the probability of extinction by adding to the background variation in the intrinsic rate of increase that is an inescapable consequence of demographic stochasticity (Macdonald

et al., 2002a). The persistence of the population of a given size is affected by the severity of the environmental fluctuations.

Threats to small populations are relevant to re-introduction since almost inevitably, re-introduced and translocated populations start small (Nolet & Baveco, 1996; Sarrazin & Barbault, 1996). The founding population should therefore be as large as possible and have a high rate of increase (Dunham, 1997; Griffith et al., 1989). Species with high fecundity (and therefore high population growth rate) will also tend to retain more of the original genetic diversity of the founders - which may mitigate adverse consequences of inbreeding depression (Caughly, 1994) - than will a species with low fecundity (Lesica & Allendorf, 1995; but see Leberg, 1993).

Following the IUCN (1998), re-introduction is an attempt to establish a species in an area which was once part of its range but from which it has been extirpated or become extinct. Animals for this purpose may be captive bred stock, or be translocated. Translocation is the deliberate and mediated movement of wild populations from one part of their range to another. Re-introductions using translocated individuals are more likely to be successful than those using captive bred animals (Griffith et al., 1989; Mallinson, 1995). However, finding sufficiently large extant populations which can act as a source of propagules may be problematic; therefore captive breeding from declining populations may be justified to fuel a re-introduction or supplementation programme (Macdonald et al., 2002a). As the national population of water voles in the UK continues to decrease (see Strachan et al., 2000), it is likely that re-introductions of captive bred individuals will become more important than from translocated populations.

Captive bred populations may have reduced genetic variation (Leberg, 1993; Sarrazin & Barbault, 1996) or individuals that exhibit behavioural deficiencies

(Shepherdson, 1994; Snyder et al., 1996) and so risk the loss of learned behaviours necessary for survival. Captive breeding is also a costly process, and these costs increase with the biomass of individuals of a species (Balmford et al., 1996). Disease problems have been common in captive populations of endangered species (Snyder et al., 1996). Wildlife re-introduction may therefore represent a significant disease risk (Viggers et al., 1993), both to the re-introduced individuals and to species extant at, and in close proximity to, the re-introduction site (Hess, 1996).

Water voles breed readily in captivity, have an extremely high rate of increase (Macdonald & Strachan, 1999; Strachan, 1998) have relatively low biomass (maximum of approximately 360g), and are likely to have fewer learned behaviours than larger, more social mammals. They are therefore an ideal candidate for re-introduction from captive breeding, and health screening of released individuals is increasingly common as a measure to avoid the spread of disease.

Re-introductions often fail. Beck et al. (1994) concluded that only 16 (11%) of 145 re-introduction projects they studied resulted in successful re-introduction. The most likely cause for failure is if the habitat into which the species is released is incorrect (Griffith et al., 1989). The correct habitat, and in the correct quantities is a necessity for the continued persistence of a given species (Gilpin & Soulé, 1986). This applies also to restoration of species. Griffith et al. (1989) state that "...without high habitat quality, translocations have low chances of success regardless of how many organisms are released or how well they are prepared for the release", and Balmford et al. (1996) state that "...by far the strongest determinant of re-introduction success is the availability of suitable habitat." Moreover, it is inappropriate to consider re-introduction or translocation as conservation tools until the causes of the

original decline have been both understood and remedied (Sarrazin & Barbault, 1996).

The correct quantity and quality of habitat is therefore crucial to the success of conservation measures to preserve or increase extant populations, and of re-introduction attempts. Variations in habitat quantity and quality ultimately determine the size of the populations that can be supported by that habitat (Ostfeld, 1985), and therefore the likelihood of extinction of those populations (Caughly, 1994).

Restoration ecology in general and re-introductions in particular are an "acid test for ecology" since they check our understanding of ecosystems (Sarrazin & Barbault, 1996). For water voles, restoration requires a thorough understanding of the species' habitat requirements, and therefore the interaction between habitat quality and quantity and population demography.

RESTORATION OF WATER VOLE POPULATIONS

Practical re-introduction strategies for water voles are still in the early stages (Strachan, 1998). At present re-introductions are performed by placing single male-female pairs into release pens separated by the distance of a female territory (Strachan, 1998). These are dug into the ground and supplied with food and water. Release pens provide three main functions: 1) they protect the released individuals from predation in the short term, post-release; 2) they allow the individuals to dig burrows into the substrate, so that by the time they escape the enclosure they have a pre-formed burrow system from which to establish a territory or home-range; 3) the spacing of the pens pre-determines the spacing of the territorial females so that each

can explore an area and establish a territory without immediate conflict with neighbouring females.

Re-introductions are more likely to be successful when large numbers of individuals are released and those individuals are able to quickly breed, increasing the population size (Dunham, 1997; Griffith et al., 1989). The spacing of release pens determines the numbers of water voles able to be released. If the pens are spaced too far apart, then the release cohort would be smaller than the optimum. If the pens were too close together, then too many individuals for a given length of habitat would be released, possibly leading to increased aggression, mortality and a reduction in breeding success. It is currently unknown how many individuals can inhabit a given quantity of habitat, how this affects their home-ranges, territories or behaviour, or indeed to what extent habitat quality may affect population density.

When restoring or managing habitat for water vole conservation, how much habitat to restore or maintain, and in what arrangement to best benefit the population under consideration, are important considerations in meeting the end-point of a self-sustaining population in the wild (Macdonald et al., 2002a; Macdonald et al., 2002b). These considerations should be complimented by the consideration of to what geographic location should the habitat be restored in order to allow dispersal between neighbouring populations; this requires knowledge of water vole dispersal rates and distances.

PREVIOUS STUDIES IN THE CONTEXT OF THIS THESIS

In this thesis I seek to supplement previous knowledge of the habitat requirements, population demography and social systems of extant water vole populations. From

this we may derive guidelines concerning the correct quantities and arrangement of habitat for water vole restoration, and best practise for re-introductions.

Water voles prefer sites with large quantities of riparian vegetation, which serves as both food and shelter (Barreto et al., 1998a; Barreto et al., 1998b; Macdonald & Strachan, 1999; Strachan, 1998; Strachan & Jefferies, 1993; Telfer et al., 2001; Woodall, 1977; Zejda & Zapletal, 1969), growing from easily penetrable earth or silt-shored banks of slow-flowing water courses into which they are able to burrow (Strachan & Jefferies, 1993; Telfer et al., 2001; Woodall, 1993; Zejda & Zapletal, 1969). All of these studies examining habitat requirements, however, have examined the *presence* or *absence* of water voles in relation to habitat features. It is possible, however, that variations in habitat quality between *extant* sites could affect population demography and hence population densities of water voles. I therefore examine the association of population parameters with variations in forage quantity between extant populations.

Female water voles are territorial during the breeding season (Macdonald & Strachan, 1999), having ranges that are typically small and non-overlapping (Efford, 1985; Leuze, 1976; Pelikan & Holisova, 1969; Stoddart, 1970). Male water voles are apparently non-territorial and have larger ranges that often overlap with each other, and may overlap with the ranges of several females (Efford, 1985; Leuze, 1976; Stoddart, 1970). Female dispersion in water voles is mediated by overt aggression during the breeding season (Leuze, 1976). Antagonistic encounters between males have also been recorded (Efford, 1985; Leuze, 1976), the frequency of which appears to relate to the presence of oestrous females within their ranges (Leuze, 1976).

It is unknown how changes in population density might affect home-ranges and social interactions of males and females, and what implications this may have for

numbers able to be released during re-introductions. Whether the size of male ranges is more restricted at high than low population densities, and what the social determinants of such a restriction would be, has not been examined in wild populations of small mammals, and in relatively few studies involving captive or enclosed populations (Bond & Wolff, 1999; Nelson, 1995a, b).

The short- and long-term patterns of range-use of both sexes of water voles are also currently unknown. It is unknown if females actively defend their entire territory over a short time period (e.g. a day; see Chapter 4), or visit their entire range over much longer periods; it is unknown whether males actively guard a selection of females within their ranges, or whether they visit their entire ranges over much longer periods. These questions can be answered by examination of the range-use patterns of each sex, and all have implications for habitat restoration and re-introduction strategies.

This thesis, therefore, analyses empirical data from extant water vole populations to derive practical guidelines for water vole conservation strategies. In doing so it addresses questions concerning background ecological theory of territoriality and ranging behaviour of small mammals.

THESIS CHAPTERS

Chapter 2

Impacts of variations in habitat quality upon population demography are addressed in Chapter 2. In this chapter I demonstrate an association between quantities of available forage and growth rates, body weights and population densities in three extant,

lowland populations of water voles. This has implications for water vole conservation in that it implies that simple habitat management strategies could influence the numbers of water voles in both extant, and re-introduced populations.

Chapter 3

Spacing and ranging behaviour and their association with population density of both males and females is addressed in Chapter 3. Chapter 3 presents evidence that the size of male water voles' ranges is limited by an optimum number of females they can overlap, and demonstrates that ranges of both males and females are smaller at higher population densities. Conversely, female ranges apparently reached a maximum size at low population densities. From Chapter 3 we can derive practical guidance for the ideal spacing of release pens for re-introductions into areas likely to contain different population densities of water voles.

Chapter 4

Temporal patterns of range-use by male and female water voles, and their association with variations in population density are addressed in Chapter 4. Chapter 4 demonstrates that female water voles exhibit drifting territoriality, possibly as a result of mating behaviour leading to flexibility in the size and position of female ranges. The degree to which female territories drifted was smaller at a site containing higher population densities. Chapter 4 also presents data concerning breeding dispersal rates of both sexes in lowland populations. From Chapter 4 we can derive guidelines for the spacing of release pens and the maximum distance between populations that

would allow dispersal, therefore partially answering questions of where to target restoration attempts with respect to existing populations.

Chapter 5

Chapter 5 presents observations from a radio-tracked population of water voles suggesting a link between the collaring of females in this population, a decline in female numbers throughout the radio-tracking period and an observed bias in the sex ratios of juveniles born during this period. This chapter contributes to our knowledge of maternal sex ratio adjustment in small mammals and has practical implications concerning the use of radio-tracking as a tool for monitoring both extant and re-introduced populations of water voles.

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Chapter 2

Habitat quality, individual growth rates and population densities of water voles (*Arvicola terrestris*)

ABSTRACT

Water voles (*Arivcola terrestris*) are an endangered species in the United Kingdom. Lowland populations of water voles are often spatially separated, and re-introductions of captive-bred animals are likely to be an important tool for the re-establishment of populations in areas of habitat too remote to be re-colonised by natural dispersal. The survival of extant, isolated populations, and the success of re-introduction attempts are likely to be influenced by population size and breeding success. Many studies of Arvicoline rodents have demonstrated that food supplementation results in larger population densities, body weights, growth rates and reproductive rates. Few studies, however, have examined effects of natural variations in forage availability upon population demography. If water vole population densities were determined by variations in food abundance, higher population densities should correlate with higher individual growth rates, body weights and larger amounts of available forage. The association of available forage with population density, body weights and growth rates was examined for three wild populations of water voles. The site with the highest population density contained the largest quantities of forage per individuals' range, and the site with the lowest density contained the smallest available quantities of forage. Higher population densities were associated with larger mean body weights and higher growth rates, such that individuals at the highest population density site reached breeding weight (approximately 140g) 20 days earlier, on average, than individuals at the lowest population density site. This suggests that the habitat of wild populations of water voles can influence growth-rates, body weights and population densities, such that increasing the quantity of available forage per unit length of waterway by 70% could potentially double the population density on site.

INTRODUCTION

Water voles (*Arivcola terrestris*) are an endangered species in the United Kingdom. Water vole numbers and distribution in the UK declined throughout the latter half of the last century (Jefferies et al., 1989; Strachan & Jefferies, 1993), representing the greatest decline of any British mammal (Macdonald & Strachan, 1999; Strachan & Jefferies, 1993; Telfer et al., 2003). The preliminary findings of the most recent national survey revealed that by the year 2000, 90% of the formerly occupied sites had been lost (Strachan et al., 2000).

Water vole populations in the UK can be roughly divided into two types. Upland populations tend to be arrayed along waterways and are typically subdivided into colonies consisting of a small number of individuals (Aars et al., 2001; Lawton & Woodroffe, 1991; Stoddart, 1970; Telfer et al., 2003). In these habitats, their distribution forms a metapopulation, in which extinction and recolonisation of habitat patches are at least partially determined by dispersal of individuals (Aars et al., 2001; Stewart et al., 1999; Telfer et al., 2001). Some lowland populations can be much more extensive, contain many more individuals and, latterly, have often become spatially separated from other such populations (Barreto & Macdonald, 2000; Barreto et al., 1998b; Carter & Bright, 2003; Telfer et al., 2001; Woodall, 1993).

This study examines the relationship between habitat quality and population demography, and concerns only lowland populations, in which relatively large numbers of individuals may live in close proximity within a given habitat.

Water voles' habitat preferences have been described in detail by many studies operating on a variety of spatial scales. Nearly all of these studies have attempted to associate the presence or absence of water voles at a given location with

its habitat characteristics (e.g. Lawton & Woodroffe, 1991; Woodall, 1993; Zejda & Zapletal, 1969). Latterly, this approach has been extended to include the effects of American mink (Barreto et al., 1998b; Bonesi et al., 2002; Macdonald & Strachan, 1999) and the proximity of other extant colonies of water voles (Bonesi et al., 2002; Telfer et al., 2001).

Studies by Barreto et al. (1998b), Bonesi et al. (2002) and Macdonald & Strachan (1999) demonstrate that occupation of habitats in lowland ecosystems are determined by three factors: 1) the presence of suitable habitat; 2) the absence of American mink; 3) the degree of isolation from other water vole colonies. Bonesi et al. (2002) found that water voles could be absent from optimal lowland habitats if conspecifics were absent from the immediate vicinity, but that if neighbouring colonies were present, then water voles could persist in sub-optimal habitat. Suitable habitat in lowland areas could remain unoccupied, even in the absence of American mink, if it were spatially isolated from extant populations of water voles.

Re-introductions of captive-bred individuals to isolated areas are likely to be employed for the recovery of lowland water vole populations (Macdonald & Strachan, 1999; Strachan, 1998). Both extant, isolated populations, and re-introduced populations can be affected by habitat quality and population size. Selection of the correct habitat is a critical concern when re-introducing a species (Balmford et al., 1996; Griffiths et al., 1989), and the correct habitat in the correct quantities is essential for species persistence (Gilpin & Soulé, 1986). Isolated populations cannot be "rescued" from extinction by immigration of dispersing individuals from larger populations (Brown & Kodric - Brown, 1977; Pulliam & Danielson, 1991), and their persistence is therefore strongly influenced by the number of individuals they contain (Caughley, 1994). Small populations are vulnerable to the combined influences of

demographic stochasticity, environmental stochasticity and inbreeding depression (Caughley, 1994), and so extant, isolated populations should be as large as possible (Ritchie, 1997).

Almost invariably re-introduced populations start small (Nolet & Baveco, 1996; Sarrazin & Barbault, 1996), and re-introduced populations should therefore have a high rate of increase (Dunham, 1997; Griffith et al., 1989) to counteract this. In lowland areas, therefore, the probability of extant populations persisting and the chances of success when re-introducing or translocating water voles may be improved by factors which increase recruitment rates or decrease predation rates, thereby increasing population size.

Restoration of large swathes of riparian habitat has been frequently cited as a necessary conservation strategy for water voles (Barreto et al., 1998a; Barreto et al., 1998b; Macdonald & Strachan, 1999; Strachan, 1998; Strachan et al., 2003). Barreto et al. (1998b) state that "expansive riverside habitats appear to be essential for self-sustaining water vole populations." No studies, however, have explored impacts of variations in habitat quality or quantity upon water vole population demography within occupied, lowland habitats. Vegetation serves as both shelter and food for water voles (Barreto et al., 1998a; Macdonald & Strachan, 1999; Strachan, 1998; Zejda & Zapletal, 1969). Effects of habitat variations upon water vole populations would therefore be expected to be mediated via access to forage and / or protection from predation (Barreto et al., 1998a).

Increasing the quantities of vegetation available to water voles may increase survival rates by providing refuges from over-winter flooding (Macdonald & Strachan, 1999) or lowering predation risk by increasing the amounts of available

cover (Barreto et al., 1998a). Increasing quantities of vegetation would also increase food abundance.

Food resources have been shown to be linked to a suite of demographic characteristics in Arvicoline rodents (for a review see Ostfeld, 1985). Many studies demonstrate higher population densities in populations of Arvicoline rodents where food resources have been artificially increased (Abdellatif et al., 1982; Andrzejewski, 1975; Cole & Batzli, 1978; Desy & Batzli, 1989; Desy & Thompson, 1983; Gilbert & Krebs, 1981; Jonsson et al., 2002; Koskela et al., 1998; Taitt & Krebs, 1981, 1983), often associated with concomitant increases in body weight and growth rates within the same study (Abdellatif et al., 1982; Desy & Thompson, 1983; Koskela et al., 1998; Taitt & Krebs, 1981, 1983).

Food abundance has the potential to influence rates of recruitment via increased reproductive success and / or immigration (Andrzejewski, 1975; Desy & Thompson, 1983; Koskela et al., 1998; Taitt & Krebs, 1981, 1983). Relatively few studies, however, have demonstrated demographic consequences of variations in food abundance in natural habitats (Ostfeld, 1985).

Water voles' ranges are often considered to be two-dimensional, comprising a relatively thin, linear *length* of habitat utilised over a given time period (Lawton & Woodroffe, 1991; Stoddart, 1970). However, habitat *width* may influence population demography by increasing levels of food and shelter available over a set length of habitat. Water voles rely upon abundant, low-quality and evenly distributed food resources which renew rapidly (Efford, 1985). They are therefore "grass-eating" or "GSH diet" (Grasses, Sedges and Horsetails) voles (Ostfeld, 1985, 1990), living in a "sea of green energy" (Wolff, 1993). It is unknown whether it is possible to demonstrate effects of the quantity of vegetation available upon water voles'

population demography since sites with extant populations are usually assumed to contain "suitable" habitat and therefore abundant quantities of vegetation.

If quantities of vegetation within water voles' habitats affected population densities, sites with higher population densities may be expected to contain wider margins of vegetation. If increased levels of vegetation mainly acted upon population density through effects of increased food abundance, rather than by reducing predation risk or risk from flooding, sites with higher population densities would also be expected to contain individuals exhibiting larger body weights and higher growth rates than sites with lower population densities.

This chapter presents data from three separate, lowland water vole populations supporting different population densities, examining the association of growth rates, body weights and population densities with the quantity of forage available at each site.

METHODS

Study sites

The Bure Marshes NNR (UK grid ref: TG 335 165) is a fenland habitat managed by English Nature, comprising fields of fen vegetation surrounded by a network of ditches in which the water voles occupy ranges. Within the study area, live traps (Sherman XLK 3 x 3.5 x 12" folding aluminium with galvanised steel doors) were deployed along 4.07 km of ditch-edge. Data for this study derives from live-trapping of water voles at this site in 2001 and 2002. Trapping occurred from April to September in 2002. Public health restrictions, due to an outbreak of Foot and Mouth

disease, prevented trapping between April 2001 and June 2001, and so this site was trapped from June to September in 2001. During 2001 and 2002 the mean population densities at the Bure Marshes were 1.45 (standard deviation +/- 0.28), and 1.04 (+/- 0.13) voles per 100m length of habitat respectively, based upon minimum number known alive over the trapped length of habitat (Chapter 3).

The Wendover Canal (SP 873 102) site comprised a single stretch of non-navigable canal with a total length of 4.12km. However, the suitable water vole habitat was interspersed with heavily wooded, over-shaded sections in which no sign of water voles was found at any time. Traps were deployed along all sections in which water vole sign was found, a total of 2.03km. Trapped sections extended 40m (two trap lengths) into the unoccupied habitat either side of the outermost field-sign of an occupied section. Throughout the study no water vole was captured more than 20m from the outermost field-sign of an occupied section, and only occupied areas are used in the following analyses. Trapping data for this study derives only from 2001. Due to Foot and Mouth disease restrictions operating in April and May 2001, this site was live-trapped from June to October in 2001. During this time, the mean population density of suitable habitat was 3.25 (+/- 0.98) voles per 100m. Over winter 2001-2002 the entire Wendover Canal population was lost due to predation by an American mink (*Mustela vison*).

The Little Bedwyn stretch of the Kennet and Avon Canal (SU 295 665) comprises a length of canal which runs parallel to the river Dun, separated from it by a mown field varying between a 20m and 60m width. Live-traps were deployed along 1.04km of the canal and 960m of the river. Traps were also set around the 120m perimeter of a small pond less than 20m from the river. The total water's side trapping at this site was therefore 2.12km. The Little Bedwyn site was trapped from June 2002

until July 2003. Mean population density for the entire site for this period was 2.08 (+/-0.48) voles per 100m.

Research design

Population densities were highest at the Wendover Canal (3.25 voles per 100m, 2001), lower at the Little Bedwyn site (2.08 voles per 100m, 2002/2003) and lowest at the Bure Marshes (1.45 voles per 100m, 2001; 1.04 voles per 100m, 2002). If food resources influence population density at these sites, the highest levels of forage, largest body weights and highest individual growth rates would be expected at the Wendover Canal, lower rates at the Little Bedwyn site, and the lowest at the Bure Marshes.

Weather conditions in a given year, however, could directly influence body weights, growth rates and population densities (e.g. Devender, 1978). Also, the portion of the 2001 season lost to Foot and Mouth Disease precautions had the potential to affect mean body weights and growth rates for that year (see Results). Direct statistical comparisons, therefore, were limited to sites trapped in the same year.

Analysis of the Bure Marshes and the Wendover Canal comprises a comparison of growth rates and body weights between low density and high density populations respectively for June-September 2001. The Bure Marshes and Little Bedwyn analysis comprises a separate comparison of growth rates and body weights between low density and high density populations respectively in 2002-2003. The June-September 2002 period can be compared directly between these sites. Comparison of the April - May period, however, is necessarily made between

separate years of the study (2002 for the Bure Marshes and 2003 for Little Bedwyn); inferences from this period are therefore made with caution. Over-winter periods were not compared between sites since food reserves are considerably less abundant during this period (Strachan, 1998).

Increases in population density may be accompanied by increases in observed survival and recruitment rates. External considerations, however, prevented robust comparison of recruitment or survival rates based on Capture Mark Recapture (CMR) data from each site. Firstly, loss of the Wendover Canal population due to predation by an American mink over-winter 2001-2002 prevented any comparison of over-winter mortality between the Bure Marshes and Wendover Canal. Secondly, radio-collaring of individuals in the Bure Marshes population at the end of the 2001 field season and during the 2002 field season may have affected recruitment, and potentially survival rates at this site (Chapter 5). Examination of survival and recruitment rates *per se* would, however, be uninformative as to mechanisms by which habitat could affect population demography at each site. Inferences, therefore, are based only upon body weights and growth rates.

Radio-collaring of individuals at the Bure Marshes is not expected to influence either mean population weights or growth rates since only individuals of greater than 180g were collared, the weight at which growth rates would be expected to be approaching an asymptote (S_{max}; Kaufmann, 1981). There was no evidence of collared animals having lost weight post-collaring. Of 18 collared individuals for which before-and-after collaring weights were available, the mean weight at collaring was 240g (standard deviation +/-20g). Of these, 9 individuals gained weight, 7 lost weight and 2 remained at the same weight. This pattern is similar for individuals of

this size at other sites, where individuals frequently exhibited negative growth at higher body weights (Results).

Females and males exhibited no differences in growth rates or mean weights in any analysis (see Results). Any skew in sex ratios of recruits due to effects of collaring (Chapter 5) would therefore not be expected to have an effect on body weights or growth rates since growth rates and weights of both sexes were similar.

Trapping protocol

Traps were positioned 20m apart and their positions recorded with a 10-figure grid reference using a *Garmin* "Etrex" GPS to a maximum error of 10m. Following the general protocol of Efford (1985), traps were baited with apple, and contained approximately 150g of carrot as an overnight food source.

All water voles captured were weighed to the nearest 5g, marked if a new capture, and sexed. In order to minimise trapping-related gains or losses of body weight, only the weight on first capture was used to represent an individual's weight for a given trapping session.

During 2001, half of the Bure Marshes and the Wendover Canal were trapped alternately, with both halves of each site trapped in each month where possible. During this period, traps were set on Monday and removed on Friday, and thus open for 4 trap nights. During 2002, the entire of the Bure Marshes and the Little Bedwyn site was trapped during each trapping session, with one trapping session each per month. At the Bure Marshes, each half was trapped in alternate mornings and afternoons, allowing one capture period per day for each half from Monday to

Saturday of each session. The entire Little Bedwyn site was trapped with one session a month of morning captures from Monday to Saturday, allowing 5 trap nights.

Analysis of factors affecting specific growth rates

Growth rate estimation follows the methods of Kaufmann (1981). *Specific growth rate* (G), the rate of growth at a specific weight, was estimated as (lnS2 – lnS1) / t for each individual, where S1 and S2 are body weight in the first and second capture sessions, separated by t days. This was plotted against ln (S), where S is the geometric mean of S1 and S2. This forms a straight line plot in which the slope (a) and intercept on the y axis (b) for the Gompertz curve are related as follows:

Equation 1 $G = -a \ln S + b$

This linear relationship allows *specific growth rate* to be used as the response variable in a General Linear Model (GLM). Similar techniques have been used to examine growth rate patterns of other small herbivorous mammals (Boutin & Larson, 1993; Virgl & Messier, 1997; Webb, 1993).

The integrated form of Equation 1 can be used to predict the age of an individual from its weight on first capture by solving the following equation:

Equation 2 $S = S_{max} \exp [-\exp -a (t + t_0)]$

where $S_{max} = \exp (b/a)$ and t_0 is the constant of integration. This study uses a constant of integration derived from water voles measured at age 16 days weighing

47.8g (data from Bristol Zoo, 3 litters, n = 14). This compares favourably with the constant (t_0) used in another water vole study: Efford (1985) used a constant of integration of 60g at 20 days (Bure Marshes growth curves in this study estimate voles at 60g as being 20-26 days old). Changing t_0 does not affect the shape or the asymptote of the growth curve, but merely moves the curve right or left along the abscissa (Kaufmann, 1981). Comparisons of growth rates and maximum weight (S_{max}) reached based upon Equation 2, and incorporating t_0, are unaffected by any error in the measurement of t_0 if compared across a set time period and from the same starting weight. In all analyses, growth rates are compared between sites over a 50 day period following t_0 (day 16, weight = 47.8g).

Habitat analysis

Quadrat based techniques have been used to compare site characteristics with water vole presence and absence in a number of previous studies (Aars et al., 2001; Lawton & Woodroffe, 1991; Telfer et al., 2001; Woodall, 1993; Zejda & Zapletal, 1969). Quadrat techniques allow objective sampling of habitat characteristics at set intervals. Since occupied habitat at each site was relatively homogenous (pers. obs.), these techniques are likely to be sufficient to represent the habitat at each site.

Habitat characteristics were recorded at each site at 60m intervals (equating to approximately 3 trapping-intervals) for each study site on the trapped side only. For consistency, all quadrats were surveyed in July at each site so that inter-site differences would be less attributable to seasonality in vegetation growth patterns. In total, 61 quadrats were analysed for the Bure Marshes, 34 for the Wendover Canal and 36 for the Little Bedwyn site.

At each site there was a clear boundary demarking the width of the riparian vegetation bordering the water course. At the Bure Marshes this was where droves (paths) were regularly cut running parallel on each side of every ditch on site. At the Wendover canal, the boundary was marked by the width of the canal bank, ending at the towpath. At the Little Bedwyn site, the boundary was marked by a fence along one half of the canal and a field margin on the other half and the river, beyond which the vegetation was regularly mown.

Quadrats were assessed for a 1m length of bank at all sampling points. Percentage cover of vegetation cover was estimated for each species in each quadrat using the Domin scale for the entire width of the vegetation present. Thus the "quadrat" was a strip of length 1m and the same width (perpendicular to the bank) as the habitat present.

Habitat measurements taken per 1m length of bank were:

1) Width of the bank vegetation, to the nearest 5cm;
2) Width of emergent vegetation (vegetation growing out of the water as opposed to out of the bank), to the nearest 5cm;
3) Overall percentage cover of bank vegetation;
4) Overall percentage cover of emergent vegetation.

Since water voles appear to have catholic vegetation preferences throughout their range (e.g. Lawton & Woodroffe, 1991; Telfer et al., 2001; Woodall, 1993; Zejda & Zapletal, 1969), incorporating at least 227 plant species (Strachan & Jefferies, 1993), analysis of food resources was based upon the overall cover of green macrophytes (termed *green forage* hereafter) at each sampling point, rather than upon individual species. *Green forage* here is distinct from *litter cover*, the inedible, un-

decayed remains of last year's vegetation (which may still offer shelter from predation). For the Wendover site, quadrats were only scored for the occupied stretches but for the Bure Marshes and Little Bedwyn, all riparian habitat at both sites was occupied and therefore surveyed.

Statistical analysis

All statistical analyses were conducted in Minitab (version 13). Two pairs of statistical analyses are presented.

Factors affecting the weight of water voles in the Bure Marshes versus Wendover Canal comparison, and in the Bure Marshes versus Little Bedwyn comparison, were assessed by using body weight as the response in a General Linear Model (GLM). Individuals may have been captured in more than one capture session and to avoid pseudoreplication such cases were randomly deleted to create a one-individual-one-datapoint set. Available factors to explain variations in body weight were *study site*, *month* of capture (entered as a covariate since a linear effect of season upon growth and body weight was expected: Devender, 1978), *sex* of each individual, and *year* of capture (Bure Marshes versus Little Bedwyn comparison only).

Factors affecting *specific growth rates* in both comparisons were assessed by using *specific growth rate* as the response variable in a GLM. Available explanatory variables were the *natural log of the weight* of each individual, ln(S); the *sex* of the vole; *study site*; *month* (entered as a covariate) and *year* (Bure Marshes versus Little Bedwyn analysis only) of capture. *Specific growth rate* was calculated from the increase in weight over two trapping sessions in different months. To avoid pseudoreplication, data from water voles that were captured in more than two capture

sessions (therefore having more than one measured *specific growth rate*) were randomly deleted to create a one-individual-one-datapoint set. The measure of *month* used in the analysis was the month in which the individual was first captured.

RESULTS

Weights of voles at the Bure Marshes and Wendover Canal

The most parsimonious GLM explaining variance in weight of water voles contained effects only of *study site* ($F_{1,232} = 9.70$, $p < 0.005$) and *month* ($F_{1,232} = 8.25$, $p < 0.005$; estimate -7.86, s.e. 2.74). Effects of *sex* were non-significant when entered ($F_{1,232} = 0.00$, $p > 0.9$).

Individuals at the Wendover Canal (marginal mean weights 189.9g, standard error 5.14) were heavier than at the Bure Marshes (168.0g, s.e. 4.77) in each month. Fig. 1 shows the decrease in mean population weight for both sites due to effects of *month* over the breeding season, and demonstrates that for all months the mean weight of individuals was higher at the Wendover Canal than the Bure Marshes.

Weights of voles at the Bure Marshes and Little Bedwyn site

The most parsimonious GLM explaining variance in weight of water voles in this comparison contained effects only of *study site* ($F_{1,176} = 19.72$, $p < 0.001$) and *month* ($F_{1,176} = 26.57$, $p < 0.001$; estimate -13.38, s.e. 2.59). Effects of the *sex* and *year* were non-significant in a model in which they were entered ($F_{1,166} = 0.03$, $p > 0.8$; $F_{1,166} = 2.27$, $p > 0.1$ for *sex* and *year* respectively). Individuals at the Little Bedwyn site

Figure 1: Mean body weight for each month at the Bure Marshes (circular points and solid line) and Wendover Canal (triangular points and dotted line) comparison (2001), showing the decrease in mean body weight at each site over each month.

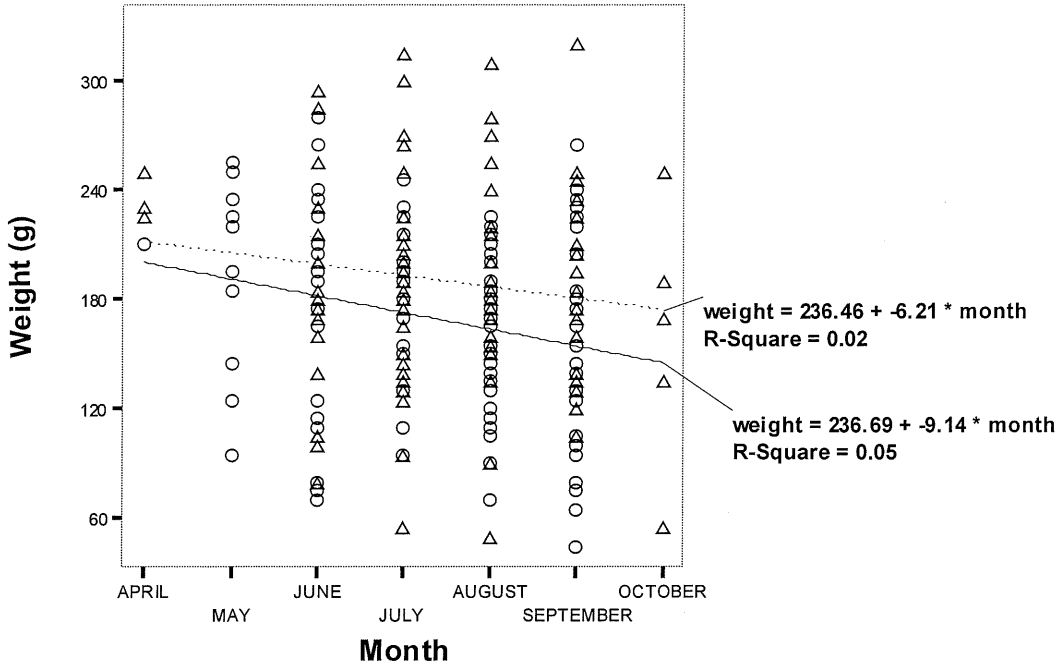
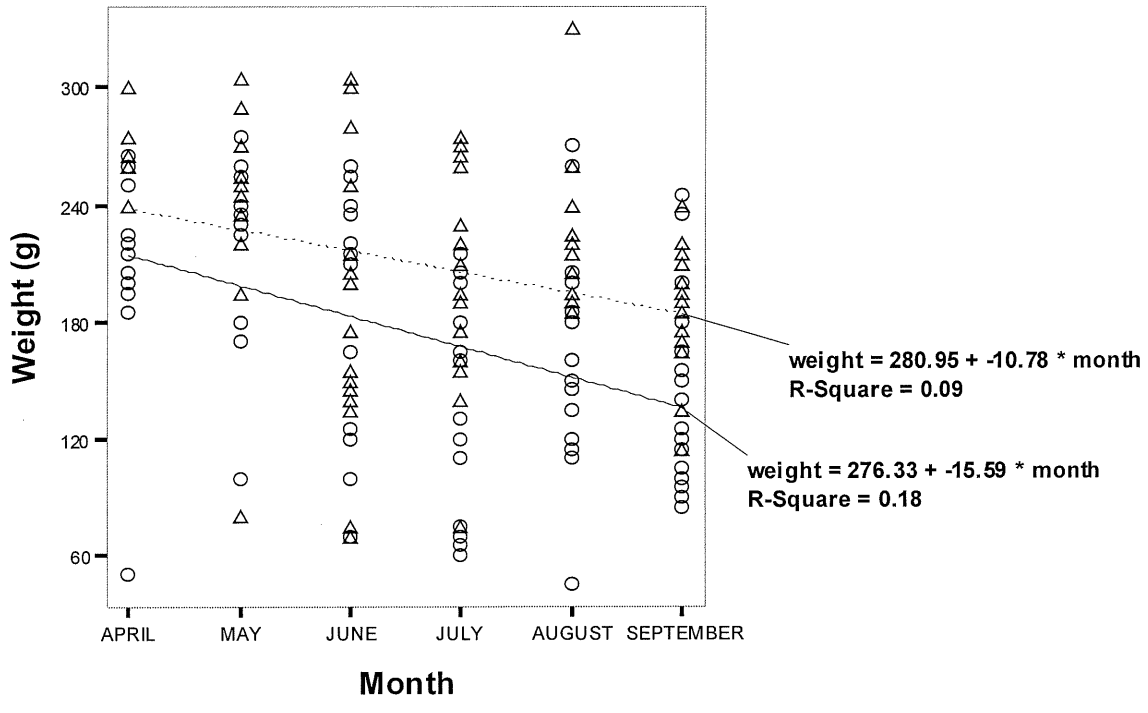


Figure 2: Mean body weight for each month at the Bure Marshes (circular points and solid line) and Little Bedwyn site (triangular points and dotted line) comparison (2002 / 2003), showing the decrease in mean body weight at each site over each month.



(marginal mean weight 207.5g, s.e. 5.94) were heavier than those at the Bure Marshes (170.1g, s.e. 5.97). For all months the mean weight of individuals was higher at Little Bedwyn than at the Bure Marshes (Fig 2).

Specific growth rates *at the Bure Marshes and the Little Bedwyn site*

The most parsimonious model explaining variations in *specific growth rate* for the Bure Marshes and Little Bedwyn site contained effects of the *natural log of weight* ($F_{1,118} = 310.42$, $p < 0.001$; estimate -0.0221, s.e. 0.0074), *month* ($F_{1,118} = 14.46$, $p < 0.001$; estimate -0.0011, s.e. 0.0003) and *study site* ($F_{1,118} = 19.89$, $p < 0.001$). Effects of *sex* and *year* were non-significant when entered in the model ($F_{1,118} = 0.84$, $p > 0.3$; $F_{1,118} = 1.34$, $p > 0.2$ respectively).

Fig. 3 shows the relationship between *specific growth rate*, the *natural log of body weight*, and *study site*. For all body weights, voles at the Little Bedwyn site had higher *specific growth rates* than those at the Bure Marshes. The slopes, intercepts, S_{max} (mean maximum weight reached) and growth rates averaged over 50 days [calculated from Equation 2, Methods, using the 50 day period after t_0] are listed in Table 1.

Table 1: Slope, intercept, S_{max}, mean daily growth rate and number of individuals calculated from the growth equations for the Bure Marshes and Little Bedwyn site

Site	Slope (a)	SE	Intercept (b)	S_{max} (g)	Mean growth rate (g/day)	Number of individuals
Bure Marshes	-0.0200	0.00165	0.1085	223.6	1.58	43
Little Bedwyn	-0.0208	0.00182	0.1160	261.4	1.92	76

Figure 3: The relationship between *specific growth rate* and ln (S) at the Bure Marshes (circular points and solid line) and Little Bedwyn site (triangular points and dotted line), indicating that for each body weight, *specific growth rates* at the Little Bedwyn site were higher than at the Bure Marshes.

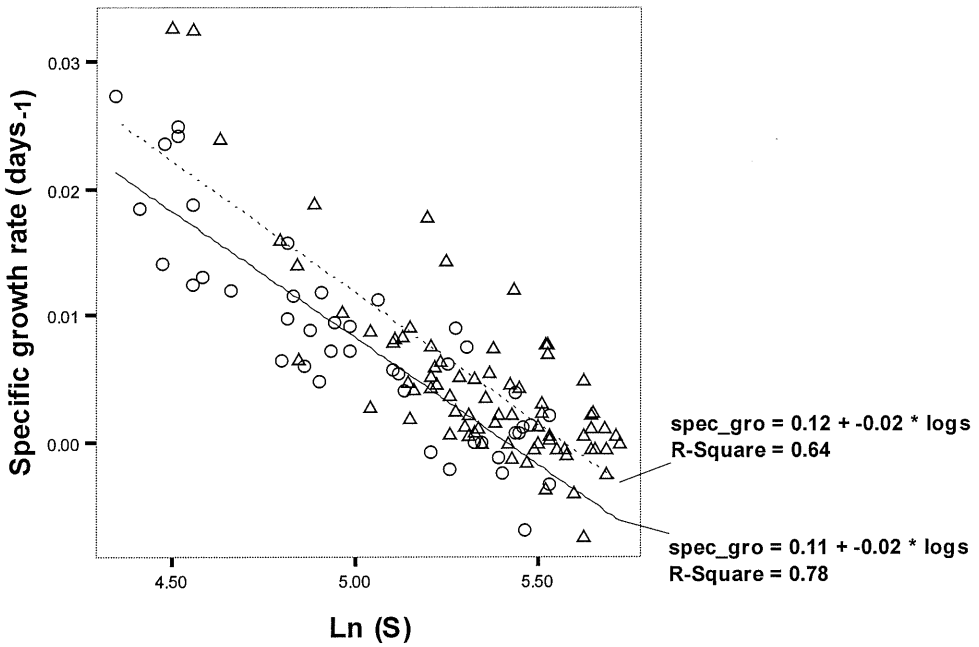


Figure 4: The relationship between *specific growth rate* and ln (S) at the Bure Marshes (circular points and solid line) and Wendover Canal (triangular points and dotted line), indicating that for each body weight above S_{max} (where *specific growth rate* = 0), *specific growth rates* at the Wendover Canal were higher than at the Bure Marshes.

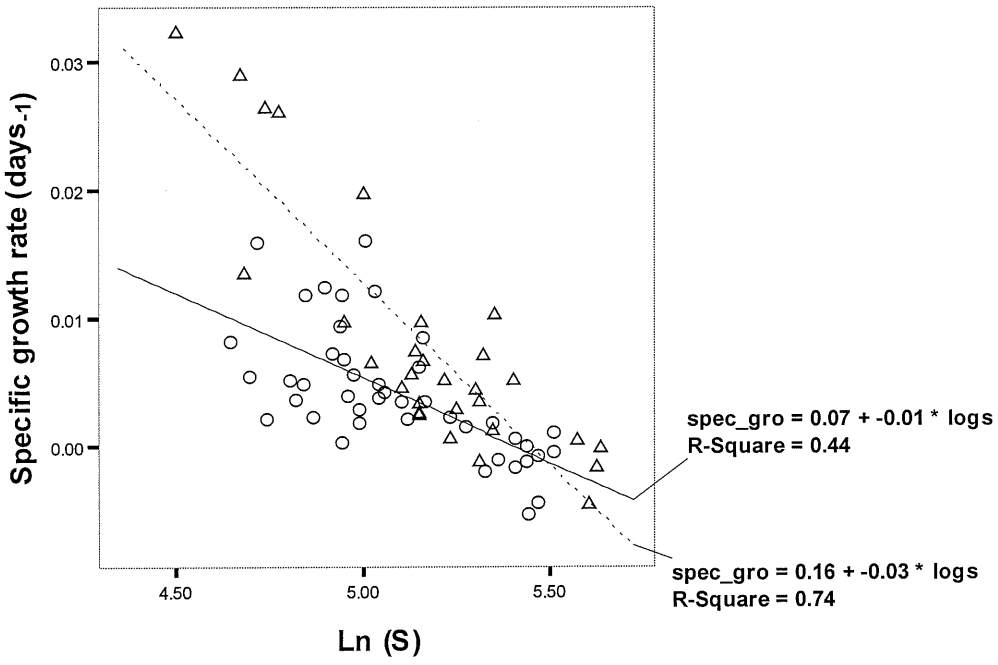


Table 1 demonstrates that individuals at the Little Bedwyn site had higher mean daily growth rates than did individuals at the Bure Marshes. This represents an approximately 17g additional increase in weight over the first 50 days following t_0. Individuals at the Little Bedwyn site also stopped growing at a higher body weight (S_{max} = 261g) than did individuals at the Bure Marshes (S_{max} = 224g).

Increasing *month* had a linear, negative effect upon *specific growth rates* over this range of months, indicating that water voles at both sites of a given body weight grew faster at the beginning of the year than at the end. This effect is unlikely to stem from inter-annual variation over the April-May period as effects of *year* were non-significant and analysis of the Bure Marshes and the Little Bedwyn site separately indicates that the same model fits both sites independently ($F_{1, 47} = 4.81$, $p < 0.05$; $F_{1,75} = 12.49$, $p = 0.001$, for the Bure Marshes and Little Bedwyn sites respectively).

Marginal mean *specific growth rates* are presented in Table 2, demonstrating the linear decline in *specific growth rate* over the year.

Calculating separate growth curves for the April-May and July-August periods allows calculation that the growth rates over the 50 days following t_0 for were 1.78g per day in April-May and 1.58g per day in July-August. This would represent a 10.17g difference in body mass gained over a 50 day period following t_0, due to the effects of season upon growth rate.

Specific growth rates *at the Bure Marshes and the Wendover Canal*

The most parsimonious GLM explaining variance in *specific growth rate* for the Bure Marshes and Wendover Canal contained only an interaction between the

Table 2: Marginal mean *specific growth rates* for each month of each analysis. Numbers in brackets represent standard errors.

Month	Bure Marshes versus Little Bedwyn	Bure Marshes versus Wendover Canal
April	7.5 (0.84)	Not trapped
May	7.0 (0.84)	Not trapped
June	6.1 (0.62)	8.1 (0.11)
July	3.9 (0.55)	6.2 (0.86)
August	3.8 (0.92)	5.9 (0.92)

natural log of weight and *study site* ($F_{1,72} = 18.08$, $p < 0.001$). Effects of *month* were non-significant ($F_{1,72} = 2.39$, $p > 0.1$) when entered. The interaction between the *natural log of weight* and the *study site* upon *specific growth rate* is presented in Fig. 4. Fig. 4 indicates that for all periods until *specific growth rate* became zero (S_{max}), growth rates at the Wendover Canal were higher than for the Bure Marshes. The interaction apparently derives from lighter individuals at the Wendover Canal having disproportionally high *specific growth rates*, coupled with a greater decrease in *specific growth rate* for each increase in body mass than at the Bure Marshes.

The slopes, intercepts, S_{max} and growth rates averaged over 50 days following t_0 are listed in Table 3.

Table 3: Slope, intercept, S_{max}, mean daily growth rate and number of individuals calculated from the growth equations for the Bure Marshes and Wendover Canal

Site	Slope (a)	SE	Intercept (b)	S_{max} (g)	Mean growth rate (g/day)	Number of individuals
Bure Marshes	-0.0133	0.00233	0.0718	221.4	1.06	43
Wendover Canal	-0.0286	0.00321	0.1558	232.0	2.24	30

Table 3 shows that individuals at the Wendover Canal had over double the growth rate of those at the Bure Marshes, representing a 58g additional increase in weight over the first 50 days following t_0. The mean maximum weight reached at the Wendover Canal was approximately 10 grams higher than that at the Bure Marshes (S_{max} = 232.0 compared to 221.4). Growth rates of individuals at the Wendover Canal over the first 50 days following t_0 were the highest of any site.

There was no significant effect of *month* in this model, probably due to the short study season (June - September). Marginal means for *month*, however, reveal that the mean *specific growth rate* for a given weight did decrease from June to September (Table 2) at these sites. The decrease in *specific growth rate* over the June-August period compares favourably with the decrease in rates for the Bure versus Bedwyn analysis for the same months.

Body weight and reproductive status

Figs. 5a and 5b present combined data from all three study sites showing the reproductive status of individuals (n = 605) captured at different body weights. Reproductive males had descended testes and reproductive females had perforate vaginas (Carter & Bright, 2003; Stoddart, 1971), with non-reproductive animals not exhibiting these characteristics. An approximate minimum of 85% of individuals of both sexes captured were in reproductive condition if captured at a weight above 140g: this "threshold" weight was within 5g of these values at all sites.

Of 307 females which were captured (all sites combined) above a 140g weight only 11 exhibited imperforate vaginas. Of these, 7 were trapped at the Bure Marshes, 2 at the Wendover Canal and 2 at the Little Bedwyn site. Six were trapped between

Figure 5a: The percentage of male water voles captured with abdominal or scrotal testes at each body weight. Data from all three study sites, n = 401 individuals. The solid line and square points represent abdominal testes and the dotted line and triangular points represent scrotal testes.

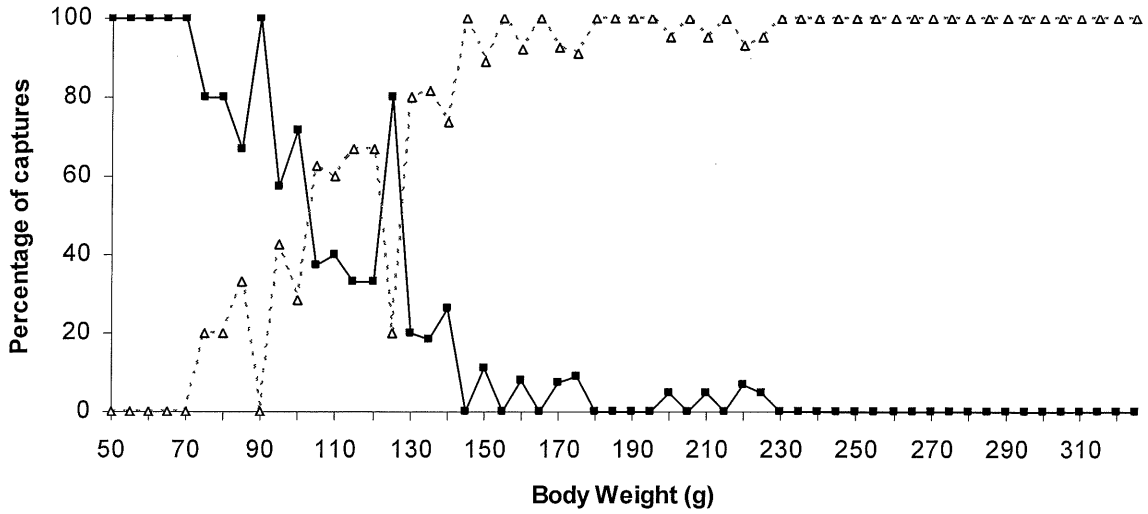
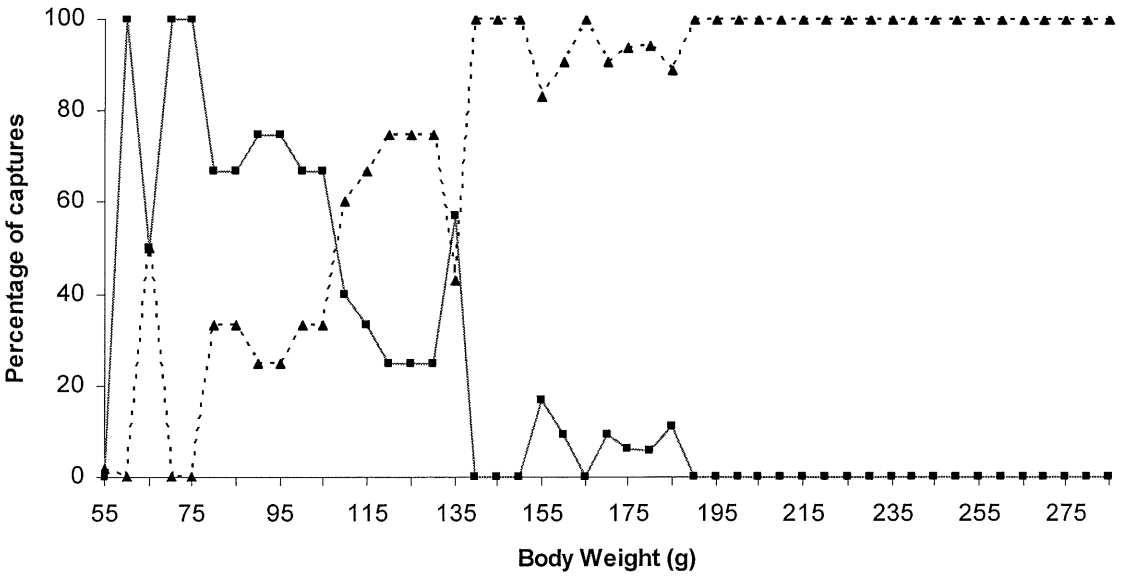


Figure 5b: The percentage of female water voles captured with perforate or imperforate vaginas at each body weight. Data from all three study sites, n = 204 individuals. The solid line and square points represent imperforate vaginas and the dotted line and triangular points represent perforate vaginas.



April and June and 5 between July and September.

Of 296 males which were captured above a 140g weight only 13 exhibited abdominal testes. Of these 3 were trapped at the Bure Marshes, 8 at the Wendover Canal and 2 at the Little Bedwyn site. Three were trapped between April and June and 10 between July and September.

Body weight apparently directly related to sexual maturation in water voles during the breeding season. There was no evidence that individuals of either sex captured in any study site or month consistently reached sexual maturity at lower or higher weights. Very few individuals of either sex captured above 140g were not in reproductive condition.

From the growth curves for each site, individuals reached 140g at a mean age of 56 days old at the Wendover Canal, 65 days old at the Little Bedwyn site and 76 days old at the Bure Marshes. Inter-site differences in growth rate could therefore have produced differences in the time that individuals took to reach breeding weight (in this case a 20 day difference in the time taken to reach 140g).

Amounts of green forage *available per water vole range*

The area of *green forage* available per metre of bank for both bank and emergent vegetation is equivalent to the measured *width* of the vegetation multiplied by its overall *percentage cover*. For example, a 3m width of emergent vegetation at 50% cover is equivalent to 1.5m^2 of emergent vegetation forage per metre length of habitat.

Figs. 6a and 6b present the mean area of *green forage* available on the bank and from the emergent vegetation per metre of bank-length at each site. Both the

Figure 6a: Area of *green forage* from bank vegetation per metre length of bank at each study site. Error bars represent standard errors.

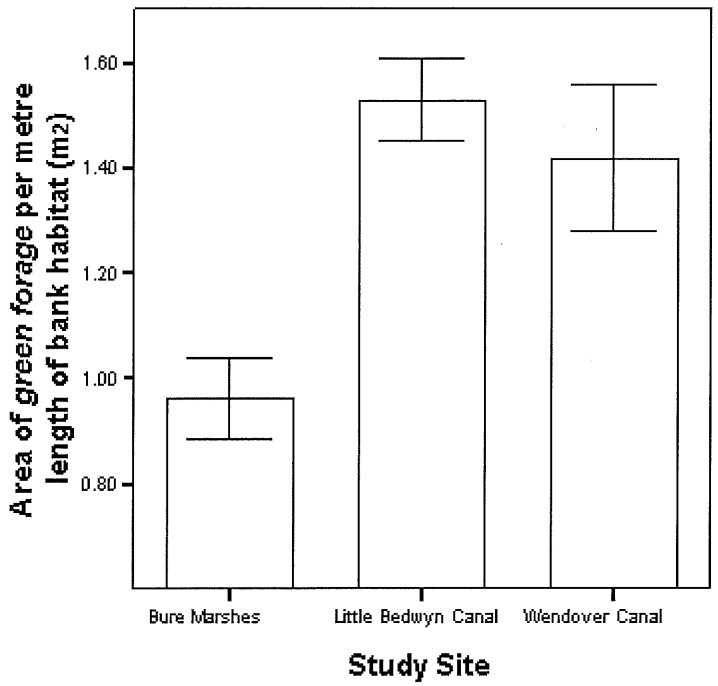
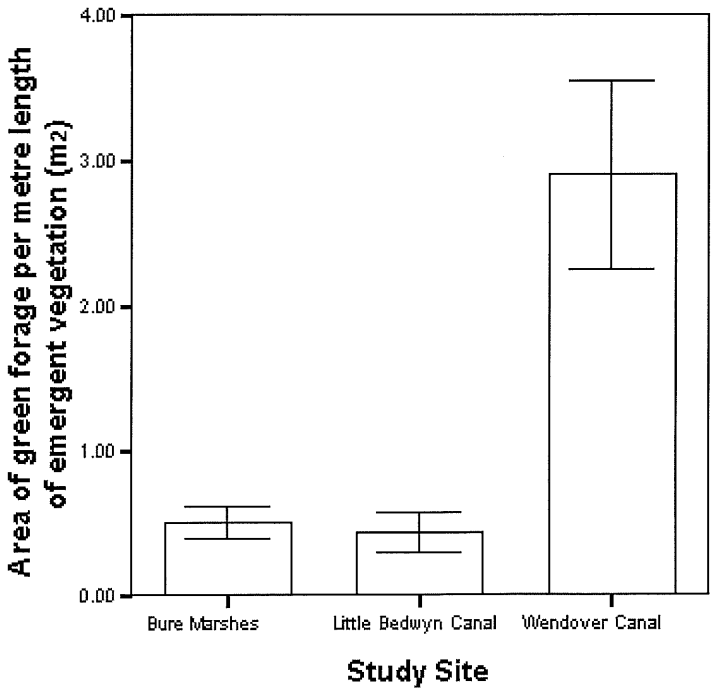


Figure 6b: Area of *green forage* from emergent vegetation per metre length of bank at each study site. Error bars represent standard errors.



Little Bedwyn site and the Wendover Canal had a greater area of *green forage* available per metre length of bank habitat than did the Bure Marshes (Kruskal-Wallis test; $H = 19.40$, d.f. $= 2$, $p < 0.001$), equating to at least an additional $0.4m^2$ of habitat per metre length of bank (Fig. 6a).

The area of emergent vegetation per metre of bank-length at the Bure Marshes and the Little Bedwyn site was similar. The Wendover Canal, however, contained over three times the area of either (Kruskal wallis test $H = 17.76$, d.f. $= 2$, $p < 0.001$; Fig. 6b). Emergent vegetation was a preferred feeding habitat for water voles at the Wendover Canal, and they were often seen feeding several metres from the bank on floating beds of Watercress (*Rorippa nasturtium-aquaticum*).

Water voles had different observed range lengths (*sensu* Pelikan & Holisova, 1969) at all three sites (Chapter 3). The amount of forage available to an individual at each site can be estimated by multiplying the *per metre* area of forage by the observed range lengths of individuals at each site. Detailed analysis of the ranging behaviour is discussed elsewhere (Chapter 3; Chapter 4).

Table 4: Areas of forage available per metre at each study site, calculated as the mean area of forage per metre multiplied by the mean observed range length of water voles at each site.

	Bure Marshes	Wendover Canal	Little Bedwyn site
Observed range length (m)	63 (62m in 2001 and 63m in 2002)	29	53
Area of bank vegetation per ORL (m^2)	60	43	81
Area of emergent vegetation per ORL (m^2)	32	97	23
Total available forage per ORL (m^2)	92	140	104

Table 4 presents the mean area of available habitat per observed range length for water voles at each site. The mean observed range lengths of water voles at the Little Bedwyn site and the Wendover Canal were shorter than those at the Bure Marshes (53m and 29m, as opposed to 63m per vole; Chapter 3). Nevertheless, the area of forage per metre of bank length was sufficient that individuals at these sites had access to larger areas of *green forage* than individuals at the Bure Marshes (Table 4).

DISCUSSION

Body weights and growth rates of individuals at the (high population density) Wendover Canal and Little Bedwyn sites were significantly larger than those at lower population densities at the Bure Marshes throughout the breeding season in both comparisons. Both sites contained more *green forage* per mean observed range length than the Bure Marshes, despite the fact that water voles at the Wendover Canal and Little Bedwyn sites had substantially shorter ranges (Chapter 3).

Individuals at the Wendover Canal and Little Bedwyn sites had higher growth rates for any body weight than individuals at the Bure Marshes for all weights below S_{max} (Fig. 3; Fig. 4). These equated to 17g and 58g respective increases in body weight gained by individuals at the Little Bedwyn site and the Wendover Canal over individuals at the Bure Marshes over a 50 day period. Similarly, mean body weights were significantly larger, by 22g and 37g for the Wendover Canal and Little Bedwyn site respectively, than at the Bure Marshes in each comparison.

Population densities were highest at the Wendover Canal, lower at the Little Bedwyn site and lowest at the Bure Marshes. Quantities of *green forage* per home

range, and per metre of habitat showed exactly this trend, being highest at the Wendover Canal and lowest at the Bure Marshes, both per metre of bank and for each observed range length. Measured growth rates for the first 50 days following t_0 were also largest at the Wendover Canal (2.24 g/day), smaller at the Little Bedwyn site (1.92 g/day) and smallest at the Bure Marshes (1.58 and 1.06 g/day for 2001 and 2002 respectively).

Water voles at the Little Bedwyn site had a higher mean body weight and S_{max} than at the Wendover Canal (body weights, 207.5g and 189.9g respectively; S_{max}, 261.4g and 232.0g respectively), contrary to expectations. This may partially result from the lack of April and May data from the Wendover Canal. During this period individuals would be heavier and grow faster (see below). Mean body weight and S_{max} at the Little Bedwyn site, excluding the April and May captures, were 194.5g and 237.6g respectively, both lower than with the April and May captures included. Growth rates and body weights were not, however, strictly comparable between the Wendover Canal and Little Bedwyn site since each site was trapped in a separate year and external factors such as weather conditions or over-winter flooding could influence growth rates (e.g. Devender, 1978).

This study demonstrates that high population densities of water voles were associated with larger quantities of *green forage*, larger body weights and higher growth rates than sites with low population densities. Increases in individual body growth rates could increase population growth rates if individuals at all sites reached breeding condition at the same weight: increasing growth rates would thereby reduce the time individual take to reach breeding condition. Individuals of both sexes at all sites attained breeding condition at 140g (Figs. 5a, 5b). Individuals reached 140g at a mean age of 56 days old at the Wendover Canal, 65 days old at the Little Bedwyn site

and 76 days old at the Bure Marshes. This difference in individual growth rates could, therefore, have affected the population rate of increase by influencing the amount of time (an additional 20 days in the lowest density site) that individuals took to reach breeding weight.

Maturation rates in some Arvicoline rodents have been shown to decrease with increasing population density (e.g. Boonstra, 1989; Rodd & Boonstra, 1988; LeDuc & Krebs, 1975; Ostfeld & Canham, 1995). It is therefore possible that any effects of increasing forage abundance, and therefore increasing individual growth rates, upon population densities could be counteracted by density-dependent social suppression of maturation. Age at sexual maturity would increase with increasing population density if a) the weight at which individuals reach sexual maturity increases with increasing population density or b) the weight at sexual maturity remains constant but growth rates decrease with increasing population density.

Very few individuals of either sex (under 5% in each case) captured at weights greater than 140g were not in breeding condition at any site or time of year: there was no evidence to support the suggestion that the weight at sexual maturity increased with increasing population density for either sex. Our results therefore concord with the findings of Ostfeld & Canham (1995) - for *Microtus pennsylvanicus* - and LeDuc & Krebs (1975) - for *Microtus townsendii* - that the weight at sexual maturity appeared effectively constant and that variations in individual growth rates would therefore directly influence the age of sexual maturity.

Although *specific growth rates* declined at all study sites through the breeding season (Table 2), growth rates, at the (high density, high forage) canal sites were larger than at the (low density, low forage) Bure Marshes site for any given month. Individuals could therefore have reached breeding weight faster, and reached higher

densities at the canal sites than at the Bure Marshes in any month, notwithstanding that *within* each site, growth rates declined throughout the breeding season.

These results suggest that between-site differences in summer plant biomass lead to substantial differences in population densities between sites in this study. Water voles, however, typically suffer high mortality rates during the non-breeding season (e.g. Macdonald & Strachan, 1999; Strachan, 1998). It is possible that any net benefit of increased summer density could be negated by over-winter food limitation and mortality. If over-winter mortality rates were uniform amongst populations then the relative densities would be expected to remain constant. If, however, mortality over winter were density dependent, higher density populations would suffer proportionally larger mortality rates, potentially negating higher summer densities and leading to a relatively reduced over-wintered cohort. Little data on relative over-winter mortality rates is available from this study, but comparison of the over-winter mortality rates at the Bure Marshes and Little Bedwyn from 2002-2003 suggest that mortality rates were approximately equal between these sites (Chapter 5). I therefore suggest that benefits of increased breeding season densities due to increased summer plant biomass may translate into a larger initial breeding cohort at the start of the following breeding season.

Many studies of food supplemented populations of Arvicoline rodents have shown that supplemented populations support individuals with increased body mass or growth rates (Andrzejewski, 1975; Desy & Thompson, 1983; Koskela et al., 1998; Taitt & Krebs, 1981, 1983), increased reproductive success (Andrzejewski, 1975; Desy & Batzli, 1989; Desy & Thompson, 1983; Koskela et al., 1998; Taitt & Krebs, 1981) and increased immigration rates (Andrzejewski, 1975; Taitt & Krebs, 1981, 1983). Population density increases have also been found in populations for which

immigration was not possible, demonstrating that increased reproductive success from supplementation alone can result in population increase (Desy & Batzli, 1989).

In wild populations of Arvicoline rodents, demographic performance (including litter sizes, body size, growth rates and proportion of female pregnancies) has been shown to vary among certain habitat types (Cole & Batzli, 1979; Getz et al., 1979; Krohne, 1980), apparently in response to food quality and floristic micropattern (Cockburn & Lidicker, 1983). It seems highly plausible, therefore, that population density differences in the present study are at least partially mediated by the levels of *green forage* available to the resident water vole populations.

These findings have implications for water vole conservation in the UK. Broad swathes of riparian vegetation, both on the banks and in the water, have been suggested to increase the viability of water vole populations (Barreto et al., 1998a; Barreto et al., 1998b; Strachan et al., 2003), but hitherto little direct evidence of this existed. In line with expectations from previous studies on food supplemented vole populations, larger areas of *green forage* available per metre length of bank were positively correlated with higher growth rates and body weights and higher population densities. The Little Bedwyn site, for example, had double the population density of the Bure Marshes (2.08 as opposed to 1.04 individuals per 100m) and approximately 70% more *green forage* per metre of waterway (2.03m^2 as opposed to 1.46m^2).

This was an observational study involving only three sites, and as such uncontrolled factors other than forage abundance could potentially have influenced population density. For example site-specific genetic differences may exist such that individuals at a given site naturally gained mass at a faster rate than at other sites. Such concerns cannot be discounted, but the large number of studies relating

increased food abundance to increased individual and population growth rates, however, argue for a causative link between forage abundance and individual / population growth rates in this study.

I cautiously suggest that that both extant and re-introduced populations could be expected to benefit from higher rates of individual growth, and hence population growth, at sites with larger quantities of vegetation. Habitat management for water vole conservation should therefore seek to increase quantities of riparian vegetation both at sites with extant populations and sites to which populations may be restored.

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Chapter 3

What limits range sizes of male water voles (*Arvicola terrestris*) at different population densities?

ABSTRACT

Range sizes of male and female small mammals at different population densities are likely to be determined by different factors. If females are territorial, their range sizes may be limited by intrasexual aggression and should therefore be smaller at higher population densities. Relatively few studies have examined factors limiting the sizes of males, and none in wild populations. Ranges of male small mammals may be limited by the density of both females and males, suggesting that there should be an optimum number of female ranges that males can overlap. Three wild populations of water voles (*Arvicola terrestris*) were studied, two at relatively high density and one at relatively low density. If male range sizes were determined by the number of female ranges they could overlap, limited by both inter- and intrasexual social interactions, it would be reasonable to expect that a) male ranges would be smaller at higher population density; b) male range-size should be related to competitive ability, irrespective of population density and; c) the number of female and male ranges that males could overlap should be constant, irrespective of population density. Both females and males had smaller range sizes at higher population density, and individuals of both sexes with larger body weights had larger ranges than smaller individuals at all sites. The numbers of females and males overlapped by males did not differ between sites in the study. The ranges of male water voles may therefore have been determined by social interactions with both females and males, restricting the number of female ranges they could overlap.

INTRODUCTION

Range sizes of male and female small mammals at different population densities are likely to be determined by different factors. A widely accepted paradigm in small mammal behavioural ecology that females compete for resources whereas males compete for females (Wolff & Peterson, 1998). Competition for limited resources may result in space use becoming exclusive amongst females, and potentially, therefore, in intrasexual territoriality. Territoriality in female small mammals may derive from competition for food resources (Ims, 1987a, 1988a; Ostfeld, 1985, 1990), defence of nesting sites to deter intraspecific infanticide (Fortier & Tamarin, 1998; Wolff, 1993; Wolff & Peterson, 1998), or potentially both factors operating simultaneously. The spacing system of males should be determined by the distribution of receptive females (Ims, 1987a, 1988a; Ostfeld, 1985, 1990).

Since female territories are exclusive, they should become smaller in response to increasing intruder pressure and / or food resource levels (e.g. Fortier & Tamarin, 1998). Male small mammals, however, often have relatively large home ranges that extensively overlap with ranges of females and other males (Bond & Wolff, 1999; Leuze, 1976). What factors operate to limit the size, and degree of overlap, of male ranges at different population densities are less clear, and relatively few studies have examined this (see Bond & Wolff, 1999; Nelson, 1995a, b).

Home range sizes of small mammals depend upon territorial behaviour, population density and food availability, amongst other factors (Maher & Lott, 2000). Increasing population density can result in smaller range-sizes of both sexes (Abramski & Tracy, 1980; Bond & Wolff, 1999; Nelson, 1995a, b; Ostfeld & Canham, 1995). Food-supplementation can also result in smaller range-sizes

(Andrzejewski, 1975; Boutin, 1990; Jones, 1990; Sullivan et al., 1983; Taitt & Krebs, 1981, 1983), but is frequently accompanied by increases in population density (Abdellatif et al., 1982; Andrzejewski, 1975; Cole & Batzli, 1978; Desy & Batzli, 1989; Desy & Thompson, 1983; Gilbert & Krebs, 1981; Jonsson et al., 2002; Koskela et al., 1998; Taitt & Krebs, 1981, 1983).

It is impossible to separate direct effects of food supplementation upon ranging behaviour from indirect effects due to increases in population density in studies not specifically designed to test this (Fortier & Tamarin, 1998; Jonsson et al., 2002). Evidence for direct effects of food supplementation is, however, equivocal. Fortier & Tamarin (1998) showed that movements of male meadow voles (*Microtus pennsylvanicus*) at low population densities were reduced by supplemental food but methodological difficulties disallowed testing for effects at high population densities. Desy et al. (1990) found no direct effects of supplemental food on home ranges of prairie voles (*Microtus ochrogaster*), and Slade et al. (1997) found that both male and female prairie voles moved further on supplemented grids. Food supplemented female bank voles (*Clethrionomys glareolus*) exhibited no difference in territory size in comparison to non-supplemented voles (Jonsson et al., 2002), and Lacki et al. (1983) found that supplemental food produced no change in home range sizes of chipmunks (*Tamias striatus*).

I examine the association of levels of population density with the observed ranges of male and female water voles. Population densities, growth rates and body weights of water voles can be higher at sites containing larger quantities of forage (Chapter 2). Effects of population density and food abundance may therefore be confounded in natural populations. Due to the equivocal nature of the evidence for direct effects of forage, however, and many studies demonstrating that increases in

population density alone can result in decreases in the home-range size of small mammals (Abramski & Tracy, 1980; Bond & Wolff, 1999; Nelson, 1995a, b; Ostfeld & Canham, 1995), interpretation of results of the present study are limited to the examination of the association of levels of population density with the size of water vole ranges.

Water voles (*Arvicola terrestris*) are an endangered species in the United Kingdom (Jefferies et al., 1989; Strachan et al., 2000; Strachan & Jefferies, 1993). In the majority of UK habitats - the only notable exceptions being reedbed populations such as those studied by Carter & Bright (2003), and the fossorial Scottish island populations studied by Telfer et al. (2003) - water voles live in populations arranged along the length of water courses in a series of home-ranges (Pelikan & Holisova, 1969; Stoddart, 1970; Woodroffe et al., 1990). In upland UK habitats, populations of water voles are typically subdivided into colonies consisting of a small number of individuals (Aars et al., 2001; Lawton & Woodroffe, 1991; Stoddart, 1970; Telfer et al., 2001; Telfer et al., 2003). Some lowland populations can be much larger, contain many more individuals and are often more spatially separated from other such populations (Barreto & Macdonald, 2000; Barreto et al., 1998b; Carter & Bright, 2003; Woodall, 1993). This study concerns only lowland populations, in which the numbers of individuals living in close proximity can be sufficient to examine spacing behaviour of relatively large numbers of males and females at different population densities.

Breeding season ranges of females are typically small and non-overlapping, whereas ranges of male water voles are larger (Efford, 1985; Leuze, 1976; Pelikan & Holisova, 1969; Stoddart, 1970), often overlap with each other, and may overlap with the ranges of several females (Efford, 1985; Leuze, 1976; Stoddart, 1970). Female

dispersion in water voles is mediated by overt aggression during the breeding season (Leuze, 1976). Antagonistic encounters between males have also been recorded (Efford, 1985; Leuze, 1976), the frequency of which appears to relate to the presence of oestrous females within their ranges (Leuze, 1976). This suggests that female water voles are territorial in these habitats whilst male water voles are not territorial but compete for access to females in breeding condition.

Ranges of male water voles in wild populations may be limited by intrasexual competition for access to females. Movements of non-territorial male field voles (*Microtus agrestis*) have been shown to be reduced in response to increasing densities of both females and males in separate experiments (Nelson, 1995a, b). When female density was kept constant and male density increased, heavier males had significantly larger ranges than lighter-weight males, implying that social dominance relationships between males determined male range size (Nelson, 1995b).

Leuze (1976) states that male water voles exhibit mate-guarding behaviour, and that cases of male-male aggression are more intense during a female's oestrus. Thus males' movements should be bounded by an upper limit to the number of females that they can successfully monitor, compete for, and inseminate (Bond & Wolff, 1999).

Male ranges may also be limited by female aggression according to the offspring-defence hypothesis (Wolff & Peterson, 1998). Unfamiliar males are potentially infanticidal, and so may be subject to overt aggression when a female is nursing (Wolff & Peterson, 1998). Some evidence for this in water voles exists: Leuze (1976) states that female water voles react more aggressively towards non-mates than mates, appearing at the nest entrance more often in the presence of non-mates. Pregnant female water voles have been shown to undertake multi-male-

matings (Jeppsson, 1986), potentially confusing paternity and perhaps thereby preventing male infanticide (Agrell et al., 1998; Jeppsson, 1986).

Males, therefore, potentially experience costs with increasing range-size due to aggressive encounters with other males and unfamiliar females. In both cases, there should be an optimum number of female ranges that can be overlapped by each male. Beyond this, costs of maintaining a range would increase at a greater rate than the benefits. These costs could be partially mitigated by increasing competitive ability such that larger males might have larger ranges (Nelson, 1995b).

Evidence for an optimum number of male-female and male-male overlaps in small mammals exists. Agrell et al. (1996) demonstrated that male field voles (*Microtus agrestis*) overlapped fewer other males at higher female population density. Bond & Wolff (1999) demonstrated that male space-use in gray-tailed voles (*Microtus canicaudus*) was influenced by degree of intrasexual competition and by the availability of females, with an upper limit of overlap with either sex of about 4-5 individuals.

We expect that ranges of adult female water voles will be smaller at higher population densities in line with the predictions of the offspring-defence and food-defence hypotheses. No studies, however, have examined the movements of male Arvicoline rodents in wild populations at different levels of population density. This study presents data relating ranges of adult male water voles, in wild populations at different densities, to the number of females they overlap. If the data supports the expectation that male range sizes are limited by an optimum number of females they can overlap, this implies that:

a) male ranges should be smaller at higher population densities of males and females;
b) male range size should be partially determined by competitive ability. I assume that this increases with body mass (e.g. Nelson, 1995b);
c) the number of female-male and male-male range overlaps should remain constant at different population densities if sex ratios remain equal (Bond & Wolff, 1999).

These predictions are valid assuming that females come into oestrus asynchronously and remain uniformly spaced (i.e. receptive females are not spatially and temporally clumped). Such clumping may theoretically induce territoriality in males (Ims, 1997b, 1988b), but has also been shown to induce greater space sharing amongst *Clethrionomys rufocanus* males (Ims, 1988). Territoriality in males would alter the expected overlapping patterns: male-male overlaps should be less tolerated and the number of female ranges overlapped by a male should decrease with increasing intruder pressure (i.e. male density). If, conversely, males responded to female clumping by space-sharing, the number of male-male overlaps should increase with increasing density, males with greater competitive ability may not have larger ranges, and male ranges may be less likely to be smaller at higher densities.

Since female water voles are territorial, often with large ranges, and come into oestrus asynchronously throughout the breeding season (Leuze, 1976) it is unlikely that sexually receptive females would be sufficiently spatially or temporally clumped to represent a defensible commodity for males. These arguments notwithstanding, the above predictions remain valid, provided males remain non-territorial, with any

departure indicating that male range-sizes were not determined by aggressive interactions with other males and females.

Ranges of water voles in the majority of habitats in the UK comprise a narrow (1-2m) width of habitat over a much larger (often over 300m, Macdonald & Strachan, 1999) length (Barreto et al., 1998a; Lawton & Woodroffe, 1991; Stoddart, 1970). Measurements of water vole ranges are therefore often considered not in terms of *area*, but in terms of *length* of occupied habitat for convenience (Stoddart, 1970).

A pre-requisite for territoriality, or indeed any effect of competition with other individuals upon range size, is sufficient detectability of intruders (Wolff & Peterson, 1998). In addition to the likelihood of detecting an intruder's scent, since water voles occupy narrow strips of habitat, an intruder passing through an occupied location would have a high chance of encountering the other occupants. Lowland water vole populations therefore provide an excellent system for studying effects of population density, since *range lengths* are likely to relate directly to social interactions, with limited capacity for mutual avoidance.

We examine observed range lengths and range overlaps of both sexes in a comparative study of three large, lowland populations of water voles during breeding seasons over a four year period. These sites were a wetland site with a low population density throughout, a canal site with a high population density and a site with two adjacent habitats: one canal habitat at high density, and one river habitat at low density. This latter site partially allows testing of whether observed ranges were site specific or whether they varied according to population density.

METHODS

Study sites

The Bure Marshes NNR (UK grid ref: TG 335 165) is a fenland habitat managed by English Nature, comprising fields of fen vegetation surrounded by a network of ditches in which the water voles occupy ranges. Within the study area, live traps (Sherman XLK 3 x 3.5 x 12" folding aluminium with galvanised steel doors) were deployed along 4.07 km of ditch-edge. This site was live trapped in 2000, 2001 and 2002, trapping ending in April 2003. Throughout the study, both sexes at this site had low population densities in comparison with both of the other sites (Fig. 1a, Fig. 1b).

The Wendover Canal (SP 873 102) comprised a single stretch of non-navigable canal with a total length of 4.12km. However, the suitable water vole habitat was interspersed with heavily wooded, over-shaded sections in which no signs of water voles were found at any time. Traps were deployed along all sections in which water vole sign was found, a total of 2.03km. Trapped sections extended 40m (two trapping intervals) into the unoccupied habitat either side of the outermost field-sign of an occupied section. Throughout the study, no water vole was captured more than 20m from the outermost field-sign of an occupied section, and only occupied areas are used in the following analyses. This site was live trapped in 2000 and 2001, throughout which both sexes had nearly double their population density at the Bure Marshes (Fig. 1a; Results). Over winter 2001/2002 the Wendover Canal population was extirpated due to predation by an American mink (*Mustela vison*).

The Little Bedwyn stretch of the Kennet and Avon Canal (SU 295 665) comprises a length of canal which runs parallel to the river Dun, separated from it by a mown field varying between 20m and 60m in width. Live-traps were deployed

along 1.04km of the canal and 960m of the river. The total water's side trapping in this site was thus 2.00 km. The Little Bedwyn site was trapped from June 2002 until July 2003. Throughout the study, population densities of both sexes on the canal were over double those on the river, and at the Bure Marshes (Fig. 1b, Fig. 1c; Results).

Research design

Male range sizes may be limited by an optimum number of females that can be overlapped, assuming that males do not become territorial at high population densities. If so, male and female territories are expected to be smaller at high population densities, male range size should increase with increasing body weight, and males should overlap constant numbers of males and females irrespective of population density, assuming equal sex-ratios. Since this hypothesis relates only to breeding individuals, only adult animals are used in any analysis.

We compared observed range lengths of water voles between sites with high and low population densities. Only sites trapped in the same year were directly compared, to minimise potential biases due to environmental conditions. In the first two years of the study (2000, 2001), comparison of observed range lengths took place between the Wendover Canal (high population density) and the Bure Marshes (low population density; Table 1). In the third year (2002), comparison was made between the (low density) Bure Marshes and the (high population density) canal habitat at the Little Bedwyn site (Table 1). Data from the river habitat at the Little Bedwyn site were excluded from comparison with the Bure Marshes. Comparison was made *within* the Little Bedwyn site between the canal (high density) and river (low density) habitats for the last two years (2002, 2003). Inclusion of the Little Bedwyn Canal in

this design increases the replicates of each population density, and tests the possibility that range differences between sites could derive from site-specific factors unrelated to population density. Population densities of water voles at each site are presented in Figs. 1a, 1b and 1c, Results.

I assume that females will be territorial and males remain non-territorial at high population densities. I follow the definition of Maher & Lott (1995, 2000) that a territory is "a fixed space from which an individual or group of mutually tolerant individuals actively excludes competitors from a specific resource or resources", but extend the definition of "competitors" to include infanticidal members of the population. To demonstrate territoriality within wild populations of water voles, I adopt the concept of exclusive use of a length of habitat in which lack of overlap with the ranges of neighbouring individuals is taken as an indication of territoriality (e.g. Kolb, 1986; Sandell, 1989). Analysis of numbers of overlaps (below) allows testing of the assumption that females remain territorial and males remain non-territorial at high population densities.

Numbers of male-female and male-male overlaps at each site were analysed in two ways. Firstly, the total number of adult individuals of each sex overlapped by a given adult at each site and of each sex was recorded. This determines if variations in population density or sex correlated with differences in the mean number of male and female overlaps recorded. Secondly, I present data demonstrating predicted adult male ranges and predicted mean numbers of females overlapped at each site for a range of male body weights. Values of range length were calculated from the statistical effects of body weight upon observed ranges derived from the analyses of observed ranges at each study site.

Trapping protocol

Trapping at all sites took place between April and October, with the exception of 2001 when public health restrictions, due to an outbreak of Foot and Mouth disease, prevented trapping between April and June, and the Little Bedwyn site during 2002, which was trapped from June onwards. Trapping periods for each site are shown in Table 1.

Table 1: Capture Mark Recapture trapping periods for the study. "Full season" implies trapping between April and October. "X" indicates not trapped in that year.

Year of trapping	Bure Marshes	Wendover Canal	Little Bedwyn Canal
2000	Full season	Full season	X
2001	June onwards	June onwards	X
2002	Full season	X	June onwards
2003	X	X	April to July

Traps were baited with apple and contained approximately 150g of carrot as an overnight food source (*sensu* Efford, 1985). Unmarked water voles captured were marked using Trovan ID-100 passive interrogation transponders, sexed, weighed and immediately released at the point of capture. Water voles were sexed on first recapture in a given capture-session and thereafter weighed and released.

Trap spacing was kept constant at each site to ensure comparability of observed ranges. Traps were positioned at 20m intervals. This is comparable with the trapping densities used in previous studies (e.g. Efford, 1985; Pelikan & Holisova, 1969), a compromise between preventing trap-saturation, ensuring effective capture of the majority of individuals and maximising the length of trapped habitat.

Trap positions were accurately established to a 10-figure grid reference using a *Garmin* "Etrex" GPS receiver. Accuracy for all trap locations was in the range of 6-10m maximum error (from internal GPS error estimation).

During 2001, half of the Bure Marshes and the Wendover Canal were trapped alternately, with both halves of each site trapped in each month where possible. During this period, traps were set on Monday and removed on Friday, and thus open for 4 trap nights. During 2002 (and 2003, Bedwyn only), the entire of the Bure Marshes and the Little Bedwyn canal sites were trapped during each trapping session, with one trapping session each per month. At the Bure Marshes each half was trapped in alternate mornings and afternoons, allowing one capture period per day for each half from Monday to Saturday of each session. The entire Little Bedwyn site was trapped with one session a month of morning captures from Monday to Saturday, allowing 5 trap nights.

Measurement and analysis of observed range lengths

Water vole capture positions were entered into ArcView GIS (version 3.1, Esri) and overlaid onto digitised aerial photographs of each study site.

The distance between the furthest capture positions for each individual in each capture-session was measured within the GIS to the nearest metre, following the contours of the watercourse in question. This measure was the *observed range length* (ORL *sensu* Pelikan & Holisova, 1969) for all water voles captured more than once in a given capture-session. Trapped ranges compared favourably with ranges from a concurrent radio-tracking study at two of these sites (Moorhouse & Macdonald, unpublished). There was no evidence that range-lengths reached an asymptote within

each capture or radio-tracking session (4-5 days) and so ORLs are here used as an index of range-size.

ORLs of adult water voles at each site formed repeated measures for each individual, and were analysed using repeated measures mixed models (Proc Mixed procedure, SAS for windows, V8), with individual nested as a random factor within study *site* and *sex*.

We predicted that male ORLs would decrease with increasing population density and increase with increasing body weight. Effects of population *density* and body *weight* upon ORL were therefore tested by entering *density* and *weight* as covariates, since population densities varied between capture sessions and sites (Fig 1). ORL may also vary with the number of *captures* per trapping session (entered as a covariate), or between study *sites*, *months* of capture or *years* of the study, due to environmental conditions. These factors were therefore included in the analysis. Interactions between *sex* and *weight* and *sex* and *density* were considered to examine the possibility that ORLs of each sex responded differently to these factors. Higher order interactions were not considered as having no *a priori* biological significance.

ORLs were transformed by taking the square-root: thus transformed the data did not depart from the assumptions of the test.

Radio-collaring at the Bure Marshes in 2002 had potential to alter ranging activities of males and female during this time. Leuze (1976) found no difference in range lengths of collared and un-collared water voles. No effect of year upon ranges in the Bure Marshes or any analysis was detected, however, and so all data from 2002 were included in the relevant analyses.

Measurement and analysis of overlaps

Overlaps between ranges of adult water voles were measured within ArcView. Individuals were defined as having overlapping ranges if they were captured more than one trapping-interval (20m) inside of the known range of another individual in a given trapping session. Cases where the overlap was only one trap were discounted as this could represent overlap at the boundary of either individuals' range.

Types of overlap were categorised as male-male, female-female or male-female. For each individual the number of each type of overlap was recorded, each overlapped individual only being counted once. Gender biases in the number of range overlaps with male and female water voles for a given individual were examined for each sex at each site. The number of recorded overlaps for each individual in a given capture session cannot be used as a direct measure of the proportion of the population undertaking each type of overlap, since trapping-related biases, such as the number of times an individual was captured, may influence the recorded number of overlaps. To eliminate these biases, analyses were confined to individuals recorded as overlapping with at least one other vole, and examined the relative proportions of males and females overlapped by individuals of each sex.

If there were no difference in the number of each sex which individuals overlapped, then the mean of [(number of males) - (number of females)] overlapped-with should be zero. If individuals of either gender overlapped with more males than females, on average, a significant increase from zero would be expected, and vice versa.

Gender bias in overlapping was compared between males and females within and between study sites. Data after May 2002 at the Bure Marshes were not included since a substantial decline (20 in May to 9 in September) in female numbers during a

radio-collaring study in this period (Chapter 5) may have affected numbers of overlaps at this site.

Predicted numbers of males and females overlapped at each site

Mean body weights of water voles varied between the study sites (Chapter 2). I use body weight as a measure of competitive ability in males (Nelson, 1995b). The influence of body weight upon competitive ability is likely to be related to the distribution of body weights of the individuals at a given site, and so direct comparison of the number of males and females potentially able to be overlapped by the range length of males for a given body weight may not compare males of the same relative competitive ability. To account for this, I calculated threshold body weights such that 25%, 50%, 75% and 95% of recorded male weights from each male population would be lower. This gives a wide range of weights from populations at different density with which to compare the predicted numbers of males and females overlapped per male range.

Threshold weights were calculated as: $pi = i / n$, where p is the proportion of animals that exhibit weights lower than a given weight and i is the rank of the weight for each animal. This method is based on the Kaplan-Meier equations for survival analysis (Kaplan & Meier, 1958), and included only individuals of greater than 140g, above which the majority of individuals would be expected to be adult (Fig 1a; Results).

The derived weights were used to predict the mean ranges of males of those weights, captured on four occasions in a given trapping session, using the coefficients from the analysis for each population analysed separately. For each site this was

calculated as: constant + (4**captures*) + (x * *weight*), where x is the threshold weight and *captures* and *weight* are the coefficients for the effect of those variables upon the square-root of observed ranges. The derived range was then back-transformed and compared to mean male and female ranges at each site to predict the mean number of males and females which a male of a given weight could overlap at that site.

RESULTS

Separation of adults and juveniles

This study relates only to individuals in breeding condition. Individuals were classified as adults or juveniles based upon reproductive status: adult males had descended testes and adult females had perforate vaginas {Stoddart, 1971 #116;Carter, 2003 #109}, with juveniles not exhibiting these characteristics. Occasionally it was not possible to score the state of perforation of the female's vagina or degree of descent of the male's testes. The majority of individuals of both genders become sexually mature at 140-145g (Chapter 2). An approximate minimum of 85% of individuals of both sexes captured were in reproductive condition if captured above this weight. This "threshold" weight was within 5g of these values at all sites. Below this weight much larger proportions of captures were not in reproductive condition. Only males and females of greater than 140g were included in the analyses.

For the analysis of overlap between individuals, individuals were assumed to be adult if demonstrating scrotal testes or a perforated vagina in a given trapping session, or if greater than 140g in weight. This allows voles in reproductive condition

to be assumed to be behaving as adults, and includes animals sufficiently large to be adult individuals but whose reproductive status may not have been accurately scored.

Population densities

Population densities were derived from the number of adult individuals inhabiting a given length of habitat. This was based upon the minimum number known alive in all cases to avoid biases from splitting sites into halves during 2000 and 2001.

Figs. 1a, 1b and 1c show that population densities were larger at the Wendover Canal and at the canal habitat of the Little Bedwyn site than at the Bure Marshes and river habitat of the Little Bedwyn site for the majority of capture sessions.

Fig. 1a presents the male and female population densities at the Bure Marshes and Wendover Canal. Population densities were averaged across two month periods in 2000 and one month periods in 2001 for clarity of presentation. The mean population densities, averaged across all capture sessions, were 1.7 (males) and 1.9 (female) times larger at the Wendover Canal than at the Bure Marshes.

Fig. 1b presents the male and female population densities for the Bure Marshes and canal habitat of the Little Bedwyn site for each trapping session in 2002. The mean population densities were 4.4 (males) and 5.3 (female) times larger at the Little Bedwyn site than at the Bure Marshes.

Fig. 1c presents the male and female population densities for each habitat within the Little Bedwyn Canal. The mean population densities were 3.5 (males) and 2.0 (females) times higher on the canal as opposed to on the river for males and females respectively.

Figure 1a: Population density of adult males (dark bars) and adult females (light bars) at the Bure Marshes (single shade) and the Wendover Canal (stippled).

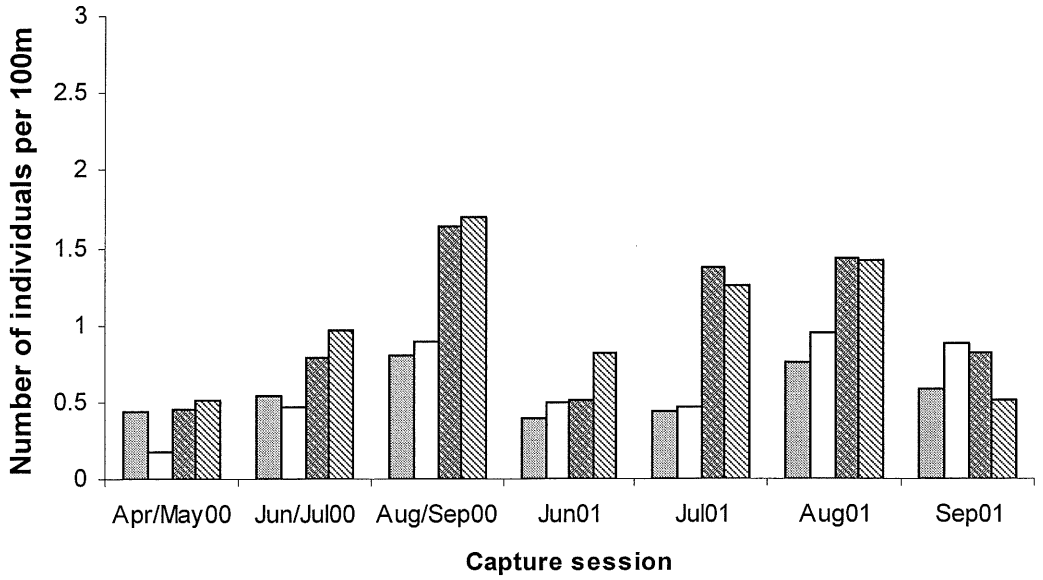


Figure 1b: Population density of adult males (dark bars) and adult females (light bars) at the Bure Marshes (single shade) and the canal habitat of the Little Bedwyn site (stippled).

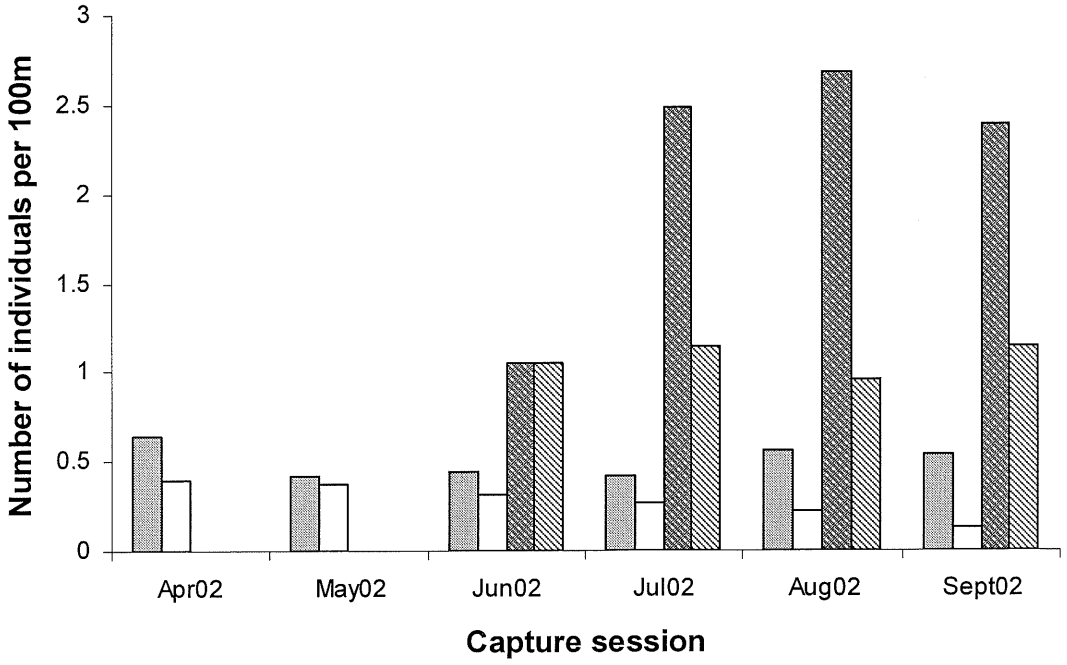
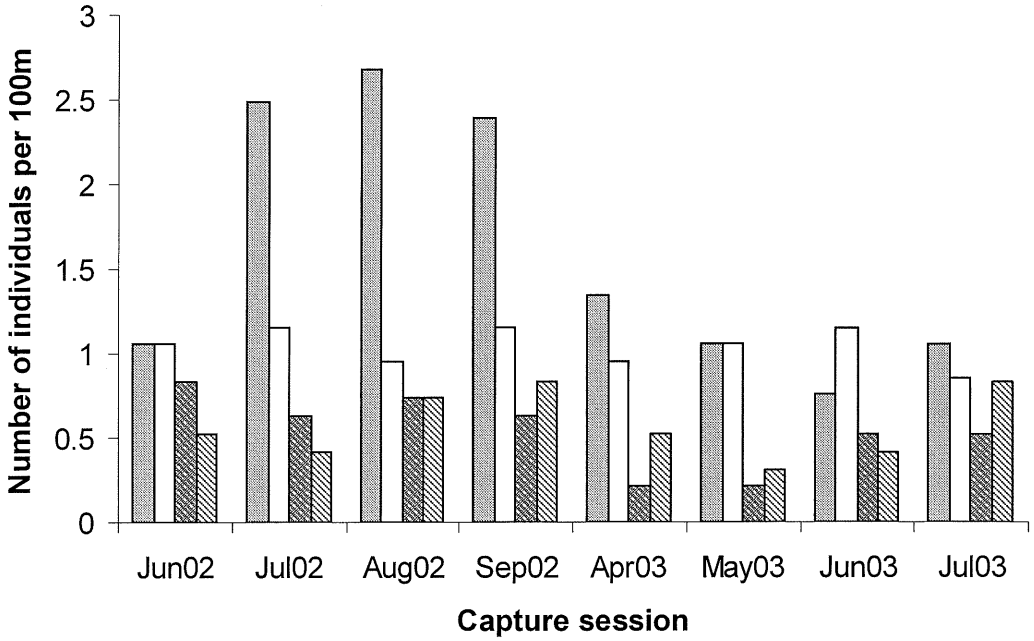


Figure 1c: Population density of adult males (dark bars) and adult females (light bars) occupying the canal habitat of the Little Bedwyn site (single shade) and the river habitat of the Little Bedwyn site (stippled).



Factors affecting ORL

In total, 688 individual water voles were captured 2746 times at the three study sites over a four year period, from April 2000 to July 2003.

Table 1 presents the results of the Proc Mixed analysis of factors affecting ORLs of water voles. ORLs of both sexes were smaller at higher population densities (Table 1; Proc Mixed, $F_{1,318} = 7.54$, $p = 0.0064$; estimate -0.852, s.e. 0.310). There was no evidence that males and females differed in their response to variations in population density when an interaction between *sex* and *density* was included in the model (Proc Mixed, $F_{1,313} = 1.42$, $p = 0.234$). Densities in the study varied between a minimum of 0.54 voles per 100m (Bure Marshes) and a maximum 3.63 voles per 100m (Little Bedwyn). Effects of population density were such that marginal mean ORL for male water voles was 69.8m at the lowest observed density and 25.3m at the highest observed density.

Figs. 2a and 2b present the mean ORLs at each site, showing that ORLs of both males and females at the (low density) Bure Marshes were larger than at the (high density) Wendover Canal and (high density) canal habitat of the Little Bedwyn site. Within the Little Bedwyn site ORLs were larger in the (low density) river habitat than in the (high density) canal habitat.

ORLs of both sexes increased with increasing body weight (Table 1; Proc Mixed, $F_{1,318} = 11.24$, $p = 0.0009$). There was no evidence that responses of males and females differed in a model including an interaction of *sex* and *weight* (Proc Mixed, $F_{1,313} = 2.16$, $p = 0.1423$). Effects of increasing body weight on the ORL of male voles are presented in Table 2.

Male range sizes and population density

Males had larger ranges than females (Proc Mixed $F_{1,294} = 12.86$, $p = 0.0004$); mean male ORL across all sites was 42.0m (95% c.i. 32.9 – 52.1m), mean female ORL was 24.7m (95% c.i.s 17.6 – 33.0m). ORL increased with numbers of *captures* of an individual in a given trapping session and varied with *month* and between study *sites* (Table 1). No effect of *year* was found in when this factor was included (Proc Mixed $F_{3,315} = 0.17$, $p = 0.91$).

Table 2: Proc Mixed Model for effects of *density*, *site*, *captures*, *sex*, *weight* and *month* upon observed range lengths. Parameter estimates are given for all covariates; numbers in brackets represent standard errors. All interactions tested were non-significant: this main effects model had the lowest AIC of any fitted.

Source	Numerator d.f.	Denominator d.f.	F	P	Estimate (s.e.)
Density	1	318	7.54	0.0064	-0.8520 (0.310)
Weight	1	318	11.24	0.0009	0.0158 (0.005)
Captures	1	318	9.75	0.0020	0.2598 (0.083)
Sex	1	294	12.86	0.0004	/
Site	2	294	7.95	0.0004	/
Month	6	318	2.52	0.0215	/

Analysis of numbers of overlaps for each sex and site

Table 3 presents the mean number of each sex overlapped for male and female water voles at the Bure Marshes and canal habitat of the Little Bedwyn site. Individuals which did not overlap with another vole are not included. Data from the Wendover Canal are not included since very few overlaps were recorded at the Wendover Canal ($n = 18$ for 2000 and 2001 combined, compared to $n = 92$ for June-September 2002 at Little Bedwyn). Water voles at this site had extremely small observed range lengths (a mean of 32m and 20m for males and females respectively). Recording range-overlaps

Figure 2a: Mean observed range lengths for males (dark bars) and females (light bars) at the Bure Marshes, Wendover Canal and canal habitat of the Little Bedwyn site. Error bars represent 95% confidence intervals.

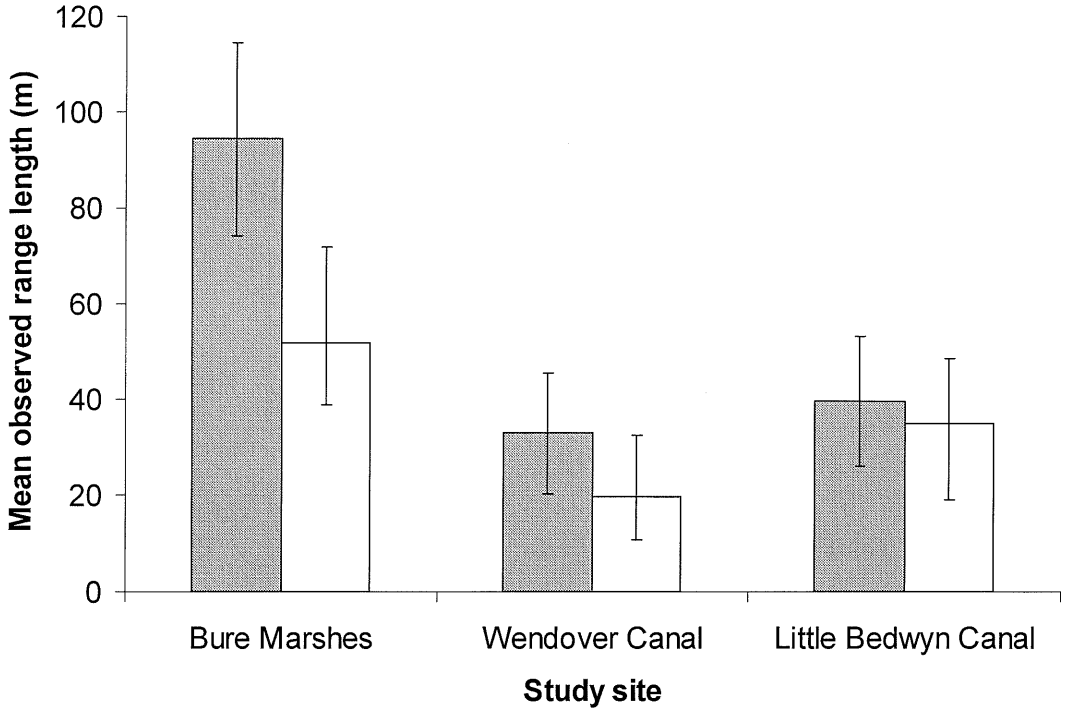
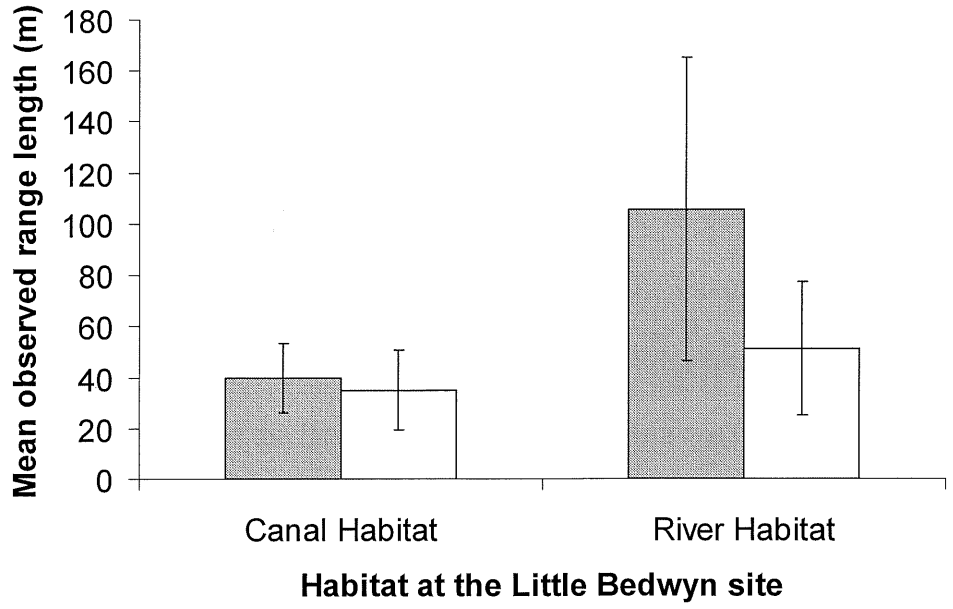


Figure 2b: Mean observed range lengths for males (dark bars) and females (light bars) at the canal habitat of the Little Bedwyn site and river habitat of the Little Bedwyn site. Error bars represent 95% confidence intervals.



of greater than one trap requires the ranges of the voles to be larger than the 20m spacing of the traps. This method is therefore not appropriate for this site and further analysis is confined to the Bure Marshes and the Little Bedwyn Canal.

Table 3: Mean number of individuals of each gender overlapped for male and female voles at the Bure Marshes and canal habitat at the Little Bedwyn site.

	Bure Marshes		**Little Bedwyn site (canal only)**	
	Male (n = 64) Mean (S.D.)	Female (n = 53) Mean (S.D.)	Male (n = 35) Mean (S.D.)	Female (n = 27) Mean (S.D.)
Number of males overlapped	1.08 (0.98)	1.38 (0.79)	1.00 (0.97)	1.19 (0.89)
Number of females overlapped	1.14 (1.40)	0.21 (0.45)	0.91 (1.04)	0.39 (0.49)
(number of males) - (number of females)	-0.06 (1.30)	1.17 (0.87)	0.09 (1.46)	0.79 (0.96)

The number of male-female and male-male overlaps were predicted to be constant irrespective of population density, assuming that females remain territorial and males non-territorial.

Males overlapped with equal numbers of males and females at both sites. There was no difference in the mean number of males or females overlapped for males at the Bure Marshes (Table 3: Mann-Whitney U test, $W = 4277.5$, d.f. = 1, $p > 0.4$) or at the Little Bedwyn Canal (Mann-Whitney U test, $W = 1285.0$, d.f. = 1, $p > 0.6$). The mean [(number of males) - (number of females)] overlapped for males did not differ significantly from 0 at either site (Table 3; Wilcoxon signed ranks test: Wilcoxon Statistic = 729, n for test = 54, $p > 0.9$; Wilcoxon Statistic = 302.0, n for test = 33, $p < 0.7$ for the Bure Marshes and Little Bedwyn Canal respectively). Similarly, the mean [(number of males) - (number of females)] did not differ between sites for male voles (Mann Whitney U test, $W = 10198.5$, d.f. = 1, $p > 0.3$). Males

were therefore not more prone to overlapping with more of one gender at either site, and overlapped equal numbers of males and females at both sites.

Females overlapped with more males than females at both sites. The number of females overlapping males, and females overlapping females differed at the Bure Marshes (Mann-Whitney U test, $W = 3974.5$, $p < 0.001$) and at the Little Bedwyn site (Mann-Whitney U test, $W = 920.5$, $p < 0.005$; Table 4). The mean [(number of males) - (number of females)] overlapped for females differed significantly from 0 at both sites (Wilcoxon signed ranks test: Wilcoxon Statistic = 1141.0 n for test = 48, $p < 0.001$; Wilcoxon Statistic = 184.0, n for test = 21, $p < 0.02$ for the Bure Marshes and Little Bedwyn Canal respectively).

At both sites females overlapped with more males than females. However, the mean of [(number of males) - (number of females)] for females differed between sites (Mann Whitney U test, $W = 844.5$, $p < 0.05$), indicating that females overlapped with a greater proportion of males at the Bure Marshes than they did at the Bedwyn Canal. This appears to result from differences in numbers of females overlapped: numbers of males overlapped did not differ for females between sites (Mann-Whitney U test, $W = 984.0$, $p > 0.25$), but there were fewer female-female overlaps at the Bure Marshes than at the Bedwyn Canal (Table 3) (Mann-Whitney U test, $W = 1276.0$, $p < 0.05$).

Within the Little Bedwyn Canal, there was no evidence that the number of male-male overlaps differed between habitats (Mann-Whitney U test, n = 48, $W = 822.0$, $p > 0.4$), the number of female-female overlaps differed between habitats (Mann-Whitney U test, n = 39, $W = 560.0$, $p > 0.5$) or that [(number of males) - (number of females)] differed for either males or females between habitats (Mann-Whitney U test: n = 48, $W = 862.5$, $p > 0.9$; Mann-Whitney U test n = 39 $W = 506.5$, $p > 0.25$ for males and females respectively).

Predicted numbers of females and males overlapped by males at each site

Due to the few overlaps recorded at the Wendover Canal, and the fact that the mean female range was less than one trapping interval (20m), comparing male ranges to the predicted number of males and females overlapped would be inappropriate for this site. The majority of recorded female range lengths were below the grain of the technique used to record them and could have been anything between 0-20m. Analysis is therefore limited to the Bure Marshes and canal habitat of the Little Bedwyn Canal.

Table 4: Calculated range lengths of adult males and predicted mean numbers of adult females and males overlapped for a range of body weights at the Bure Marshes (low population density) and canal habitat of the Little Bedwyn site (high population density). Number of overlaps are based on mean female ranges of 51.8m and 35.1m, and mean male range lengths of 94.4m and 39.7m at each site respectively (Fig. 3a). For each site, ranges of males were calculated as: constant + (4**captures*) + (x * *weight*), where x is a given body weight and *captures* and *weight* are the coefficients for the effect of those variables in separate analysis of males only at the site.

Percentage of population below weight	**Bure Marshes**				**Little Bedwyn Canal**			
	Male weight (g)	Male range (m)	Number of female overlaps	Number of male overlaps	Male weight (g)	Male range (m)	Number of female overlaps	Number of male overlaps
95%	265	159.8	3.1	1.7	305	108.8	3.1	2.7
75%	233	138.7	2.7	1.5	270	87.6	2.5	2.2
50%	200	118.4	2.3	1.3	230	66.2	1.9	1.7
25%	165	98.6	1.9	1.0	193	49.1	1.4	1.2

Table 4 presents the calculated range lengths and predicted numbers of males and females overlapped for each male body weight such that 95%, 75%, 50% and 25% of weights from each population were smaller at the (low population density) Bure Marshes, and (high population density) canal habitat of the Little Bedwyn site.

Increases in body weight translated into substantial increases in calculated range length at each site (a mean of approximately 60m extra for a 100g increase at the Bure Marshes and 54m for 100g at the Little Bedwyn site; Table 4).

Although body weights of males were larger at the Little Bedwyn site, calculated range lengths were smaller than at the Bure Marshes, reflecting the association of high population density and smaller male ranges. The predicted number of females overlapped by the calculated range was approximately equal for both sites, suggesting that population density would not affect the number of male-female overlaps for an individual of a given body weight. The predicted number of males overlapped was slightly larger for all weights at the Little Bedwyn site than at the Bure Marshes. However, the difference between the sites resulted in only one extra individual overlapped for the top 95% of body weights.

DISCUSSION

If male range sizes were limited by the number of females they could overlap, range sizes of male and female water voles should be smaller at high population density, more competitive males should occupy larger ranges, and numbers of females and males overlapped by males should remain approximately constant, irrespective of population density, assuming sex-ratios remain equal. Failure to meet these criteria

would suggest that male ranges were not determined by social limitations to an optimum number of females they could overlap.

Both males and females exhibited progressively smaller ORLs with increasing population density. Effects upon mean male ranges were sufficient that males had approximately 44m shorter ranges at the highest densities observed in this study compared to the lowest observed densities. This represents an approximately 75% reduction in range size due to effects of population density. Since ranges of both sexes were smaller at higher population densities (no significant interaction between *sex* and *density* was found), these results support the prediction that both male and female ranges should be smaller at higher population densities.

For some small mammal species, increasing body weights are likely to confer a competitive advantage in aggressive encounters (Efford, 1985; Leuze, 1976; Nelson, 1995b). At all three sites, male range lengths increased with increasing body weight. The fact that male range lengths were smaller at higher population densities, and that larger males had larger range lengths, suggests that male movements were influenced by social interactions, and therefore range size was related to the competitive ability of a given male. This was also found by (Nelson, 1995b) in an experimental population of field voles where male ranges contracted due to male-male competition.

I examined numbers of overlaps of both sexes in two ways: by direct observation from the populations, and prediction of the number of males and females that males of a given size would be able to overlap, based on observed ranges at high and low population density.

Overlaps between individuals at the Wendover Canal were unable to be studied since the mean male (32m) and female (20m) range lengths were sufficiently

small to limit the number of one-trapping-interval overlaps recorded. At this site the emergent vegetation was very broad in places (range 0 – 15m in width, mean 3.8m; s.d. 4.6m), and dense enough for water voles to feed away from the bank (pers. obs.). This increased habitat width may have resulted in the high population densities at this site (Chapter 2) and therefore the extremely short ORLs. The wider habitat would not invalidate the assumption that both sexes could detect, and respond to the presence of intruders within their ranges and should not, therefore, affect the outcome of the analysis of ORLs.

Male-male overlaps were as common as male-female / female-male overlaps at both the Bure Marshes and Little Bedwyn Canal (Table 3). Significantly fewer female-female overlaps were recorded than female-male overlaps at each site. This supports the assumption that males remain non-territorial at higher population densities and shows that female water voles are territorial whereas males will tolerate a degree of range overlap with other males (Efford, 1985; Leuze, 1976; Pelikan & Holisova, 1969; Stoddart, 1970). Population densities of males and females were similar within each site: respectively 2.1 and 2.6 times larger at the Little Bedwyn Canal than at the Bure Marshes. Thus the sex ratios of adult voles are expected to be to be approximately equal at both sites.

Numbers of recorded male-male or male-female overlaps did not alter between sites. At both the Bure Marshes and the Little Bedwyn site, males were recorded as overlapping with a mean of approximately one male and one female (Table 3). Females overlapped with slightly larger numbers of females at the Little Bedwyn Canal than at the Bure Marshes (a mean of 0.39 as opposed to 0.21 females overlapped per female; Table 3). This is not necessarily an indication of the relaxation of territoriality. Female voles may share ranges with close kin (e.g. adult and sub-

adult daughters (Lambin, 1994; Lambin & Yoccoz, 1998; Wolff et al., 2001) and increasing population densities may increase the costs of female dispersal, meaning that females are more likely to remain in their natal range.

In analysing the predicted number of males and females able to be overlapped by males of a given body weight (Table 4), I used body weights derived from distributions of weights for each population rather than an absolute value of body weight. This is reasonable since a male with a given body weight in a population of heavier individuals may have a relatively reduced competitive ability.

Although the threshold body weights of males used were larger at the Little Bedwyn site, range lengths predicted from these weights were smaller than at the Bure Marshes. The number of females potentially overlapped by the calculated range, however, was approximately equal for both sites, suggesting that population density did not affect the number of male-female overlaps for an individual of a given body weight. Predicted numbers of males overlapped were slightly higher at high population densities than at low population densities. This does not necessarily contradict the conclusion from the observed overlaps that males overlapped with the same number of males at both population densities, since observed overlaps represent the population average from a range of weights. The discrepancy in predicted number of males overlapped reached one individual only for the top 95% of body weights.

In conclusion, the results demonstrate that higher population densities were associated with shorter range lengths of both female and male water voles. This suggests that the size of male ranges was bounded by social interactions, since male range lengths increased with increasing body weight irrespective of population density. I was unable to separate the effects of interactions with females and males in constraining male ranges in this study; previous studies in captive populations have

shown that male range sizes are limited by the population density of both males and females (Bond & Wolff, 1999; Nelson, 1995a, b). There was little difference in the observed or predicted numbers of male-male or male-female overlaps with increasing population density in this study.

It is possible that the smaller male ranges at high population densities could derive from direct effects of forage abundance, rather than due to social factors, since population densities and forage abundance co-varied in this study (Chapter 2). It is also conceivable, if this were the case, that larger males would have larger ranges and that numbers of male-male and male-female overlaps may remain constant irrespective of population density. This explanation cannot be entirely discounted, but reported direct effects of forage upon ranges of small mammals vary from reduced ranges (at low densities only: Fortier & Tamarin, 1998) to no effect (Jonsson et al., 2002; Lacki et al. 1983) and increased ranges (Slade et al.,1997). A number of studies have emphasised that receptive mates, rather than food or habitat characteristics, are the key factors in male fitness (e.g. Bond & Wolff, 1999; Ims, 1987b, 1988a,b; Ostfeld, 1990): if so male competition and the distribution of receptive females, rather than variations in forage abundance, are more likely to affect male range-sizes.

I cautiously interpret the data presented in this study to mean that range sizes of male water voles in wild populations may be determined by social restrictions from other males and females resulting in an optimum number of female ranges they can overlap.

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Chapter 4

Temporal patterns of range-use in water voles (*Arvicola terrestris*)

ABSTRACT

A widely accepted paradigm in small mammal behavioural ecology that females compete for resources whereas males compete for females. Female competition for resources may lead to intrasexual territoriality. The *food defence* and *offspring defence* hypotheses explaining female territoriality both predict that females should exclude competing females from territorial boundaries. For water voles, either hypotheses allows for either "static" territoriality, in which the locations of females' territories remain constant, or drifting territoriality in which the locations of female's territories constantly drift. If females defended their entire range over short periods, gains and losses of habitat should be actively competed for, potentially resulting in static territoriality. If females visited their entire range over longer periods, drifting territoriality could result, since peripheral habitat may be less well defended. Female water voles may be more likely to actively defend entire ranges at relatively high population densities. At low population densities, therefore, territories may drift; at high densities territories may be more static. Male and female water voles were radio-tracked at two study sites, one at low population density, and one at high population density. At both sites, range-use patterns revealed that ranges of neither sex reached asymptotes with increasing observations, but the position of the ranges constantly shifted via gains and losses of habitat. This apparently resulted from mating behaviour in which male – female pairs shared discrete locations within their ranges over a number of days. Therefore, entire ranges were not visited over relatively short time periods. At the high population density site, the degree to which ranges of both males and females shifted was smaller than at the low population density site. I conclude that female water voles exhibit drifting territoriality, but speculate that at population densities higher than those in this study their ranges could become static.

INTRODUCTION

Female small mammals are expected to compete for resources with which to raise offspring, and may, therefore, exhibit territorial behaviour, whilst males are expected compete for access to females, and therefore, according to some authorities, are not expected to exhibit territoriality (Ims, 1987, 1988; Ostfeld, 1985, 1990). Patterns of home-range use by each sex at different population densities, and over different time periods, are therefore likely to be determined by different factors.

Two competing paradigms are generally evoked to explain the evolutionary significance of territoriality in female small mammals; the *food-defence hypothesis* and *offspring-defence hypothesis* (Fortier & Tamarin, 1998; Ostfeld, 1990; Wolff, 1993). Both predict that females should defend habitat-related resources; it is possible, therefore, that females are simultaneously motivated to defend both food and nesting sites. To the extent that territorial behaviour arising from these motivations can be separated, the FDH predicts that females should compete for exclusive access to sufficient food resources for rearing young (Boonstra et al., 1987; Ims, 1987; Ostfeld, 1985, 1990), whilst the ODH suggests that territoriality is independent of the type and distribution of food resources and that females maintain exclusive territories in order to defend a nest site and deter intraspecific infanticide (Wolff, 1985, 1993; Wolff & Peterson, 1998).

According to Ims (1988) and Ostfeld (1990), male small mammals are not predicted to be territorial when females exhibit territoriality, but their spacing behaviour should reflect that of the females (Bond & Wolff, 1999; Fortier & Tamarin, 1998; Ims, 1987, 1988; Nelson, 1995a, b; Ostfeld, 1985, 1990). Males in most small mammal species do not engage in parental care and so their individual reproductive

success is largely limited by access to females; if females are territorial (and therefore uniformly distributed across the landscape) males would be unable to monopolise them by defending territories (Ostfeld, 1990).

Male ranging behaviour is likely to reflect a balance between many factors, amongst which influential ones may be the need to monitor the breeding condition of a number of females (e.g. Bond & Wolff, 1999), and secure access to females in oestrus by active mate guarding (e.g. Bond & Wolff, 1999; Leuze, 1976; Macdonald & Strachan, 1999). These two factors might be balanced by males that visited their entire range over relatively long time periods, and in the short term occupied discrete locations in the company of a single female.

In this study I examine the behavioural expression of female territoriality in water voles by examining their range-use patterns over different time periods. Patterns of male range-use may influence female movements via mating behaviour and potentially infanticidal behaviour. Whilst this study concerns the expression of female territoriality, therefore, I also examine the movements of male water voles.

In the majority of habitats in the UK water voles live in colonies arranged along the length of the water course in a series of home-ranges (Pelikan & Holisova, 1969; Stoddart, 1970; Woodroffe et al., 1990a). Breeding season ranges of female water voles are small and non-overlapping, whereas ranges of male water voles are larger (Efford, 1985; Leuze, 1976; Pelikan & Holisova, 1969; Stoddart, 1970; Chapter 3), often overlap with each other, and may overlap with the ranges of several females (Efford, 1985; Leuze, 1976; Stoddart, 1970).

Ranges of water voles in the majority of habitats in the UK comprise a narrow (1-2m) width of habitat over a much larger (often over 300m, Macdonald & Strachan, 1999) length (Barreto et al., 1998a; Lawton & Woodroffe, 1991; Stoddart, 1970).

Measurements of water vole ranges are, therefore, often considered not in terms of *area*, but in terms of *length* of occupied habitat for convenience (Stoddart, 1970). A pre-requisite for territoriality or competition between individuals, is sufficient detectability of intruders (Wolff & Peterson, 1998). In addition to the likelihood of detecting an intruder's scent, since water voles occupy narrow strips of habitat, an intruder passing through an occupied location would have a high chance of encountering the other occupants. This makes them a good model species for studying territorial behaviour in small mammals.

This study concerns only populations in lowland habitats in the UK, which can be much larger, and more spatially separated than some upland populations (Barreto & Macdonald, 2000; Barreto et al., 1998b; Carter & Bright, 2003; Woodall, 1993) and in which the numbers of individuals living in close proximity can be sufficient to demonstrate ranging activities of both sexes within the context of the surrounding individuals.

I follow the definition of Maher & Lott (1995, 2000) that a territory is "a fixed space from which an individual or group of mutually tolerant individuals actively excludes competitors from a specific resource or resources", but extend the definition of "competitors" to include infanticidal members of the population.

If territoriality in female water voles adapted entirely to defence of food resources, territory size (the length of habitat from which other females are excluded) should be determined by the length of habitat required to contain a sufficient quantity of food to raise offspring (Ims, 1987; Ostfeld, 1985, 1990). Richer resources of available food per unit length of habitat should result in smaller territories, all else being equal (e.g. Fortier & Tamarin, 1998). If territoriality in female water voles adapted entirely to defend altricial young in nesting sites, and territoriality was

therefore independent of the type and distribution of food resources (Wolff & Peterson, 1998), territory size should be optimal to keep competitors as far from a nest as economically possible, and territories should be maintained throughout the breeding season to maintain exclusive space for subsequent litters (Wolff, 1993).

For both the FDH and ODH, therefore, territorial behaviour in water voles should reflect a female's requirement to safeguard sufficient resources contained within a given length of habitat, and should preserve the boundaries of this defended area against intruding females. Water voles occupy relatively homogenous habitats (Efford, 1985; Leuze, 1976; Chapter 2) and the ranges of female water voles often contain many burrows and nesting sites (Efford, 1985; Leuze, 1976; Strachan, 1998; pers. obs). The predictions of both the FDH and ODH may, therefore, be equally satisfied if the position of females territories was stable over time, or if they exhibited drifting territoriality (*sensu* Doncaster & Macdonald, 1991; Taber & Macdonald, 1992), in which the geographical position of female territories constantly drifted.

The boundaries of water voles' territories are mediated by overt aggression (Leuze, 1976), but potentially also by passive range exclusion (*sensu* Stewart et al., 1997; Stewart et al., 2001) via the placement of latrines demarking territorial boundaries (Leuze, 1976; Stoddart, 1970; Woodroffe et al., 1990b). Latrines are regularly maintained by females, representing a considerable time investment in patrolling the territory (Leuze, 1976; Stoddart, 1970). In either case, therefore, the defended area of habitat is likely to represent the extent of a female's movements over a given time period.

If competing females were excluded from the entire length of a female's range, the size and position of female territories may be expected to remain relatively constant, and extension of the territory to occur only via direct competition or upon

the death or dispersal of a neighbour (Leuze, 1976). Maintaining exclusivity implies that the entire territory should be defended over a relatively short time period. It is possible, however, that the ranges of female water voles could be larger than a minimum territorial requirement (Chapter 3). This could potentially lead to some areas of a range being less rigorously defended than others, and the entire range being visited over much longer periods.

It is currently unknown over what time periods water voles use their entire ranges. Stoddart (1970) concluded that water voles visited the important latrines within a range at least once in each 24 hour period, most often twice, but that peripheral areas may only be visited up to once every 24 hours. Ranges of water voles can be over 300m in length, but are usually substantially shorter (Efford, 1985; Leuze, 1976; Macdonald & Strachan, 1999; Stoddart, 1970; Chapter 3). Water voles have been recorded moving as far as 800m in a single day (Macdonald & Strachan, 1999), and 100m in an hour (pers. obs.). A 6 - 8 hour period, or "day" of tracking (see Methods), should, therefore, be more than sufficient time for females to visit the entire of their territories at least once. If so, observed ranges could reach an asymptote after a day of tracking.

If female water voles actively defended an entire territory with set boundaries, it would be expected that:

a) the territory holder should visit the entire territory over a period of one day, sufficient to defend both ends of an entire length of habitat;
b) since intruding females should be excluded from an entire length of habitat, female ranges should be relatively inflexible with respect to losses and gains of habitat;

c) ranges should therefore retain a relatively constant size and position and reach an asymptote with increasing numbers of observations.

This would represent static territoriality, in which the positions of female territories remain relatively constant over time. Conversely, if females did not actively patrol their territorial boundaries on a daily basis, some habitat within a female's territory could be undefended at any point in time, and potentially used by neighbouring females. Thus each territory could have flexibility with respect to its size and position, due to losses and gains of habitat, and territory size would not reach an asymptote with increasing observations. Female water voles may therefore exhibit drifting territoriality.

Evidence suggests that female ranges may reach a maximum size at low population densities, at which habitat is apparently not actively competed for, whereas at higher densities range sizes apparently vary with competitive ability (Chapter 3). Female water voles at high density populations may therefore be expected to occupy more static territories, since ranges would be relatively small and potentially more actively defended (Chapter 3). At low population densities, females may exhibit drifting territoriality, since competition for habitat may be less intense, and areas of the range may remain relatively undefended.

In assessing the degree to which territories drift, it is necessary to exclude dispersing individuals. Dispersal (definition *sensu* Stenseth & Lidicker Jr., 1992, and Clobert et al., 2001) is a one-way movement of an individual away from a previous home-range to a new location, comprising three stages: 1) leaving the previous range 2) a transience phase (travelling to a new location) and 3) arriving at the new location (and establishing a new home-range). For female water voles, dispersal is therefore a

movement made *between* successive territories, and such movements would not constitute evidence of drifting territoriality.

Extra-home range movements representing a failure to complete any of the above stages fall into three categories (Clobert et al., 2001). These are *nomadism*, the failure to establish a new home range; *exploration*, making excursions outside of the home-range, but failing to leave permanently; *shifting*, moving a home range by adding territory to one edge and removing territory from another. Constant shifting of a home-range would be symptomatic of drifting territoriality in female water voles.

I present analyses of data on the range-use patterns of radio-collared water voles of both sexes over the short and long term. Short term (i.e. comparison of ranges measured over a single day with those measured over multiple days of tracking) movements are appropriate to determine whether time-budgets of females and males indicate that the entirety of their ranges are used over short time periods. Analyses of longer term movements (over a number of tracking sessions) demonstrate whether recorded ranges reach an asymptote with increasing observations, whether habitat is lost or gained by each individual over time and, if so, whether this is due to shifting or dispersal behaviour.

METHODS

Overview and study sites

A total of 688 individual water voles were live-captured 2746 times at three study sites over a four year period, from April 2000 to July 2003. These sites were the Bure Marshes NNR, Norfolk, UK (UK grid ref: TG 335 165); the Wendover Arm of the

Grand Union Canal, (SP 873 102); and the Little Bedwyn Stretch of the Kennet and Avon Canal (SU 295 665). Intensive radio-tracking of water voles took place at the Bure Marshes from April-September 2002 and at the Little Bedwyn Canal from April-July 2003. In total 20 males and 18 females were collared at the Bure Marshes and 8 males and 6 females at the Little Bedwyn Canal.

The Bure Marshes is a fenland habitat comprising fields of fen vegetation surrounded by a network of ditches in which the water voles occupy home ranges. Within the study area, live traps (Sherman XLK 3 x 3.5 x 12" folding aluminium with galvanised steel doors) were deployed along 4.07 km of ditch-edge. This site was live trapped in 2000, 2001 and 2002, trapping ending in April 2003.

The Wendover Canal (SP 873 102) comprised a single stretch of non-navigable canal with a total length of 4.12km. However, the suitable water vole habitat was interspersed with heavily wooded, over-shaded sections in which no sign of water voles was found at any time. Traps were deployed along all sections in which water vole sign was found, a total of 2.03km. Trapped sections extended 40m (two trap intervals) into the unoccupied habitat either side of the outermost field-sign of an occupied section. Throughout the study no water vole was captured more than 20m from the last field-sign of an occupied section and only occupied areas are used in the following analyses. This site was live trapped in 2000 and 2001.

The Little Bedwyn stretch of the Kennet and Avon Canal (SU 295 665) comprised a length of canal which ran parallel to the river Dun separated from it by a mown field varying between a 20m and 60m width. Live-traps were deployed along 1.04km of the canal and 960m of the river. Traps were also set around the 120m perimeter of a small pond less than 20m from the river. The total water's side

trapping in this site was thus 2.12km. The Little Bedwyn site was trapped from June 2002 until July 2003.

Individuals were radio-tracked in 12 tracking-sessions at the Bure Marshes and 5 sessions at the Little Bedwyn Canal (see below). There were two distinct habitats at the Little Bedwyn site, with differing population densities (Chapter 3). Only water voles on the canal habitat, at higher population densities, were collared and tracked. No individual dispersed onto the river habitat at any point during the study.

During the radio-tracking periods, the mean adult population density was 1.0 (standard deviation, +/- 0.1) voles per 100m at the Bure Marshes and 2.1 (+/- 0.2) voles per 100m for the canal habitat of the Little Bedwyn site. During trapping comparisons, population densities at the Wendover Canal were approximately double those of the Bure Marshes, and at the Little Bedwyn Canal were over four times those of the Bure Marshes for all comparable time periods (Chapter 3).

Research design and data analysis

Radio-tracking data were divided into *daily*, *weekly* and *total* ranges (see below). In each case, for convenience "range" refers to the length of habitat visited over each time period (*daily*, *weekly*, *total*). Thus, "*daily* range" equates to the length of habitat visited over a day of tracking (see below).

If female water voles defended an entire territory with set boundaries and males actively monitored all of the females in their ranges, *daily* and *weekly* ranges should be of a similar size, demonstrating that the entire range was visited on an approximately *daily* basis. I therefore compare *daily* and *weekly* ranges, and also

present behavioural observations from male and female radio-tracked individuals which overlapped ranges, to explain the patterns of *daily* and *weekly* ranges observed.

The size and position of *weekly* ranges, and how these relate to *total* recorded ranges for each individual, demonstrate the degree of stability in the geographical location of the ranges. Analysis of the types and frequencies of extra-territorial movements would determine whether any alterations in the position of range were due to dispersal. I therefore present analyses of dispersal rates to explain patterns of *weekly* and *total* ranges.

Dispersal rates and distances were recorded from radio-tracking data at the Bure Marshes and Little Bedwyn Canal and from trapping data at all three trapped sites, with high population densities at the Wendover Canal (untracked) and Little Bedwyn Canal, and lower population densities at the Bure Marshes. The dispersal rates from the trapping data are relevant since they indicate overall dispersal rates from each population as a whole.

Radio-tracking data consisted of repeated measures from a number of individuals at each site. These data were analysed in SAS (the SAS System for Windows, V8) using the Proc Mixed procedure, with *vole* nested as a random factor within *sex* and *study site*. For non-repeated measures data, analysis was conducted in Minitab (version 13), using General Linear Models. In all cases the range lengths were transformed by taking the square-root in order to meet assumptions of normality and homogeneity of variance. For analysis of proportional data, I arcsine transformed the square-root of the proportions.

Trapping protocol

The trapping and handling protocol, and analysis of ranging patterns from trapping data are described in detail elsewhere (Chapter 3). Traps were positioned 20m apart and their positions recorded with a 10-figure grid reference using a *Garmin* "Etrex" GPS to a maximum error of 10m. Following the general protocol of Efford (1985) traps were baited with apple, and contained approximately 150g of carrot as an overnight food source. All water voles were weighed to the nearest 5g, marked if a new capture, and sexed.

Collaring protocol

Radio-collars were purchased from Biotrack Ltd., Dorset, UK, with a TW-4 transmitter and Ag386 cell, weighing 4.5g. Collars were attached only to adult voles weighing more than 180g (and thus weighed 2.5% or less of any individual's body weight). Handling took an average of 2 minutes, did not require anaesthesia, and the collared voles were released immediately at their point of capture. Each animal was fitted only once with a radio-collar, which was removed at the end of the study period.

Water voles were collared throughout the 2002 field season at the Bure Marshes from mid-April until mid-August, attempting to ensure that 16 collared individuals (8 male, 8 female) were present on site at all times. Water voles were collared only in April and May at the Little Bedwyn Site, resulting in 8 male and 6 female individuals tracked from May onwards.

Radio-tracking protocol

There were 12 tracking sessions between April and October 2002 at the Bure Marshes, and 5 tracking sessions between April and July 2003 at the Little Bedwyn Canal. Radio-tracked positions of each individual were accurately established to a ten-figure grid reference using a Garmin "*Etrex*" GPS receiver. Accuracy for all tracked locations was in the range of 6-10m maximum error. The time of each fix was recorded to the nearest minute. To minimise disturbance to the tracked animals, a minimum distance of 5m was maintained perpendicular to the water course. This did not affect the accuracy of the fix since individuals were located by tracking linearly along each waterway, and triangulating the individual's position parallel to the water-course.

Radio-tracking took place only during daylight hours. Water voles were tracked for 5 days in each radio-tracking session. Each fix was taken by following a set route including all extant individuals. Individuals in close proximity, therefore, had fixes that were spatially and temporally adjacent for a given round of tracking. Fixes on any one individual were separated by a minimum of one hour as a compromise between reducing autocorrelation between consecutive fixes and maximising the number of fixes for each individual per day. The largest mean weekly range length in trapping studies of water voles at these sites were 94.4m (standard deviation, 102.2m) for males and 51.7m (s.d. 57.6m) for females at the Bure Marshes (Chapter 3). Water voles can move 100m in an hour (pers. obs.); I therefore assume that the majority of individuals could have traversed their entire ranges over a one-hour period.

The number of fixes that could be obtained per vole depended to some extent upon an individual's activities but in the majority of cases 5 fixes per day per vole were obtained for most days during each session (Table 1, Results). For each vole in a given tracking session, the *weekly* range comprised 5 *daily* ranges of approximately 5 fixes each.

Radio-collaring at the Bure Marshes was associated with a skewed sex ratio amongst water voles' offspring, potentially caused by effects of stress on collared females (Chapter 5). It is possible that this could have affected the behaviour of collared water voles. Leuze (1980), however, found no difference between range sizes of 30 collared and 14 un-collared females over a 5 month period. This provides some assurance that range lengths recorded in this study were not adversely affected by radio-collaring.

Measurement of daily *and* weekly *ranges*

Both trapped and radio-tracked positions were entered into ArcView GIS (version 3.1, Esri) and overlaid onto digitised aerial photographs of each study site. All measurements of range lengths were made within the GIS.

Observed radio-tracked ranges were measured to the nearest metre, following the watercourse. *Daily* ranges were derived by measuring the distance between the furthest tracked positions for each individual on each day of tracking. *Weekly* ranges were measured between the furthest tracked positions for each individual in each tracking session. *Total* ranges comprised the entire range of an individual over the entire period for which it was tracked.

Measurement of male / female radio-tracking range overlaps

I present behavioural data from male / female pairs recorded as having overlapping ranges from the radio-tracking data at both study sites. Since the positions of each individual were recorded in a given hour during each day's tracking, individuals in close proximity had spatially and temporally adjacent fixes. I recorded the proximity of interacting individuals to one another by scoring the number of fixes, occurring at similar times (usually within 5-10 minutes), within 10m, 20m, 30m and 40m of the fix for the other individual over the course of each week of tracking. Thus for each male-female pair, the number of pairs of fixes at approximately the same time within each distance class were recorded over the course of each 5 days of tracking. This eliminates the possibility that individuals could be sharing the same space but exhibiting temporal avoidance. Fixes in the same place, but separated by an hour or more, were discounted.

Measurement of breeding dispersal from trapping data

This study records only breeding dispersal (the movement of adults between two successive breeding areas or social groups, *sensu* (Clobert et al., 2001; Cockburn, 1992; Greenwood, 1980) since this relates to the movements of territorial and breeding individuals, rather than juveniles.

In some upland areas, dispersal can be directly inferred from trapping data via the movement of individuals between colonies or the colonisation of unoccupied habitats (Telfer et al., 2001; Telfer et al., 2003), both of which necessitate all three stages of dispersal to have occurred. In lowland populations, such as those in this

study, trapping occurs *within* spatially separate populations. Thus only within-population dispersal events can be detected from trapping data in this study, and dispersal is more difficult to separate from range-shifting.

Individuals could be trapped whilst dispersing, or dispersal could be inferred from individuals captured in two consecutive trapping sessions with relatively large distances between the nearest points of the consecutive ranges (i.e. a large minimum between-sessions distances). In both cases attributing dispersal is contingent upon demonstrating ranges before and after the dispersal event that were spatially distinct.

I use a working definition of dispersal to separate dispersal events from within-home range movements based upon the size and type of movement within the context of individuals' ranges. For these purposes, I define a "range" as a series of observations made over a tracking or trapping session, demonstrating a length of habitat within which the individual spends the majority of its time.

I employed a threshold movement distance that allowed separation of dispersal events from range-shifts and within-range movements on the basis of the likelihood of the movement being observed from a distribution of within-range movements. Observed range lengths for each week of trapping were used as the basis for a non-parametric cumulative probability distribution of the frequency of various range lengths occurring at each site and for each sex. This method is based on the Kaplan-Meier equations for survival analysis (Kaplan & Meier, 1958), calculated as: $p_i = i / n$, where p is the proportion of animals that exhibit ranges shorter than a given distance and i is the rank of the observed range length for each animal. I take the threshold for dispersal as a distance of x meters being larger than 95% of observed range lengths from the distribution. This measure includes all of the ranges of

individuals, potentially including dispersal events, and so is a conservative threshold for dispersal.

Ascribing movements to "dispersal" required that the movement resulted in a displacement of a previous range to a new location, separated by a sufficient distance at the nearest points from the previous range, and therefore;

a) that ranges before and after were recorded: if the individual was trapped whilst dispersing those ranges must have been significantly smaller than the range whilst dispersing;
b) the distance moved was larger than 95% of recorded ranges of individuals of the same sex in the population and so unlikely to represent a within home-range movement or range-shift;
c) the movement took place during a trapping session or between adjacent trapping sessions to minimise the possibility that the separate ranges could derive from multiple range shifts. Over-winter dispersal could not, therefore, be recorded.

Measurement of breeding dispersal from radio-tracking data

The majority of radio-collared individuals were monitored over several weeks. Since *weekly* radio-tracked ranges were based upon many more observations at both sites than were the trapped ranges (see Table 1; Results), the *weekly* ranges give a robust estimate of the range-lengths of each individual, and establish a context from which dispersal can be inferred. The threshold for separation between shifting a *weekly* range and dispersing based on radio-tracking data is, however, not clear. The

separation of these types of movement was necessarily arbitrary, and I defined dispersal as having occurred if there was a minimum between-sessions distance that was larger than either of the *weekly* ranges between which the dispersal occurred.

This incorporates information concerning the range-lengths each individual, and is conservative in that an individual would have to move the distance of a range-length away from its previous range in order to count as dispersal.

RESULTS

Of the 38 water voles collared at the Bure Marshes, 25 (15 males and 10 females) retained their collars for a week or more. Of the 14 at Little Bedwyn, 10 (6 males and 4 females) retained their collars for a week or more. Only individuals collared for a week or more were included in the analyses. Of these voles, the mean time spent collared was 4.9 weeks at the Bure Marshes and 4.0 weeks at the Little Bedwyn Canal.

Daily *and* weekly *radio-tracked ranges*

Mean *daily* ranges were a less than half of the size of *weekly* ranges at both study sites (Fig. 1). The proportion of each *weekly* range represented by each *daily* range differed between study sites but not between sexes ($F_{1,32} = 12.4$, $p < 0.002$; $F_{1,32} = 1.38$, $p > 0.2$ respectively). Fig. 1 presents the marginal means of the effects of site, showing that at the Bure Marshes, the mean *daily* range was 0.38 of the mean *weekly* range, whereas at the Little Bedwyn Canal it was 0.49.

Fig. 2 presents the mean percentage increase in cumulative range length of the *weekly* range for each day of tracking. Fig. 2 demonstrates that even after 4 days of tracking, *weekly* ranges of both males and female still increased by up to 20% with an additional day of tracking. Fig. 2 also shows that percentage increases in range-length for days two - four were larger at the Bure Marshes than at the Little Bedwyn Canal. This supports the observation that *daily* ranges represented lower proportions of the *weekly* ranges at the Bure Marshes.

Daily ranges did not differ significantly between sexes or study sites (Proc Mixed, $F_{1, 32} = 1.45$, $p > 0.2$; $F_{1,32} = 0.24$, $p > 0.6$ for effects of sex and site respectively). *Weekly* ranges significantly differed between sexes (Proc Mixed, $F_{1,32} = 4.31$, $p < 0.05$), such that males had larger ranges (106m as opposed to 78m). *Weekly* ranges did not differ significantly between sites ($F_{1, 32} = 2.54$, $p > 0.1$).

Weekly ranges did not reach an asymptote over the 5 days of tracking in each session, suggesting that neither males nor females visited their entire ranges over this period. Indeed, neither male nor female ranges reached an asymptote over the entire period of the tracking study at either site (see below).

Daily ranges at both sites increased with increasing numbers of fixes (Proc Mixed, $F_{1, 657} = 41.42$, $p < 0.001$; parameter estimate 0.5828, s.e. 0.091), and the mean proportion of each *weekly* range represented by each *daily* range increased with increasing number of fixes per day (Proc Mixed, $F_{1,657} = 36.43$, $p < 0.0001$; parameter estimate 0.0751, s.e. 0.012). It is therefore possible that the difference between *daily* and *weekly* ranges could be an artefact from insufficient fixes per day, rather than the movements of the individuals tracked. Fig. 3 presents the mean *weekly* trapped and tracked, and *daily* tracked ranges of a sample of male and female water voles from the

Figure 1: Proportion of mean *weekly* ranges represented by *daily* ranges (solid bars) and mean *total* ranges represented by *weekly* ranges (hashed bars) for the Bure Marshes (dark bars) and Little Bedwyn Canal (light bars). Error bars represent 95% confidence intervals.

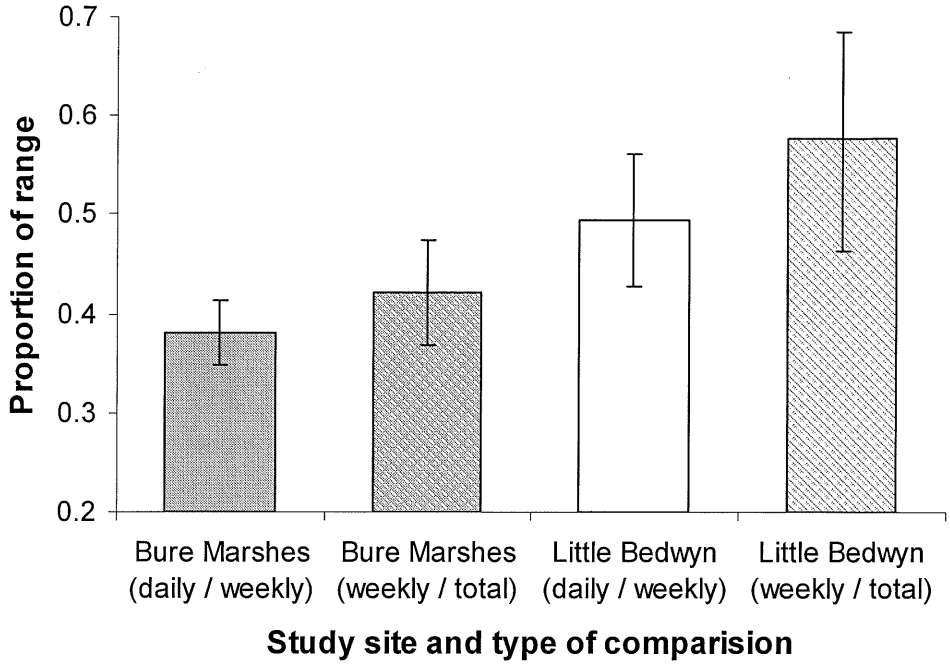


Figure 2: Mean percentage increase in cumulative range-length for each day of tracking for males (square symbols) and females (triangular symbols) at the Bure Marshes (solid lines and symbols) and the Little Bedwyn Canal (dotted lines and open symbols). Error bars represent standard errors.

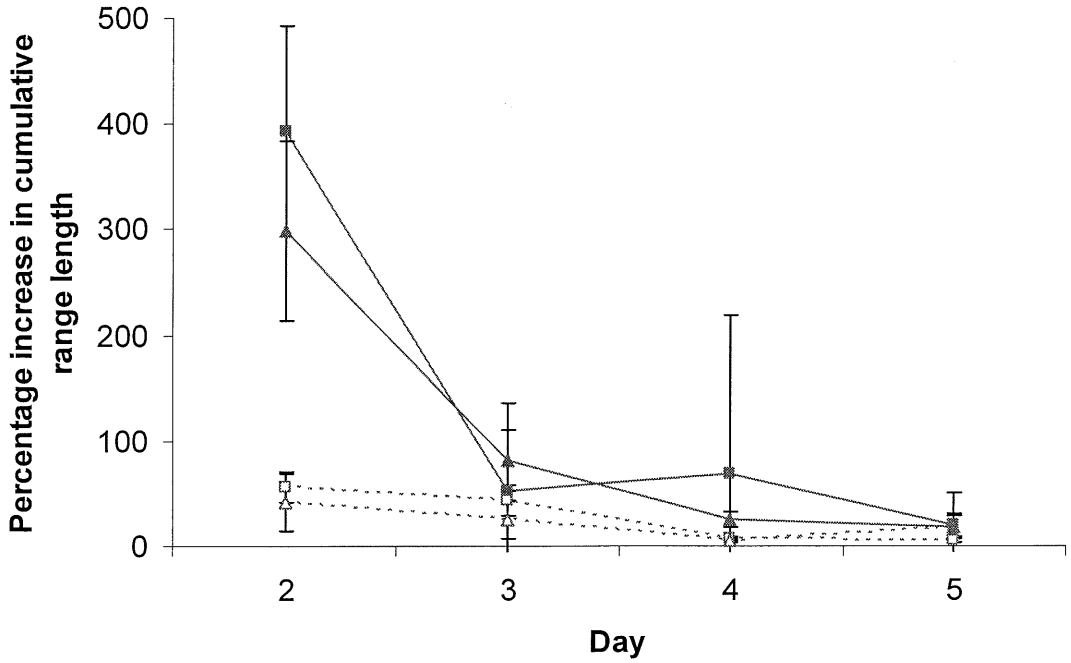
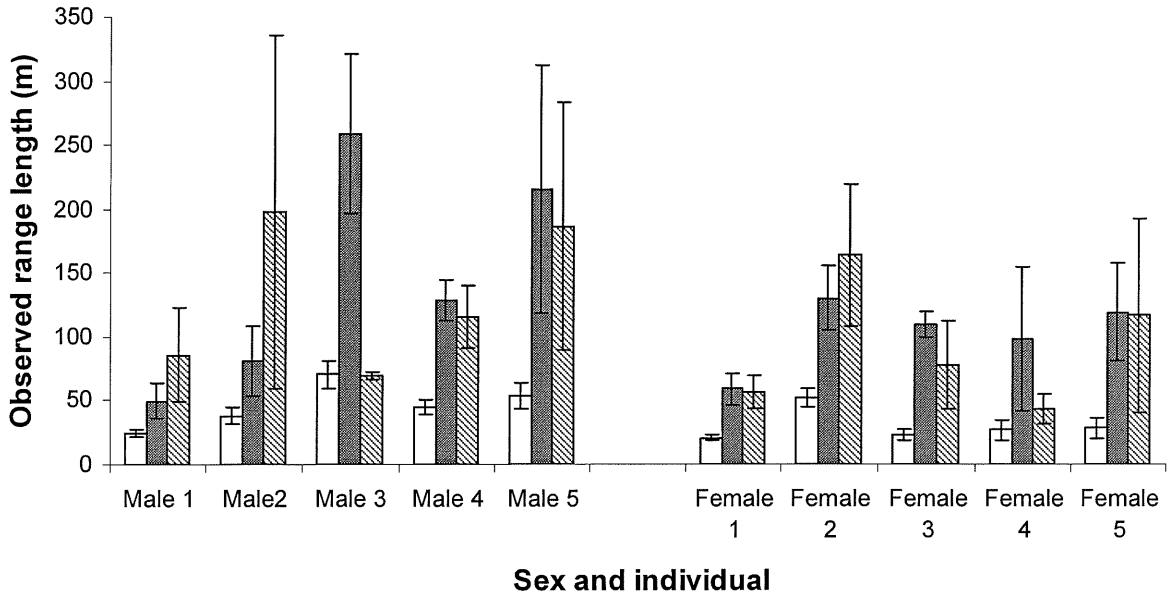


Figure 3: Mean *weekly* trapped (hashed bars), *daily*-tracked (white bars) and *weekly*-tracked (black bars) range-lengths of individual males and females at the Bure Marshes. Error bars represent standard errors.



Bure Marshes, and Table 1 presents the number of fixes (or captures) that each range size was based upon at each site.

Table 1: Median number of fixes (or captures) that each range size was based upon. Numbers in brackets represent the maximum and minimum number of fixes / captures.

	Bure Marshes	Little Bedwyn Canal
Weekly trapped range (m)	3 (2-6)	3 (2-6)
Weekly tracked range (m)	19 (14-25)	25 (24-25)
Daily tracked range (m)	4 (3-6)	5 (3-6)

Neither the radio-tracked nor trapped *weekly* ranges were consistently larger, despite the radio-tracked ranges being recorded with a much larger number of fixes (Fig. 3). The majority of trapped *weekly* ranges at the Bure Marshes for both males and females was larger than the tracked *daily* tracked ranges, even though the *daily* ranges were based upon more fixes than the trapped *weekly* range (Table 1).

Weekly *and* total *ranges*

Analysis of *total* ranges (the total length of habitat that each vole occupied throughout the study) was restricted to individuals tracked for two weeks or more, and which were not classed as having dispersed during tracking (n = 4; see below).

Mean *total* ranges were larger than mean *weekly* ranges which were larger than mean *daily* ranges at both sites (Fig. 4). *Total* ranges for each individual increased with increasing number of weeks over which the individual was radio-tracked (GLM, $F_{1,28} = 8.12$, $p < 0.01$; Fig. 5; parameter estimate 0.745, s.e. 0.261).

Similarly, the mean proportion of the *total* range that each *weekly* range represented decreased with increasing number of weeks of tracking at both sites (Proc Mixed, $F_{1,106} = 7.60$, $p < 0.01$; parameter estimate -0.0341 s.e. 0.0132).

Fig. 5 presents the percentage increase in cumulative *total* range for each week of tracking for both sexes at each site. Individuals' ranges could increase by up to 40% after four weeks and could increase even after 7-8 weeks of tracking (weeks were not necessarily consecutive).

Table 2: Mean amounts of range gained and lost per week per vole at each site. Numbers in brackets represent the standard deviation.

	Bure Marshes		Little Bedwyn Canal	
	Males (n= 13)	Females (n=9)	Males (n=6)	Females (n=4)
Mean range gained per week per vole (m)	49.5 (42.9)	27.6 (18.3)	20.0 (16.4)	13.6 (6.4)
Mean range lost per week per vole (m)	65.9 (51.9)	54.1 (42.6)	9.7 (7.8)	6.5 (3.8)

Table 2 presents the mean amount of new range length gained and previous range unused after each tracking session for individuals at each site and of each sex. Mean male and female ranges were respectively 94m and 52m at the Bure Marshes and 40m and 35m at the Little Bedwyn Canal (Chapter 3). Individuals therefore gained and lost substantial percentages of range-length with each tracking session. This shows that the length and the position of water vole's *weekly* ranges continually altered throughout tracking, forming much larger *total* ranges.

This evidence suggests that the position of *weekly* ranges was not constant and that the size of water voles' ranges did not reach an asymptote with increasing observations, implying that male and female water voles at both sites exhibited drifting territoriality.

Figure 4: Back-transformed marginal mean range-lengths for *daily*, *weekly* and *total* ranges at the Bure Marshes and Little Bedwyn Canal. Error bars represent 95% confidence intervals.

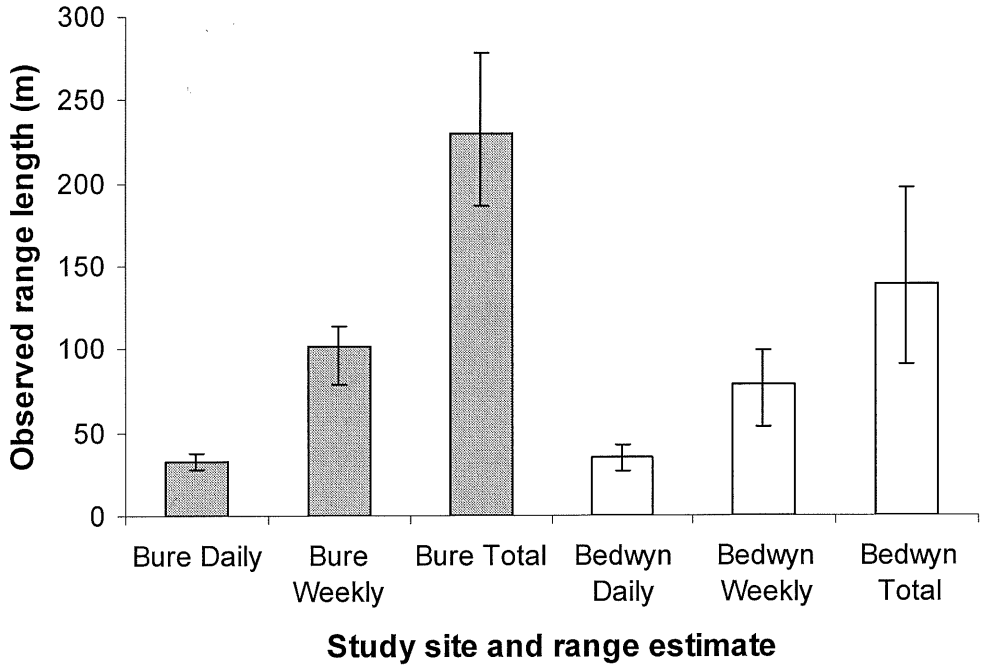
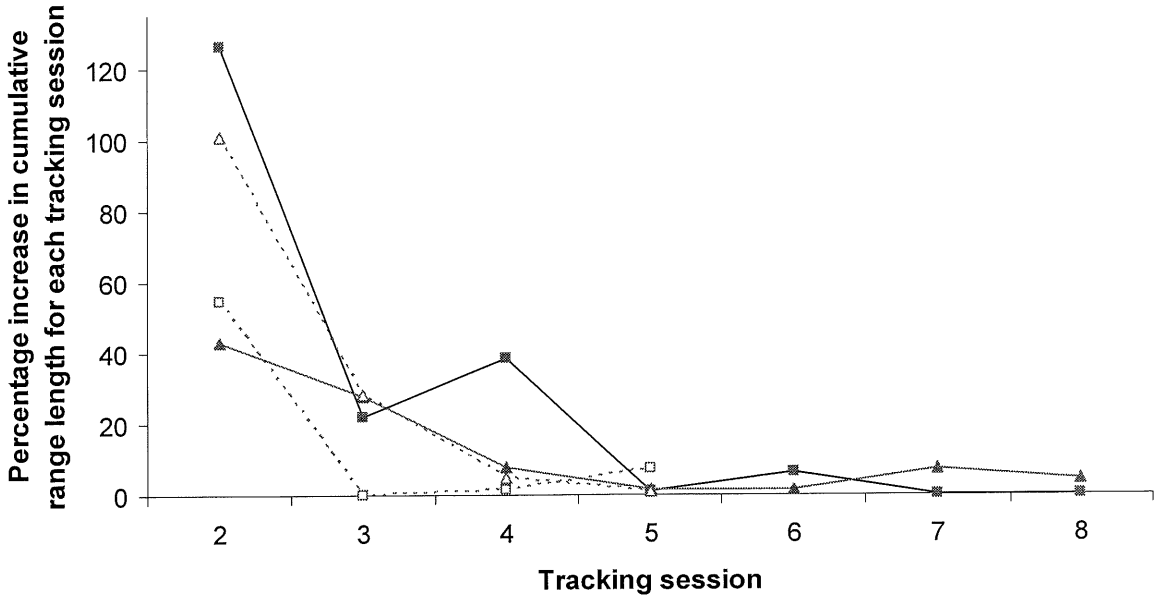


Figure 5: Increase in cumulative *total* range as a percentage of the previous week's range for males (squares) and females (triangles) at the Bure Marshes (solid line and symbols) and the Little Bedwyn Canal (dotted line and outline symbols). Error bars omitted for clarity.



Neither *total* ranges nor the proportion of *total* ranges represented by *weekly* ranges differed significantly between the sexes (GLM $F_{1, 28} = 1.68$, $p > 0.2$; Proc Mixed $F_{1,25} = 0.03$, $p > 0.5$, respectively). *Total* ranges were smaller at the (higher population density) Little Bedwyn site than at the (lower population density) Bure Marshes (GLM $F_{1,28} = 6.14$, $p < 0.05$; Fig. 4), and the proportion of *total* ranges represented by *weekly* ranges was larger at the Little Bedwyn site than at the Bure Marshes (Proc Mixed $F_{1,25} = 5.96$, $p < 0.05$; Fig. 1). This, and the data in Table 2, suggest that the amount by which the ranges shifted was larger at the low population density site than at the higher population density site, although the effects of other site-specific factors cannot be discounted.

The above analyses did not include the 4 individuals recorded as dispersing at the Bure Marshes. Inclusion of these individuals in separate analyses did not substantially alter the relationships described. The proportion of *total* ranges represented by *weekly* ranges still decreased with increasing weeks (Proc Mixed $F_{1,119} = 5.17$, $p = 0.025$; parameter estimate -0.0279, s.e. 0.0123), and was larger at the Little Bedwyn site than at the Bure Marshes (Proc Mixed $F_{1,29} = 9.30$, $p < 0.05$; marginal mean proportion 0.59 and 0.39 respectively). Similarly *total* ranges were larger at the Bure Marshes than at the Little Bedwyn site (GLM $F_{1,32} = 6.58$, $p = 0.016$; marginal mean ranges 290m and 138m respectively).

Although individuals defined as dispersing were removed to prevent this different movement type from influencing the study, the removal of these individuals did not in itself alter the results of the analyses.

Interactions between radio-collared individuals

Four types of male / female range overlap were recorded at the Bure Marshes and Little Bedwyn Canal from radio-tracking data. These were:

1) One male and one female overlap for all or part of a week, remaining within 40m of one another for the duration (n=14 overlapping male / female pairs);
2) One male overlaps two or more females and divides his time between them, within 40m of at least one of them for all or part of a week (n=6);
3) Two or more males overlap one female whilst she divides her time between them, within 40m of at least one of them for all or part of a week (n = 2).
4) A male and female overlap ranges for all or part of a week but are not recorded within 40m at any time (n = 2).

Un-collared, "invisible" individuals could influence the movements of collared animals. The above therefore cannot be used to derive frequencies of such overlaps occurring for each individual, but are representative of the types of interaction observed.

In 12 cases of the first overlap-type, the male moved into the female's range. In two cases the female approached the male. One female-female overlap was observed, in which the ranges overlapped extensively with 6 fixes within 10m of each other: this could be characteristic of mother-daughter associations (Chapter 3). Three male-male overlaps were observed. In one case, only one fix within 40m was recorded. In the other two cases, numbers of fixes at 10 and 20m apart were recorded, and the males spent 5 and 3 days within 40 metres of each other.

Table 3: The mean number of days spent within 40m, and the mean number of fixes per day of overlap in each distance class that each pair participating in the first type of overlap (single male - single female; above) spent. Numbers in brackets represent standard deviations.

Mean days within 40m	Percentage of fixes within distance class			
	40m	30m	20m	10m
3.5 (1.4)	75.3 (17.6)	65.6 (18.3)	50.6 (17.0)	31.3 (20.6)

Table 3 shows that the mean number of days per week that a given male-female pair spent within 40m was 3.5. On each day, an average of 30% of fixes was 10m or less apart, showing that pairs typically interacted closely for a proportion of each day. The percentage of fixes within 40m was not 100% since this incorporates days at the end of the overlap period when the individuals may have moved away, and days when individuals may have moved greater than a 40m distance and returned.

I re-analysed factors affecting *weekly* ranges, including only data from individuals undertaking male-female overlaps that remained within 40m of one another for at least one full day, and which overlapped with only one other vole. The most parsimonious model to explain variation in *weekly* ranges of overlapping individuals contained only main effects of *sex* and *number of days* that the overlap lasted, entered as a covariate (effects of *sex*: $F_{1,25} = 7.9$, $p = 0.01$; effects of *number of days*: $F_{1,25} = 5.66$, $p < 0.05$, estimate -1.056, s.e. 0.444), effects of *site* being non-significant when entered ($F_{1,24} = 1.49$, $p > 0.2$). Effects of increasing number of days were negative: the larger the number of days that males and females overlapped, the smaller their *weekly* ranges. Mean *weekly* ranges were 28m shorter with a 5 day overlap. This suggests that whilst males and females were occupying the same

location in close proximity, their ranges remained small, but that females' ranges were more affected than males.

Rates and distances of breeding dispersal

Table 4 presents the threshold distances above which movements from trapping data were candidates for breeding dispersal, based on the upper 5% of a cumulative probability distribution of trapped, observed ranges. These thresholds are conservative in that the distributions of range-lengths on which they are based include dispersal events and range shifts, increasing the number of large *weekly* ranges.

Table 4: Threshold values for dispersal having occurred for each sex and site, from trapping data, such that 95% of observed *weekly* ranges from the trapping data were smaller.

Study Site	Upper 5% of observed range lengths (m)	
	Males	Females
Bure Marshes	325	122
Wendover Canal	104	84
Little Bedwyn Canal	178	139

From the combined trapping data for all study sites, 32 individuals were classified as dispersing according to these criteria. In total 17 adult males and 16 adult females dispersed, suggesting there was no sex-bias in breeding dispersal. Approximately equal frequencies of dispersal were recorded in each month of the breeding season (range 5-8 individuals per month from May-September).

Dispersal could be detected only in individuals captured in more than one trapping-session. At the Bure Marshes, 309 individuals were captured, 153

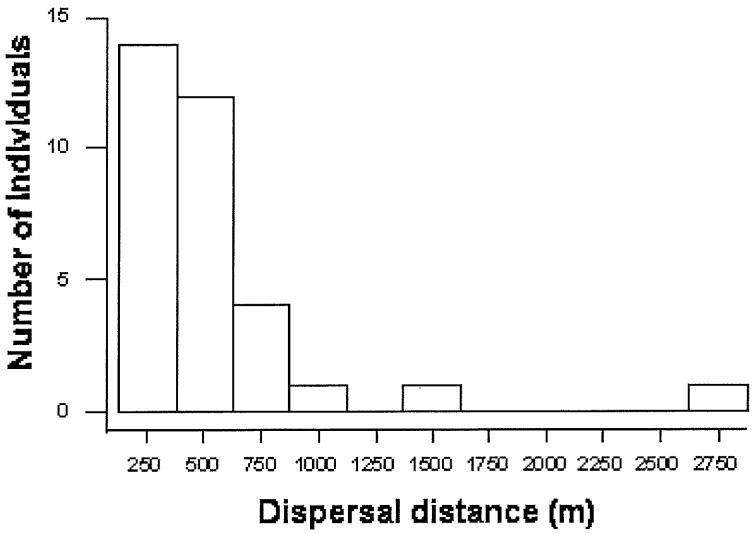
individuals were captured in more than one session, and 17 (approximately 11%) individuals were classified as dispersing. At the Little Bedwyn Canal, 191 individuals were captured, 59 in more than one session and 8 individuals (approximately 14%) dispersed. At the Wendover Canal, 188 individuals were captured, 18 voles in more than one session and 6 individuals (approximately 33%) dispersed.

Most dispersal distances were between 125-375m (n = 14) and 375-625m (n = 12; Fig. 6), with relatively few occurring in the 625-1125m range (n = 6; Fig. 6). Two extremely large dispersal movements (2704m, male, and 1412m, female; Fig. 6) were recorded at the Wendover Canal. Such movements could not be recorded at the Bure Marshes or Little Bedwyn Canal since the trapped area was not sufficiently large in either case.

There were no significant differences between *sites* or *sexes* with respect to the distances recorded for dispersal (GLM; $F_{2,32} = 2.63$, $p > 0.08$; $F_{1,32} = 0.00$, $p > 0.9$ for *site* and *sex* respectively). Removing the two large dispersal movements at the Wendover Canal from the data removed the suggestion of differences between *sites* ($F_{2,30} = 0.13$, $p > 0.8$, for effects of site).

Of 38 water voles radio-tracked at the Bure Marshes, 24 animals were tracked in more than one week. Dispersal was detected in 4 cases, two males and two females. In three cases, dispersed distances were below 375m (186m, 326m, 347m). One female dispersed 949m whilst being tracked. Of the water voles radio-tracked at the Little Bedwyn Canal, 10 individuals were tracked in more than one week. No radio-collared individual dispersed during tracking.

Figure 6: Frequency histogram of dispersal distances classified from trapping data at the Bure Marshes, the Wendover Canal and the Little Bedwyn Canal.



DISCUSSION

If the territories of female water voles did not drift, and were therefore static, the size of *daily* ranges would be expected to approximate the size of *weekly* ranges, and females' territories should be relatively inflexible with respect to losses and gains of habitat. Territory sizes should therefore reach an asymptote with increasing numbers of observations. Females may actively compete for habitat at higher, but not lower population densities in water voles (Chapter 3), leading to predictions that at higher population densities, ranges of female water voles should be more static and more likely to drift at lower population densities.

Daily ranges were smaller than *weekly* ranges for both sexes at both sites, such that *weekly* ranges built up over a number of days with no evidence that even 5 days of tracking was sufficient for the *weekly* range to reach an asymptote (Fig. 2). It is possible that sampling issues may have influenced the size of *daily* ranges; this is unlikely for two reasons. Firstly, water voles frequently appeared to occupy discrete locations for numbers of hours or days during tracking (pers. obs). Secondly, most *daily* ranges were smaller than, but based upon more observations than *weekly* trapped ranges (Table 1; Fig. 3). Traps were set at 20m intervals; the trapping interval was therefore small in relation to the length of individuals' ranges (Chapter 3). Individuals frequently returned to the same trap (often for every capture in a given week), and could not progress further than the trap in which they were captured. It is unlikely, therefore, that trapping methods would be inherently more likely to record large movements than radio-tracking. This suggests that the movements of the voles themselves, rather than inadequate sampling determined the extent of *daily* ranges.

Females did not visit the entire of their ranges on a *daily* basis, and males did not visit all of the females within their ranges every day. Instead, the length of *daily* and *weekly* ranges apparently reflected mating behaviour. Male-female interacting pairs often remained in close proximity for a number of days (a mean of 3.5) and spent a mean of approximately 30% of each day within 10m of each other (Table 3), often within the same tussock sedge (*Carex paniculata*), at both sites (pers. obs.). Tussock sedges have previously been shown to be preferred nesting sites of female water voles at the Bure Marshes (Leuze, 1976).

The more days a male-female pair remained within 40m of one another, the shorter their respective *weekly* ranges were. For interacting water voles, therefore, *weekly* ranges comprised small *daily* ranges, followed by large movements in the absence of an interaction. I cautiously suggest that the observed patterns of *daily* and *weekly* range-use reflect interactions between males and females taking place in discrete locations over prolonged periods, implying that females' short term range-use derives from mating behaviour centred upon nesting sites.

At both sites and for both sexes, mean *weekly* ranges were less than 60% of the size of mean *total* ranges (Fig. 1; Fig4). Increasing the number of weeks over which *total* ranges were measured increased the size of *total* ranges and decreased the proportion of the *total* ranges represented by *weekly* ranges at each site. Thus *total* ranges of both sexes at both sites derived from a series of *weekly* ranges, each of which was smaller than the *total* range, and the position of which was not stable over time. From this I conclude that the geographical location of each individual's range altered throughout tracking and the size of water vole's ranges did not reach an asymptote with increased observations. These range use patterns comply with

expectations if female territories drifted (Doncaster & Macdonald, 1991; Taber & Macdonald, 1992).

In these analyses, I used 100% ranges for each time period (*daily*, *weekly*, *total*), as opposed to a probabilistic measure of the range with an arbitrary cut-off (e.g. 95% range). It is possible that the use 100% ranges may allow females that performed frequent exploration movements (in which an individual makes excursions outside of the range but the position of the range does not alter: Clobert et al., 2001) to appear to exhibit drifting territoriality, when the position of their territories was, in fact, constant. However, only 4 individuals were observed to make extra-range movements not leading to a range-shift, on 4 separate days of tracking (from 738 vole-days of tracking). Given the extremely low incidence of observed exploration movements, the analysis and conclusions appear robust to the usage of 100% ranges.

The range-use patterns observed could be explained if water voles maintained stable ranges and underwent frequent dispersal events. From the trapping data, the percentages of the population classed as dispersing at the Bure Marshes and Little Bedwyn Canal were relatively low (between 11-13%). However, 33% of trapped voles were classed as dispersing at the Wendover Canal. The apparent larger dispersal rate at the Wendover Canal may reflect habitat fragmentation: approximately half of the habitat on site was unsuitable and occupied sections were a mean of 243m in length, surrounded by unsuitable habitat. Any individuals leaving a suitable patch would necessarily have to disperse in order to locate further, suitable habitat.

Dispersal appeared to be additional to the background pattern of range-shifts, rather than causing it. Dispersal may counterbalance stochastic local extinction through immigration of breeding individuals into populations which would otherwise go extinct (Brown & Kodric - Brown, 1977; Hanski, 1999), and occupancy of suitable

habitat by water voles in both lowland and upland habitats has been shown to be partially determined by proximity to extant populations (Barreto et al., 1998b; Bonesi et al., 2002; Macdonald & Strachan, 1999; Telfer et al., 2001). Analysis of breeding dispersal is therefore relevant to the conservation and restoration of water vole populations.

There was no evidence of a greater frequency of breeding dispersal of either sex in any month during the breeding season, or of differences in dispersal distances between sites or sexes. The majority of dispersal events recorded were between 125-650m (n = 26) in length. Only 8 dispersal events were larger, of which the two largest were 2.7km and 1.4km respectively, both occurring at the Wendover Canal. This suggests that male and female water voles from extant populations would be equally capable for reaching lowland habitat 2.7km away but that the rates of immigrants into habitat more than approximately 1km away would begin to decline rapidly (Fig. 6).

Of 34 radio-collared voles for which dispersal could be detected, four were classed as dispersing. Analysis of the proportion of *total* ranges represented by the *weekly* ranges did not include these individuals, but still showed that mean *weekly* ranges were less than 60% of the size of mean *total* ranges at both sites. The proportions of *total* ranges represented by *weekly* ranges decreased as the number of weeks of tracking increased for each individual; I therefore conclude that at both sites female water voles exhibited drifting territoriality, and that male ranges also followed this pattern, the position of their ranges constantly drifting over time.

Patterns of range-use were similar for both sexes at both study sites, but higher population densities were associated with smaller *total* and *weekly* ranges for both sexes. *Daily* ranges of collared voles did not differ between the low population density (Bure Marshes) and high population density (Little Bedwyn) sites (32m and

35m respectively). *Weekly* ranges were larger at the Bure Marshes than the Little Bedwyn Canal (101m and 78m) but this difference was non-significant at $p > 0.1$. The mean proportion of the *weekly* range represented by each *daily* range was, however, significantly larger at the Little Bedwyn site than at the Bure Marshes (0.49 as opposed to 0.38; Fig. 1), suggesting that *weekly* ranges were, in fact, larger at the Bure Marshes. Mean *total* ranges were significantly smaller at low population density that at high population density (230m and 139m respectively), and the proportion of *total* ranges represented by *weekly* ranges was larger at higher population density (0.59 as opposed to 0.39; Fig. 1).

These observations stimulate speculation that there is a minimum range-length requirement for female water voles, equating to the defended area of habitat within their ranges. The results suggest that discrete areas within the females' ranges were defended, but this defended area represented a greater proportion of the overall range at higher population densities. Since *daily* ranges did not alter with increasing population density, and represented a larger proportion of *weekly* ranges at higher densities, it is possible that *daily* ranges approximate the defended territory within a larger range. Territories of females at higher population densities than those recorded in this study, therefore, may have potential to become static as opposed to drifting if the overall range size was reduced sufficiently that the defended area represented the entire of a female's range.

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Chapter 5

Sex ratio variation in water voles: an explanation, and a caution concerning radio-collaring

ABSTRACT

Sex ratio manipulation amongst litters of mammals is an important feature of population biology, and both of the hypotheses commonly invoked to explain it refer to the condition of mothers. One technique often used in the study of such issues, and indeed used ubiquitously in studies of wild vertebrates is radio-tracking. A fundamental assumption - with scientific and welfare implications - is that data gathered on the tagged animal accurately reflects the biology of un-tagged animals. During a study of two populations of water voles (*Arvicola terrestris*), one site was live-trapped from April-September for two years (2000, 2001), and then members of the population were fitted with radio-collars and concurrently radio-tracked and trapped in the final year (2002). The second site was trapped only during 2002. The sex ratios of recruits born to both populations did not differ markedly from each other or from parity during the live-trapping phases (mean for each year: male = 25.7, s.d. = 2.1; female = 29.0, s.d. = 7.0), whereas following the period during which it was radio-tracked the sex ratio of recruits to that population became heavily male biased (43:13).

The altered sex ratio in the radio-tracked population was attributable to a 48% decrease in the number of female water voles being born, a decrease similar to the proportion (0.49) of the female population that was collared. No similar decline in male births was evident, suggesting that the radio-collaring of female water voles caused the sex ratio of offspring to be skewed in favour of males. These results may accord with Clarke's (1978) Local Resource Competition hypothesis which predicts that under sub-optimal conditions females will produce more of the dispersing sex; in this case males.

INTRODUCTION

It is well established that population parameters respond to changes in the environment and that such responses reflect the consequences of change at the level of individuals. Evolutionary theory suggests that parental investment may favour the sex expected to produce the most grandchildren per unit investment, where this investment influences the fitness of one sex more than the other. Two hypotheses link natal sex ratios and environmental quality as it is expressed in terms of female condition.

First, the local resource competition hypothesis predicts that mothers with access to poor resources should produce offspring of the sex that is most likely to disperse, in order to reduce competition for resources in the natal range (Clark, 1978; Silk, 1983). This model, recently formalized quantitatively by Julliard (2000), assumes differences between male and female dispersal rates; it also assumes spatial variability in that reproductive success is better in some habitats than others, presumably because the females in those habitats are in better condition.

Second, Trivers & Willard (1973) proposed that the optimal reproductive strategy for a mother is to produce offspring of the sex that can most benefit from the level of resources that she can provide. Thus, in polygynous societies, a mother in good condition is predicted to produce more sons, insofar as her condition bestows subsequent competitive advantage on them and this translates into higher reproductive success.

Water voles in the UK are not sexually dimorphic (Macdonald & Strachan 1999), but the above hypotheses hold in so far as they are polygynous with males the non-philopatric sex (Leuze, 1976).

Both models connect offspring sex ratio with the availability of food resources, expressed through maternal condition. There is some evidence of natal sex ratio variation amongst water voles (*Arvicola terrestris*). Bazhan et al. (1996) showed that food deprivation during pregnancy almost halved the number of weaned young produced by captive female water voles, and the sex ratio of these litters was skewed in favour of males by over 2:1. They also demonstrated an increase in levels of corticosterone in food deprived females, suggesting a stress response. Nazarova & Evsikov (2000) demonstrated that captive female water voles which gained relatively little weight during pregnancy weaned smaller litters with an increase in the proportion of males, compared to females that gained larger amounts of weight during pregnancy.

Water voles are endangered in the UK, largely through the impact of invasive American mink (*Mustela vison*) (Macdonald & Harrington, in press; Macdonald & Strachan, 1999; Woodroffe et al., 1990), although this impact may be worsened by the linearisation and fragmentation of their habitat in lowland agricultural landscapes (Barreto et al., 1998).

Habitat fragmentation, and its impact on metapopulation and source-sink dynamics is a fundamental interest in ecology (Hanski, 1999), and applicable to water voles (Bonesi et al., 2002; Telfer et al., 2001). Understanding the link between water vole populations and the quality and heterogeneity of their habitats is thus of fundamental and conservation importance (Rushton et al., 2000). We therefore set out to study the population dynamics, dispersion and movement patterns of water voles in two contrasting populations. To do this we used, amongst other methods, radio-tracking.

Radio-tracking is a ubiquitous tool in field studies of wild vertebrates. An important assumption is that the behaviour of tagged individuals is representative of those in the population at large. This scientific concern, and the related one that subjects' welfare should not be compromised by tagging, have been emphasized since the technique's inception (see Amlaner & Macdonald, 1980, and papers therein) and remains so today (Kenward 2001). Although many studies using radio-tracking do not test its effects, several of those that have done have revealed them to be negligible (de Mendonca, 1999).

In a review of five journals, Withey et al. (2001) found 96 articles that assessed the effects of radio-transmitters on animals, of which 79% were conducted upon bird species. Of these 96, 47% reported an adverse effect. Amongst the effects recorded are effects on reproduction (Cotter & Gratto, 1995; Ramakka, 1972), weight (Perry, 1981; Reynolds, 1992; Tuyttens et al., 2002), condition (Greenwood & Sargeant, 1973; Jackson et al., 1985; Perry, 1981), behaviour (Cotter & Gratto, 1995; Ramakka, 1972) and survivorship (Webster & Brooks, 1980; Werner & Etter, 1983). Such impacts could have profound consequences, and some discussion of them has been controversial (e.g. Burrows et al., 1994, 1995, versus Ginsberg et al., 1995; see Woodroffe, 1997). Tuyttens et al. (2003) have argued that the ways in which effects of tagging are manifest may be subtle, and emphasized the importance of studying this topic.

In the present context, it is noteworthy that Leuze (1976, 1980) found no significant difference between radio-collared and other female water voles in either their body weight or the mean number of weanlings produced. Furthermore, many studies reporting no direct impact of radio-collaring also involved small rodents (e.g.

Berteaux et al., 1996; de Mendonca, 1999; Johannesen et al., 1997; Ormiston, 1985; Reynolds, 1992; Smith, 1980).

In our study of water vole ecology we observed a marked change in the sex ratio of recruits into one of our study populations. Our analysis reveals that the most likely cause of this change was a shift in the sex ratio of young raised by radio-collared females, a result with relevance to both sex ratio allocation theory and conservation research.

METHODS

Study sites

This study was conducted at two sites, the Bure Marshes National Nature Reserve, Norfolk, UK and the Little Bedwyn stretch of the Kennet and Avon Canal, Wiltshire, UK.

The Bure Marshes NNR (UK grid ref: TG 335 165) is a fenland habitat managed by English Nature, comprising fields of fen vegetation surrounded by a network of ditches in which the water voles occupy home-ranges. Within the study area, we deployed live traps (Sherman XLK 3 x 3.5 x 12" folding aluminium with galvanized steel doors) along 4.07 km of ditch-edge. The population was open to immigration and emigration in that further, occupied ditches were accessible from three sides of the site. This site was live trapped from April to September in 2000 and 2002 and during April 2003. Public health restrictions, due to an outbreak of Foot and Mouth disease, prevented us from trapping between April 2001 and June 2001.

The Little Bedwyn (SU 295 665) stretch of the Kennet and Avon Canal comprises a length of canal which runs parallel to the river Dun separated from it by a mown field varying between a 20m and 60m width. Live-traps were deployed along 1.04km of the canal and 960m of the river. We set traps also around the 120m perimeter of a small pond less than 20m from the river. The total water's side trapping in this site was thus 2.12km. The site was bounded on one side by unsuitable habitat but on the other was linked to further, small patches of suitable habitat via the river, and therefore potentially open to dispersal. The Little Bedwyn site was trapped from June 2002 until July 2003.

Trapping protocol

Traps were positioned 20m apart and their positions recorded with a 10-figure grid reference using a *Garmin* "Etrex" GPS to a maximum error of 10m. Following the general protocol of Efford (1985) traps were baited with apple, and contained approximately 150g of carrot as an overnight food source.

During 2000 half of the Bure Marshes site was trapped in alternate months. During 2001, the two halves were trapped in consecutive weeks. During both years, traps were set on Monday and removed on Friday, and thus open for 4 trap nights. During 2002, the entire Bure Marshes site was trapped during each trapping session, by trapping each half in alternate mornings and afternoons, allowing one capture period per day for each half from Monday to Saturday of each session. The entire Little Bedwyn site (2002) was trapped with one session a month of morning captures from Monday to Saturday, allowing 5 trap nights.

Collaring protocol

Radio-collars were purchased from Biotrack Ltd., Dorset, UK, with a TW-4 transmitter and Ag386 cell, weighing 4.5g. Collars were attached only to voles weighing more than 180g and thus weighed 2.5% or less of any individual's body weight. Handling took an average of 2 minutes, did not require anaesthesia, and the collared voles were released immediately at their site of capture. Each animal was fitted only once with a radio-collar, which was removed if it was still attached at the end of the study period.

Water voles were first collared at the Bure Marshes at the end of the 2001 field season from 23/08/01 to 07/09/01 (and thus after the population had been live-trapped routinely for 9 months over a two year period). 15 water voles (8 female, 7 male) were collared. Only one of these individuals survived the over-winter period, but lost its collar doing so; high over-winter mortality rates appear to be characteristic of the species (Macdonald & Strachan, 1999). Water voles were collared throughout the 2002 field season from 17/04/02 until 27/08/02, attempting to ensure that 16 collared individuals (8 male, 8 female) were present on site at all times. In total 18 females and 20 males were collared. The total number of collared females on site at the end of each trapping session is shown in Table 3.

Birth date estimation

Birth dates of water voles for each year at the Bure Marshes were estimated using the growth curve estimation techniques described by Kaufmann (1981). These have been used previously to construct age-weight growth curves for water voles (Efford, 1985)

and for estimating the birth-dates and growth rates of other small herbivorous mammals (Boutin & Larson, 1993; Virgl & Messier, 1997; Webb, 1993).

Growth rate estimates were based upon changing weights of individuals between successive capture sessions. Only the weight on first capture in a given session was used for estimation in order to minimize the impact of trapping-related weight losses or gains. Both Gompertz and Bertalanffy curves were fitted to the data. As determined by the coefficient of variation (R^2) for the fit of the regression from the straight line plot (Kaufmann, 1981), both fit the data equally well. Following Efford (1985) we used only the Gompertz curve, on the grounds that these techniques may be inappropriate for fitting the Bertalanffy curves (Kaufmann, 1981). Growth curves were fitted separately for each sex in each year.

Specific growth rate (G), the rate of growth at a specific weight, was estimated as (lnS2 – lnS1) / t, where S1 and S2 are weight in the second and first capture sessions separated by t days. This was plotted against ln (S), where S is the geometric mean of S1 and S2.

The slope (a) and intercept on the y axis (b) for the Gompertz curve are related as follows:

$$G = -a \ln S + b$$

The integrated form of the above equation can be used to predict the age of an individual from its weight on first capture by solving the following equation:

$S = S_{max} \exp [-\exp -a (t + t_0)]$, where $S_{max} = \exp (b / a)$ and t_0 is the constant of integration assuming that a water vole at age 16 days weighs 47.8g (data from Bristol Zoo, 3 litters, n = 14). Birth date estimation is reliant upon a robust constant of integration. The value of t_0 used here compares favourably with other data. Efford

(1985) used a constant of integration of 60g at 20 days (estimate from Bure Marshes growth curves puts voles at 60g between 20-26 days old).

Usage of this method for birth date estimation assumes that no individuals consistently grow faster or slower than the average (Kaufmann, 1981). This assumption can be validated by examining the difference between estimated birth dates for a given individual if captured more than twice.

Birth dates were estimated only for individuals below 180g on first capture, since this was the lowest body weight from which any individuals first lost weight between sessions, indicating that they were approaching S_{max}. Only a percentage of animals born would enter the trapped population, and the number of births estimated for each month is based only upon individuals captured between the weight when first able to be captured (45-50g) and 180g. The numbers of each gender born in each month cannot, therefore, be assumed to represent the actual number of births, but are useful as a comparative tool for examining birth sex ratios.

MARK analysis

All analysis of survival and recruitment rates, and population size estimates was conducted using Program MARK (White & Burnham, 1999). Males and females at each site were analyzed separately. All survival rates and population sizes were estimated using the Robust Design (Kendall, 1999; Kendall & Nichols, 1995; Kendall et al., 1997) and recruitment rates of each gender were estimated using Pradel's model for survival and recruitment estimation (Pradel, 1996), both implemented within MARK.

Best fitting models were selected by use of Akaike's Information Criterion, implemented within MARK (AIC: Anderson & Burnham, 1999).

Numbers of voles recruited in each session were calculated by multiplying the recruitment rates (defined as the number of new animals at time t = 2 captured per extant member of the population at t = 1) from Pradel's model by the Robust Design population estimate in the previous trapping session.

Following Kendall *et al.* (1995, 1997) the intervals between trapping sessions are termed the *primary sampling periods* (hereafter "*primary periods*") in which gains (birth and immigration) and losses (death and emigration) to the population can occur.

Model of female recruitment rates versus proportion collared

We present a model of female recruitment rates versus proportion of the female population collared, based upon the recruitment and survival rates measured in the MARK analysis. This model makes the following assumptions:

1) That collared females give birth to only male offspring;
2) That the ratio between recruitment rates for each *primary period* would stay the same if more females were recruited in previous sessions;
3) That survival rates of females would be unaffected by increased birth rates of juvenile females.

Not meeting the first assumption would decrease the expected male-biased shift in sex ratio for each collared female and we would expect to find increasingly less correlation between numbers of females collared and female recruitment rates.

The second assumption is reasonable as the relative difference between female recruitment rates in each session during 2002 was similar to that of the male Bure Marshes recruitment rates and female and male recruitment rates at Little Bedwyn during this period (see Results).

The third assumption is reasonable if juvenile female survival rates are similar to those of adults after entering the trapped population. No data exists from the current study to support or refute this assumption.

In the model, the collared proportion was averaged across all capture sessions. How the exact proportion of collared voles in each capture session would affect the recruitment for the next month was unknown. Reducing the recruitment by the average collared proportion across all capture sessions simplified the model and removed this source of uncertainty.

Experimental design

Although our original aim was a comparison between two sites, the emerging results caused us to consider the design in terms of testing the hypothesis that changes in sex ratio were attributable to radio-collaring at the Bure Marshes. This experimental design is necessarily unreplicated, and follows the form of a Before-After-Control-Impact-Pairs (BACIP) design (Stewart-Oaten et al., 1992). This design determines if the state of a perturbed system differs significantly from what it would have been in

the absence of the perturbation. In this case, the perturbation is the fitting of radio-collars to individuals of the Bure Marshes population.

The Bure Marshes population was live trapped in all three years of the study; collaring took place only at the end of the 2001 field season, and throughout the 2002 field season. The Little Bedwyn population was live trapped and not radio-tracked during the 2002 field season. Water voles were collared at the Little Bedwyn site from April 2003. Data from this period is excluded from comparison with the Bure Marshes population.

The *Before* period comprises live trapping at the Bure Marshes with the absence of radio-collaring in 2000 and 2001. Although water voles were first collared at the end of 2001, no collared individuals survived the winter and so the 2002 breeding season was unaffected by the presence of collared females until collaring in late April (except potentially by altered recruitment between September 2001 and April 2002 - see Results). The *Perturbation* period, therefore, comprises live-trapping and concurrent radio-collaring from April 2002 onwards. The *Control* is the live trapping only at the Little Bedwyn site running concurrently with the radio-tracking and trapping at the Bure Marshes.

This design departs from the BACIP in one respect which is that the Little Bedwyn site was not trapped before 2002, making a statistical pair-wise comparison impossible. The robustness of the present experimental design relies upon proving that sex ratios and hence numbers of male and female water voles born at the Bure Marshes in 2002 (*Perturbation* period) following the onset of collaring were demonstrably different from sex ratios and birth rates at the Bure Marshes in the preceding years (*Before* period) and at the Little Bedwyn site during 2002 (*Control*).

RESULTS

Fates of collared animals in 2002

9 female voles slipped collars or died within a week of being collared. Of these, 5 were definitely predated, 3 were probably predated (they were never recaptured) and 1 slipped its collar, remaining alive in the population. 7 male voles slipped collars or died within a week of collaring. Of these, 4 collars were slipped or malfunctioned and were removed, 1 vole was definitely predated as probably were 2 others. For voles that retained a collar for more than one week, the mean time spent collared was 69 days for females (n=9, standard deviation, 33, range 20-119) and 76 days for males (n = 13, s.d., 45, range 22-161).

Population estimates and the female decline

Details on model selection and parameter estimates are presented in Appendix II. Fig. 1 shows the Robust Design population estimates for the Bure Marshes and Little Bedwyn. Whereas these were stable in both areas during the periods for which they were live-trapped only (*Before* period and *Control*), the numbers of females in the Bure Marshes declined throughout 2002 (*Perturbation*) to reach a minimum of only 5 in April 2003. Scrutiny of the data from April to September 2002 reveals a steady decline in females from 20 to 9 over this period, the only reversal being an estimated increase from 13 to 15 from June to July. In contrast, between April and September 2002 the estimated number of males increased from 28 to 35.

Figure 1: Estimated population sizes from 2001 - 2003 at the Bure Marshes and Little Bedwyn Canal. Solid lines represent Bure Marshes populations, dotted lines represent Little Bedwyn populations. Triangular points represent males, rhomboid points represent females. Error bars represent standard error of population estimate.

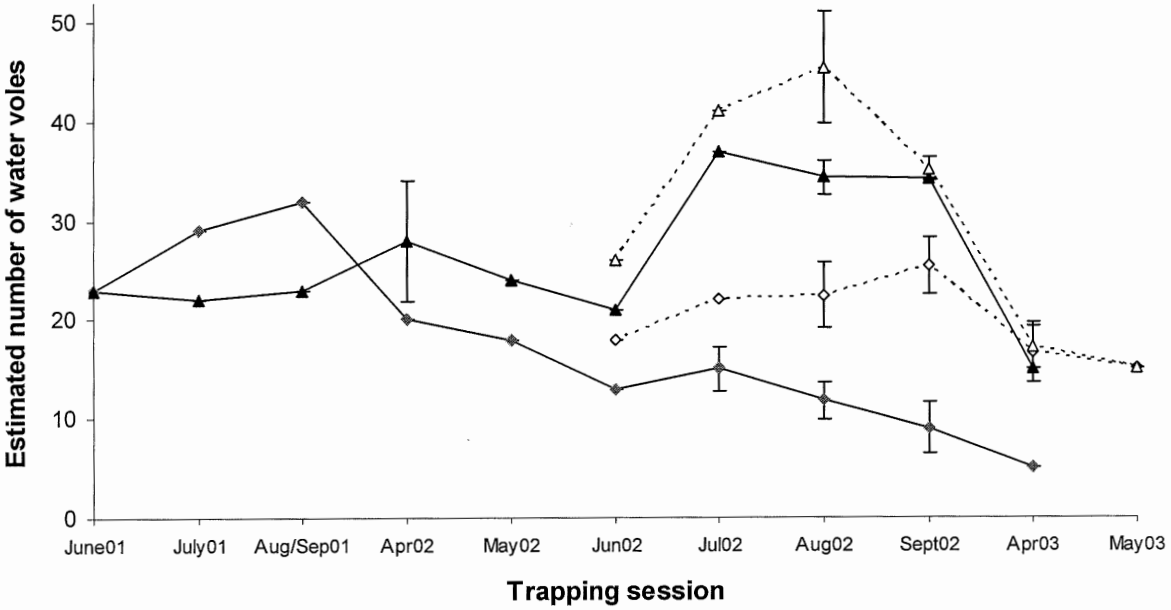
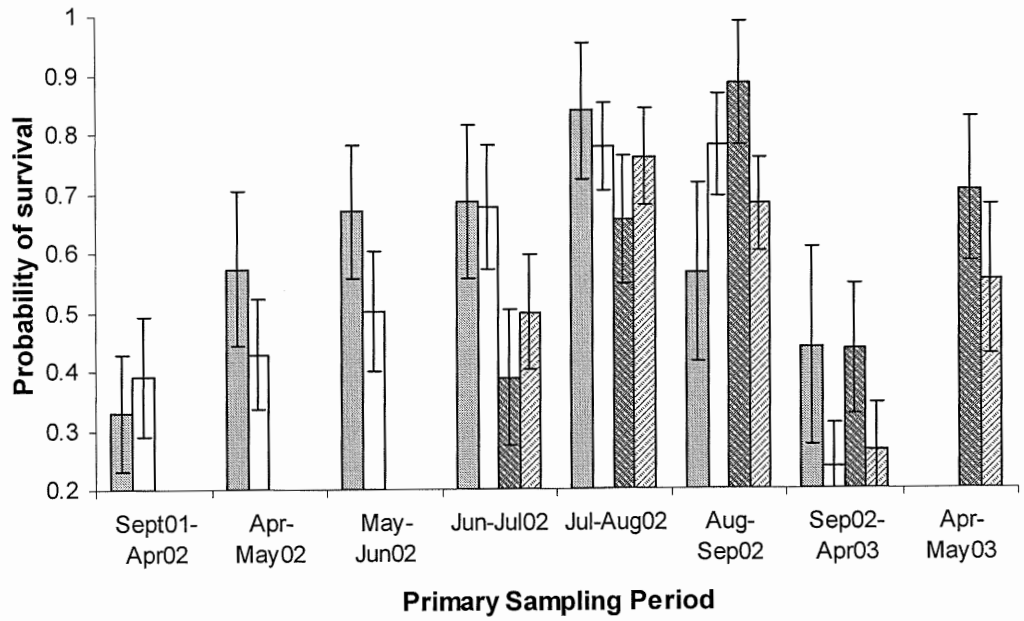


Figure 2: Survival probabilities during primary sampling periods from 2001 to 2003 at the Bure Marshes and Little Bedwyn sites. Solid bars represent Bure Marshes populations, hashed bars represent Little Bedwyn Populations. Light bars represent males, dark bars represent females. Error bars represent s.e. of survival estimate.



Survival rates

Fig. 2 shows the survival rate estimates for *primary periods* from 2001 to 2003. Survival rates were higher for females than for males at the Bure Marshes from the outset of the *Perturbation* (April 2002 onwards); indeed, the survival rate of females at the Bure Marshes was higher than the survival rates of either sex at Little Bedwyn up to August-September. In short, the decline in numbers of females at the Bure Marshes occurred whilst their survival rates were the highest of either gender or population.

The best fitting model to estimate survival rates did not incorporate emigration (Kendall, 1999; Kendall & Nichols, 1995; Kendall et al., 1997). Any emigration of females would therefore result in lowering the survival probability for a given *primary period* and we can therefore exclude the possibility that the decline in numbers of females at the Bure Marshes could be attributed to unacknowledged emigration. Rather, the observed decline must have resulted from low recruitment rates of females into the population.

Recruitment

Fig. 3 presents the estimated number of males and females recruited into both study populations during each *primary period* from 2001 to 2003. In all cases the estimated number of recruits for any site or gender in a given month was within 3 individuals of the actual number of new animals captured, suggesting that the MARK estimates were a good representation of the data.

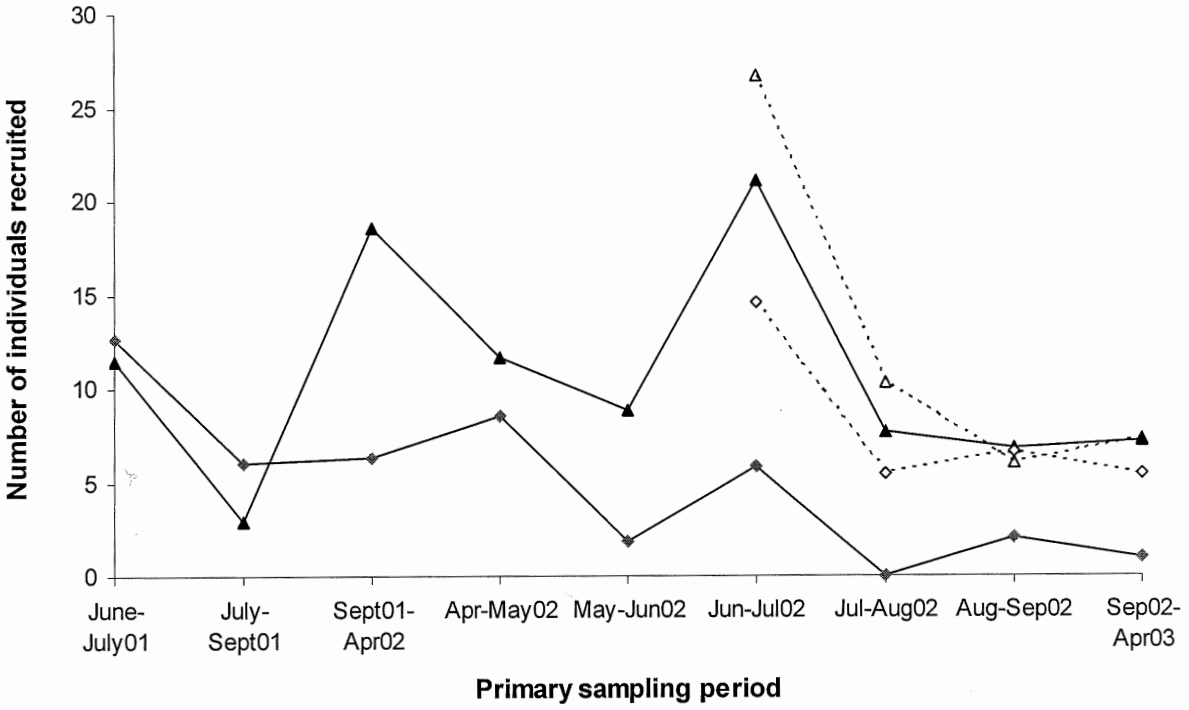
Radio-collaring and birth sex ratios

After September 2001, the numbers of females recruited to the Bure Marshes (and the percentage of recruits that were female) were consistently lower than had been the case during the *Before* period (with the exception of the April-May 2002 period: see below), or was ever the case at Bedwyn (*Control*). In the Bure Marshes population (*Before* period), 51 females and 45 males were recruited in 2000, and 19 females and 15 males from June-September 2001. In the Little Bedwyn population (*Control* site), 32 females and 53 males were recruited from June 2002 to April 2003. Over the same time period (*Perturbation* period) 43 males but only 9 females were recruited into the Bure Marshes population.

Immigration and emigration rates

A proportion of recruits in any session could be immigrants from outside of the trapped area. Dispersal rates of females at the Bure Marshes were relatively low: no radio-collared female moved beyond the trapped area of the site during 2002 and, from the trapping data, only 8 females were recorded as making weekly or between-sessions movements of over 100m (mean female weekly trapping-derived range for all years 36.25m). Of these, only 5 could be classed as true dispersal movements (definition *sensu* Stenseth & Lidicker Jr., 1999 and Clobert et al., 2000; Chapter 4), size of movements in range 239m-902m). Similarly for the 2001 season (June-September 2001) only 4 females were recorded as making movements of greater than100m, of which only one (619m) could be defined as dispersal. The scarcity of female dispersal (detected in c. 9% of the female population over two years) was such that it is unlikely that a substantial proportion of female recruits to the population were immigrants.

Figure 3: Estimated numbers of males and females recruited during each primary sampling period between 2001 and 2003 at the Bure Marshes and Little Bedwyn. Solid lines represent Bure Marshes populations, dotted lines represent Little Bedwyn populations. Triangular points represent males, rhomboid points represent females. Error bars omitted for clarity.



Fit of growth models

R^2 for the fit of the regression of G on ln(S) is shown in Table 1. In all cases, body size (lnS) explained 40-70% of the variance in Specific Growth Rate.

Table 1: R^2 for the regression of size (ln(S)) on Specific Growth Rate (G) for each year, site and gender.

	Bure Marshes		Little Bedwyn	
Year	Males	Females	Males	Females
2000	46.3	52.6	/	/
2001	61.4	41.2	/	/
2002	69.9	55.7	54.2	55.9

Table 2 shows the mean and standard deviation for the maximum discrepancies between estimated dates of birth for each individual for which data are available during each year, this being an indication of the goodness of fit of the growth curve.

Table 2: Mean maximum discrepancies (in days) between estimated dates of birth for the same individuals for the Bure Marshes study site in each year.

	Bure 2000	Bure 2001	Bure 2002
Mean	17.82	15.23	14.5
Standard Deviation	10.70	12.74	11.46
N	11	26	26
Range	3-38	1-42	1-40

Table 2 demonstrates that the assumption that no individual consistently grew faster or slower than the population average is upheld sufficiently to allow most dates of birth to be estimated to within two to three weeks. This is an acceptable accuracy considering that the relevant level of resolution for the purposes of this study is the month of birth.

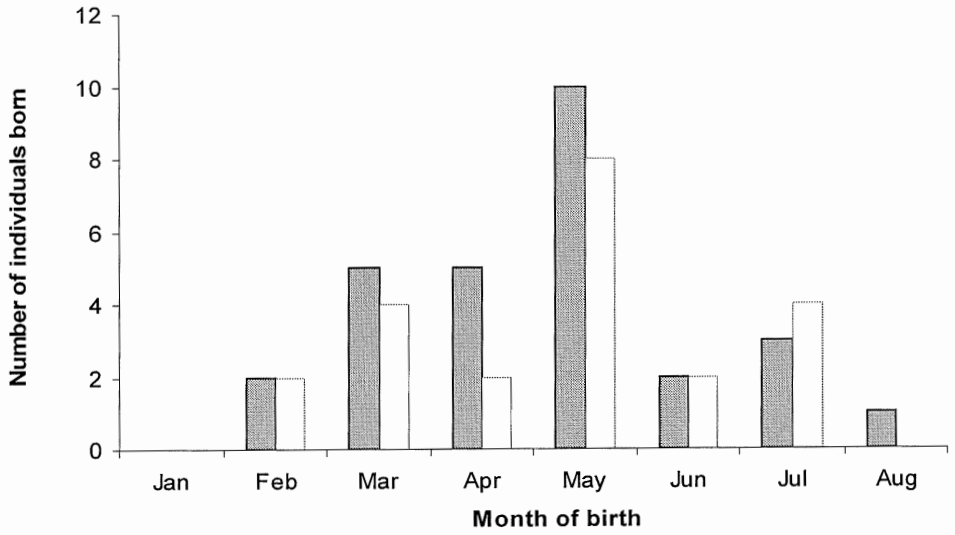
Figs. 4a, 4b and 4c show the numbers of juveniles of each sex born in each month during 2000, 2001 and 2002 respectively at the Bure Marshes, based upon extrapolation from the weight and date of first capture. Fig. 5 shows the juvenile water voles of each gender (voles < 135g for males and < 140g for females, see below) actually captured in each month of 2002. The pattern of captures is fundamentally the same as that demonstrated in Fig. 4c, but offset by a month in most cases because only juveniles above 50-60g (approx. 20 days after birth) were available to be trapped.

Extrapolated birth dates and recruitment

During the *Before* period (2000, 2001; Figs. 4a and 4b respectively) the numbers of each gender born at the Bure Marshes were approximately equal in each month. Similarly in March and April 2002, pre-perturbation, numbers born were approximately equal (Fig. 4c, Fig. 5). During the *Perturbation* period, between May and September 2002, the total number of females [estimated from voles first captured at < 180g] born was 4 compared to 38 males (Fig. 4c). The first collaring in 2002 occurred during the session 15-24th of April, in time potentially to influence the May births, but not those in April. At the *Control* site, Little Bedwyn, births of males and females in each month were roughly similar throughout (Fig. 4d).

Figure 4: Number of individuals of both genders born during each month during the field season, based upon back-extrapolated dates and weights of first capture for a) Bure Marshes 2000 field season b) Bure Marshes 2001 field season and c) Bure Marshes 2002 field season d) Little Bedwyn 2002 field season. Dark bars represent females, white bars represent males.

a)



b)

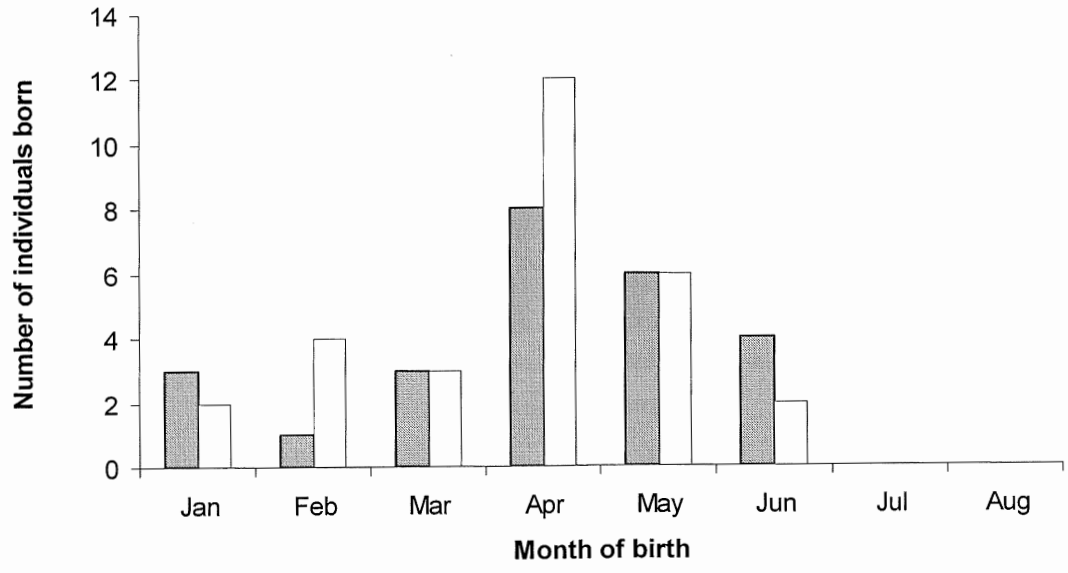
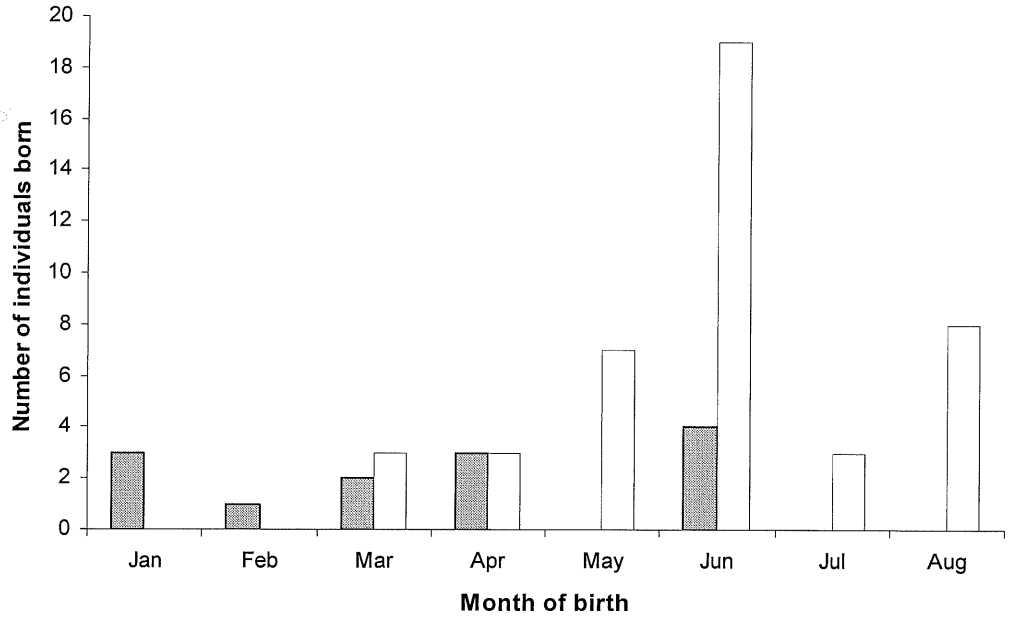


Figure 4 cont[d]:

c)



d)

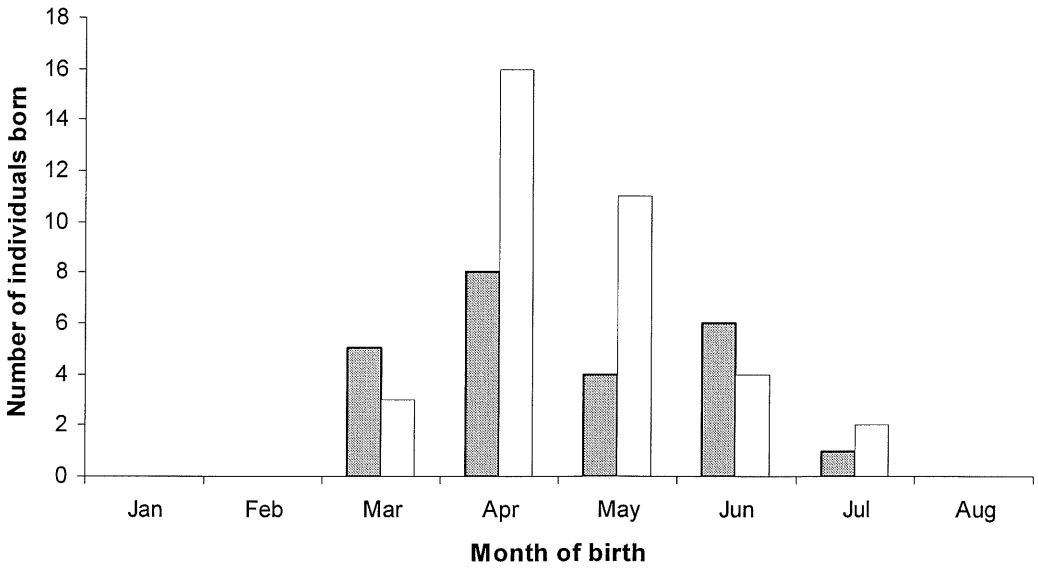
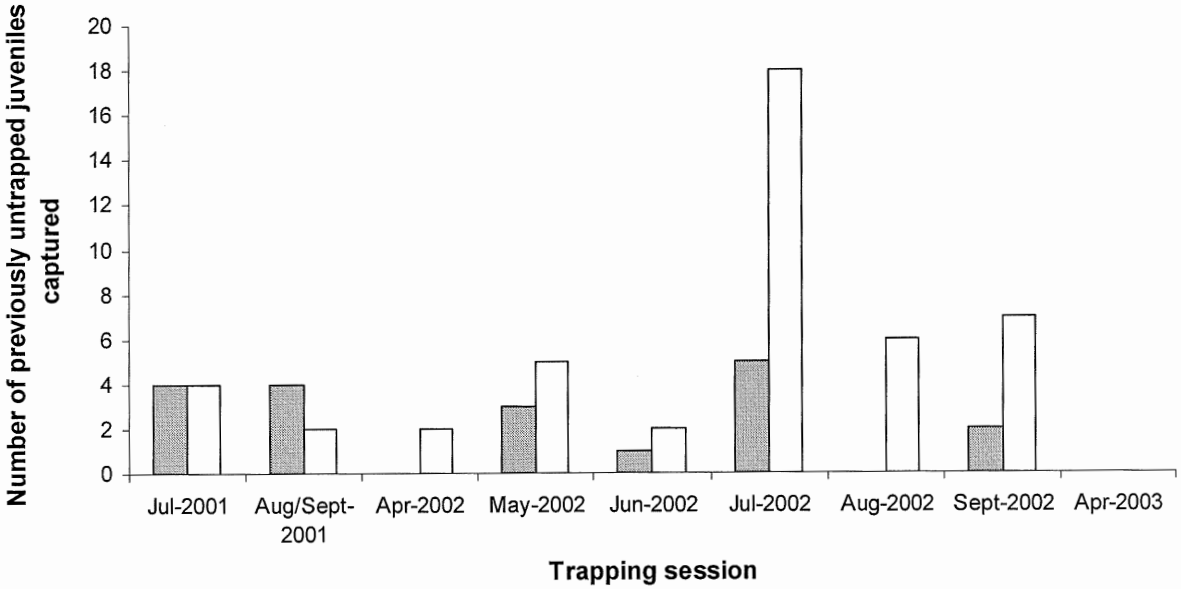


Figure 5: Number of previously un-trapped juvenile water voles of each gender captured in each session between September 2001 and April 2003 at the Bure Marshes. Dark bars represent females, white bars represent males.



There is an initial peak in male recruitment at the Bure Marshes after September 2001 (Fig. 3), probably resulting from the collaring in 2001. The Pradel estimate recruitment rates for April-May for males and females were approximately equal (0.42 and 0.43 respectively; Appenix II), suggesting that the majority of animals first captured in May were born before collaring took place. Thereafter both the recruitment rate and number of animals recruited were lower for females than for males at the Bure Marshes.

Modelling the effects of the proportion of the female population collared

Table 3 presents the proportion of females above breeding weight fitted with collars by the end of each trapping session. Definition of breeding weight for female water voles was based upon the weight above which the majority of water voles had perforate vaginas upon capture (140g; Fig. 1b in Chapter 3).

Table 3: The proportion of female water voles above breeding weight fitted with radio-collars at the end of each capture session.

	Sept01	April02	May02	June02	July02	August02	Sept02
Number of female voles (robust estimate)	32	20	18	13	15	12	9
Number above breeding weight (trapping data)	23	13	15	12	11	8	4
Number collared	8	6	8	8	6	3	2
Proportion above breeding weight collared	0.35	0.46	0.53	0.66	0.54	0.38	0.50

A proportion of the collared females was predated or disappeared within a week of collaring. These animals are nevertheless included in the collared proportion for each session in Table 3 according to the following logic:

1) The first-week loss of collared animals could be attributable to natural predation. If so, a similar proportion of un-collared animals should be predated in that month, keeping the relative proportions the same.
2) The first-week loss could result from an increase in predation attributable to collaring. Predated females would give birth to neither male nor female offspring, lowering the female recruitment rates to the same extent as if the animals had survived but produced entirely male litters. The concurrent reduction in male births would be compensated for by the increased birth rate of males from other collared females if collaring skewed the sex ratios.

Numbers of females at the Bure Marshes during the *Perturbation* period can be reconstructed from the Robust Design survival rate estimates and the Pradel recruitment rate estimates from the MARK analysis. Table 4a shows the actual numbers on site (from the closed captures estimates of the Robust Design model) and the estimated numbers reconstructed from the survival and recruitment rates. There is close agreement throughout, the maximum discrepancy being 3 individuals in April 2002.

Table 4a: Reconstructed numbers of females from the Robust Design survival estimates and the Pradel recruitment rates.

Session	Sept01	April02	May02	June02	July02	Aug02	Sept02	April03
Actual Numbers	32	20	18	13	15	12	9	5
Estimated numbers	32	16.9	16.9	13.0	14.8	12.4	9.2	5.0
Number Survived		10.5	9.7	11.3	9.0	12.4	7.0	4.0
Number Recruited		6.3	7.2	1.7	5.8	0.0	2.1	1.0

By keeping the survival rates the same but increasing recruitment rates by 1.923 we can derive Table 4b, which represents sustainable survival and recruitment in which numbers of females in September 2001 and September 2002 are equal.

Table 4b: Reconstructed numbers of female water voles with recruitment rates increased until the population does not change (sustainable recruitment).

Session	Sept01	April02	May02	June02	July02	Aug02	Sept02	April03
Actual Numbers	32	20	18	13	15	12	9	5
Estimated numbers	32	22.7	31.7	27.5	42.5	35.6	32.0	20.7
Survived		10.5	13.0	21.3	18.9	35.6	20.2	14.1
Recruited		12.2	18.7	6.2	23.6	0.0	11.8	6.6

The recruitment rates in the "sustainable model" used in Table 4b compare favourably with the measured rates from Bure males and Bedwyn males and females. Sustainable female recruitment rates for Table 4b were in the range 0.00 to 0.86. Rates for Bure males ranged from 0.21 to 1.01, Bedwyn females from 0.21 to 0.81 and Bedwyn males from 0.13 to 1.03 over the same time periods.

The mean measured female recruitment rate at the Bure Marshes for 2002 (*Perturbation* period) was [1/1.923 =] 0.52 of the theoretically sustainable recruitment rate in Table 4b. This requires a 0.48 proportional reduction in the sustainable female

recruitment rate to achieve the measured rate. The mean proportion of the female breeding population that was collared was 0.49, averaged across capture sessions. If collared females produced only male offspring, this would create a 0.49 reduction in female recruitment rates.

Table 4c: Effect of reducing the "sustainable" female recruitment rates (Table 4b) by the proportion of collared females.

Session	Sept01	April02	May02	June02	July02	Aug02	Sept02	April03
Actual Numbers	32	20	18	13	15	12	9	5
Estimated numbers	32	16.7	16.6	12.8	14.4	12.1	8.9	4.9
Survived		10.5	9.6	11.2	8.8	12.1	6.8	3.9
Recruited		6.2	7.0	1.7	5.6	0.0	2.0	0.9

Table 4c shows the estimated number of females in each trapping session based upon a 0.49 reduction in the recruitment rate in Table 4b for each *primary period.* This leads to a decline similar to that recorded.

DISCUSSION

From June 2002 to April 2003 at the Bure Marshes (*Perturbation* period) the ratio of males to females recruited was 4.8:1. At the Little Bedwyn (*Control*) site this was 1.6:1. From April - September 2000 and June - September 2001 at the Bure Marshes (*Before* period) the sex ratios were 1:1.1, and 1:1.3 respectively, with more females recruited than males. During the *Perturbation* period, therefore, the bias in sex ratios at the Bure Marshes was reversed with respect to the *Before* period, and three times larger than the bias at the *Control* site. This indicates a dramatic skew in the birth sex ratios at the Bure Marshes during the *Perturbation* period.

There is a strong correlation between the collaring of water voles at the Bure Marshes and the decline in numbers of female water voles at this site. This decline occurred only during a period when voles were being simultaneously radio-collared and live-trapped. No such decline occurred at the Little Bedwyn site or in two previous years at the Bure Marshes during which only live-trapping took place. This suggests that neither trapping nor annual variation were likely to have caused this decline.

We interpret this to mean than that the decline in female numbers derived from male-skewed offspring sex ratios at the Bure Marshes mediated by a deterioration in maternal condition in response to the attachment of radio-collars to females during the 2002 field season. This interpretation relies upon two assumptions both of which appear valid.

Firstly, we assume that the decline in female numbers derives from low recruitment of females rather than any other explanation. We exclude the possibility that the decline resulted from poor female survival rates as survival rates across the majority of *primary periods* in 2002 were higher for females at the Bure Marshes than for other voles of either sex or site. The decline could not have resulted from increased, permanent emigration of females since this would lower the MARK estimates of female survival rates. Moreover, none of the 18 radio-collared females left the study area during 6 months of tracking, and trapped female water voles demonstrated low prevalence of dispersal. The decline is unlikely to result from abnormally low immigration: there is little reason to suspect that emigration rates from the un-trapped area would be higher than those of the study site. During the *Perturbation* period fewer females were born in any month relative to males in any year or relative to female births during the *Before* period (Figs. 4a, 4b and 4c) or at

the *Control* site (Fig. 4d), based upon the extrapolated birth dates. This supports the above assumption.

Our second assumption is that the number of females collared and the resulting proportional reduction in female birth rates would be theoretically sufficient to account for the observed decrease in recruitment rates. The model of survival and recruitment rates of females (Tables 4a, 4b and 4c) demonstrates that keeping survival rates unaltered but reducing a theoretically stable female recruitment rate by the proportion of the female breeding population that was collared is sufficient to account for the decline in numbers witnessed during 2002. This evidence suggests the existence of a causal link between collaring female water voles and skewed sex ratios.

Our interpretation of the causes of the female decline requires radio-collaring to exert a detrimental influence upon the females collared, resulting in skewed sex ratios. Evidence for a detrimental influence of collaring upon small mammals has been shown in a number of studies. Berteaux et al. (1994) demonstrated decreased body mass and activity levels of meadow voles (*Microtus pennsylvanicus*) following collaring. Reduced wheel-running activity has been demonstrated for collared house mice (*Mus musculus*) (Mikesic & Drickamer, 1992) and meadow voles (Hamley & Falls, 1975). Pouliquen et al. (1990) found that activity and social interactions of mice (*Mus domesticus*) were low immediately after collar attachment and Wolton & Trowbridge (1985) noted that most of the wood mice (*Apodemus sylvaticus*) in their study that died wearing collars did so within two days of collaring.

Leuze (1976, 1980) found no effects of radio-collars upon body weight or fecundity of water voles. However, she recorded only numbers of weanlings seen with the mother, not offspring sex ratios or numbers weaned. Nazarova & Eviskov (2000) showed that low-weight females not only had male-biased litters, but a

reduced ability to wean offspring successfully. Therefore, Leuze could have missed alterations in both sex ratios and fecundity resulting from collaring.

In our study there was mortality in the first week following collaring (5 confirmed and 3 suspected cases of predation for females versus 2 and 1 respectively for males). For voles surviving the first week, the mean times spent collared were 69 days for females and 76 days for males, suggesting immediate short-term adverse effects from collar attachment.

Skewed sex ratios have been described in stressed and malnourished females of different species (Labov et al., 1986; McGinley, 1984). Female water voles exhibit decreased litter sizes, male-biased offspring sex ratios and stress responses in response to decreased food availability and body weight (Bazhan et al., 1996; Nazarova & Evsikov, 2000). This suggests a link between stress and offspring sex ratios that is in keeping with the predictions of Clark (1978), Juliard (2000), Silk (1983) and Trivers & Willard (1973).

If radio-collars cause stress to small mammals, as implied by the initial first-week post-collaring mortality in this study, that of Wolton (1985) and by the other studies demonstrating adverse effects (Berteaux et al., 1994; Hamley & Falls, 1975; Mikesic & Drickamer, 1992; Pouliquen et al., 1990), this would supply a mechanism for the observed effects of radio-collars upon birth sex ratios of water voles.

The implications of this study for further radio-collaring studies of small mammals are likely to be species-specific (Withey et al., 2001), and further work is required to establish a causal link between collaring water voles and skew in offspring sex ratios. This study casts doubt on the assumption that the use of radio-collars does not fundamentally affect the biology of collared water voles.

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Chapter 6

Discussion

OVERVIEW

Sinclair (1991) states that wildlife management requires a scientific approach, and conversely that the science of wildlife ecology requires management in order to carry out experiments. Practical conservation guidelines may be derived from empirical research into a species' ecology, and research to produce conservation guidelines may have countervailing benefits in providing data with which to test ecological theory.

This thesis examined factors that may influence the success of re-introductions and habitat restoration for the conservation of water voles, studying interactions between their habitat requirements, population density, individual growth rates, social structure and dispersal biology. In this discussion I analyse the results of each of the preceding Chapters by firstly examining their implications for our understanding of the dynamics of water vole populations, and then interpreting them in terms of practical measures for the conservation of water voles.

FOOD RESOURCES, GROWTH RATES AND POPULATION SIZE

It is well established that increasing food abundance can increase densities within small mammal populations (Abdellatif et al., 1982; Andrzejewski, 1975; Cole & Batzli, 1978; Desy & Batzli, 1989; Desy & Thompson, 1983; Gilbert & Krebs, 1981; Jonsson et al., 2002; Koskela et al., 1998; Taitt & Krebs, 1981, 1983), increase individual growth rates and body weights (Andrzejewski, 1975; Desy & Thompson, 1983; Koskela et al., 1998; Taitt & Krebs, 1981, 1983), and decrease the size of individual's ranges (Andrzejewski & Mazurkiewicz, 1976; Boutin, 1990; Sullivan et al., 1983; Taitt & Krebs, 1981, 1983), either by direct means (Fortier & Tamarin,

1998) or indirectly through the effects of population density upon ranges (Abramski & Tracy, 1980; Ostfeld & Canham, 1995). Body weights, growth rates, reproductive success, population densities, home-range and territory sizes and social interactions of water voles may all be influenced to some degree by the availability of food resources, and therefore habitat quality.

Nearly all of the studies of the effects of food abundance upon small mammal populations have involved captive or enclosed populations; very few studies have demonstrated effects of variations in natural levels of food abundance upon populations of small mammals in the wild (Ostfeld, 1985). Water voles rely upon abundant, low-quality and evenly distributed food resources which renew rapidly (Efford, 1985). They are therefore "grass-eating" or "GSH diet" (Grasses, Sedges and Horsetails) voles (Ostfeld, 1985, 1990), living in a "sea of green energy" (Wolff, 1993). It was unknown whether it would be possible to demonstrate effects of the quantity of forage upon demography of water vole populations since sites with extant populations are usually assumed to contain "suitable" habitat and therefore abundant quantities of vegetation.

Chapter 2 demonstrated that higher population densities were associated with larger widths and percentage cover of bank and emergent vegetation, both per metre-length of bank, and per mean observed range length. Higher population densities and forage levels correlated with higher growth rates and body weights of individuals. Evidence from this study was associative in nature, so a causative link between forage levels and population density was not able to be demonstrated. Two lines of evidence, however, suggest that the population density responded to levels of forage. Firstly, had population density been influenced only by effects of vegetation upon predation rates (hence cover), it would not be expected that body weights and growth rates of

individuals would vary with population density. Growth rates and body weights were higher at higher population densities, suggesting that sufficient extra food had to be available for this to occur. Secondly the growth curves demonstrated that individuals reached breeding weight an average of 20 days earlier at the highest population density site than at the lowest. This suggests a mechanism for the action of increased forage quantities upon reproductive success. I conclude that it is likely that the water vole populations responded numerically to increases in the quantities of available forage acting upon individual growth rates.

Implications for conservation

Larger populations are likely to remain in existence for longer periods than smaller populations (Caughly, 1994), and re-introductions in which the release cohort has a high rate of increase are likely to be more successful than those with lower rates of increase (Dunham, 1997; Griffith et al., 1989). Whilst acknowledging that Chapter 2 studied only three populations, and so extrapolation to the wider landscape must be made with caution, these results suggest that increasing the width of habitat in extant populations and targeting re-introductions at extant or restored sites with wider swathes of habitat should result in larger, more robust populations for a given length of habitat. Population densities of more than double (2.08 as opposed to 1.04 individuals per 100m) were associated with a mean increase in the per-metre area of green-forage to 2.03m^2 from1.46m^2, suggesting large potential benefits from relatively small increases in habitat width. Since this was an observational study, however, many uncontrolled factors could potentially have influenced population density and these figures should be treated with caution.

This study implies that we can increase numbers of water voles via simple changes to habitat management techniques. However, populations would still be vulnerable to catastrophic events such as over-winter flooding or predation by American mink. Seven populations, four extant and three reintroduced were studied throughout the fieldwork for this thesis. Of these, three (two extant and one re-introduced) were predated upon by American mink. In two cases, the entire population was lost, one of which was a site containing over 100 individuals which had been live trapped for two years (the Wendover Canal). In the third case, the population was part of a much larger, well interconnected area containing water voles. Although all of the previous inhabitants were extirpated, a number of juveniles dispersed into the trapped area in the following month. This suggests that large, interconnected habitats may well present a buffer to the effects of American mink (Barreto et al., 1998; Carter & Bright, 2003; Macdonald & Strachan, 1999), but emphasizes that in cases where the population cannot be rescued from extinction by dispersing individuals, the effects of mink are indeed "catastrophic" (Strachan et al., 1998). I therefore suggest that prophylactic mink trapping should be a necessary part of management or any re-introduction attempt involving water voles.

POPULATION DENSITY AND SPACING BEHAVIOUR

Chapter 2 suggests that management to increase habitat width is likely to result in increases in the numbers of water voles a length of habitat can support. The relationship between population densities and the social structure and movements of individuals within water vole populations was previously unknown, and examined in Chapters 3 and 4.

Female water voles are territorial (Leuze, 1976). Reasons for female ranges to be smaller at higher population density are provided by both the *offspring-defence* (Wolff, 1985, 1993; Wolff & Peterson, 1998) and *food-defence* hypotheses (Boonstra et al., 1987; Ims, 1987; Ostfeld, 1985, 1990). Under the FDH, female ranges may contract in response to increasing food resources and population densities (Fortier & Tamarin, 1998). Under the ODH, females contract their territories in response to increasing intruder pressure (Wolff & Peterson, 1998).

Predicted effects of increasing population density upon movements of non-territorial male small mammals were less clear. Three studies have shown that male small mammals' range-sizes may be limited by both intrasexual competition and by the population density of females (Bond & Wolff, 1999; Nelson, 1995a, b). Males ranges were apparently limited by a maximum number of females they could overlap (Bond & Wolff, 1999). This has hitherto been demonstrated only in two species - field voles (*Microtus agrestis*) and grey-tailed voles (*Microtus canicaudus*) - and only in enclosure experiments in which population densities were artificially manipulated by the addition and removal of individuals. Chapter 3 presents the first evidence from a wild population of small mammals that male ranges may be limited by an optimum number of females they can overlap.

Habitat quality could have influenced movements of water voles directly or indirectly via variations in food availability and / or population density (Fortier & Tamarin, 1998). It was impossible to separate these direct and indirect effects in any of the studies in this thesis since they were observational studies of wild populations, and did not include experimental manipulation (Fortier & Tamarin, 1998; Jonsson et al., 2002). For the purposes of Chapter 3, I concentrated upon explanations of movements only in terms of effects of population density. This is justifiable since

evidence for direct effects of forage upon movements of small mammals is equivocal and frequently contradictory (Desy et al., 1990; Fortier & Tamarin, 1998; Jonsson et al., 2002; Lacki et al., 1983; Slade et al., 1997), and many studies consistently demonstrated smaller ranges of small mammals at higher population densities (Abramski & Tracy, 1980; Bond & Wolff, 1999; Nelson, 1995a, b; Ostfeld & Canham, 1995).

I acknowledge the possibility that ranges of both males and females may react directly to food abundance (Fortier & Tamarin, 1998). However, evidence from Chapter 4 implies that range-use patterns of water voles may be mainly influenced by mating behaviour, suggesting that ranges of both sexes were more likely to relate to social interactions and hence population density, rather than to the amount of food available.

Increasing population density was associated with decreased observed ranges from trapping data (Chapter 3), and decreased *weekly* and *total* ranges of radio-tracked individuals (Chapter 4) for both sexes. The social structure of the water vole populations studied were similar at different levels of population density (Chapter 3), with females remaining territorial and males apparently remaining non-territorial. The number of males and females overlapped by members of either sex also remained approximately equal.

I interpreted the positive correlation of male range lengths with increasing body weight, and the smaller male range lengths at higher population densities, as evidence that male range lengths were limited by social interactions, partially mitigated by the competitive ability of the males, which I assumed positively correlated with body weight (Nelson, 1995b). I presented a statistical model predicting that males of a given relative competitive ability overlapped with

approximately equal numbers of females and equal numbers of males irrespective of population density. This suggests that males had an optimum number of females and males with which they could overlap, and that this limited the size of their ranges.

If so, factors limiting male ranges could have resulted from one, or a combination of a) male-competition for females in oestrus, such that attempting to overlap with a greater number of females increased the number of aggressive encounters with other males (e.g. Nelson, 1995b) or b) aggression from unfamiliar females nursing young (Wolff & Peterson, 1998). In both cases, increases in the size of male ranges should be a balance between the advantages of access to a larger number of females, and costs incurred due to increasing frequency of aggressive encounters (Bond & Wolff, 1999; Ostfeld, 1990). These costs would be expected to be less for males of greater competitive ability, and this provides a ready explanation for the larger ranges of larger males.

Ranges of female water voles were disproportionately smaller at low population densities than would be predicted from the size of the male ranges (Chapter 3). Females' ranges at low population density apparently reached a maximum size, below which competition for resources arose. This interpretation is supported by the observation that female ranges at low population densities did not increase with increasing body weight, whereas they did at high population densities, suggesting that habitat-related resources were competed for at high but not at low densities. It is unclear whether this maximum range size related to quantities of forage or sufficient nesting sites, or some other factor since access to both commodities were likely to increase with increasing territory size at any of the study sites (e.g. Leuze, 1976).

Implications for conservation

The success of a re-introduction is likely to be influenced by the number of individuals released (Griffith et al., 1989), their immediate survival and the speed with which they are able to start breeding and successfully raise young (Dunham, 1997; Griffith et al., 1989).

Release pen methods for water vole re-introduction rely upon placing single pairs of males and females into release pens separated by the distance of a female territory (Chapter 1). This establishes female territories at the correct distance and provides a safe environment from which both sexes can explore (Chapter 1).

During the course of this study we undertook four re-introductions using this method, although data from these are largely anecdotal and therefore not included in the main body of the thesis. We tracked 32 collared individuals (17 female and 15 male) from two successful releases. Although many of these voles slipped collars or were predated on escaping their release pen (14 cases of predation in the first two weeks following escape from the pen), the data is sufficiently robust to show that in the majority of cases, the individuals remained within 100m of their pen for a number of weeks: only 6 individuals were recorded as making excursions of larger than 100m in the first two weeks following escape from the pen. The numbers of females released into a given habitat, and their relative spacing, are therefore influenced by the numbers and spacing of release pens used. Ideal spacing of release pens should reflect the anticipated territory sizes of females.

Range lengths of both female and male water voles are smaller at sites with higher population densities and widths of habitat (Chapter 2; Chapter 3). This suggests that release pens should be sited closer together in habitats with relatively

broad swathes of vegetation and further apart in habitats with narrower margins. The mean of female observed ranges at the Bure Marshes was 52m (standard deviation 58m), and this site contained the largest female ranges recorded. However, caution must be exercised in interpreting these results for practical purposes. The period over which range were measured was a maximum of 6 days in any study, and this may not have been sufficient to record the entire of a female's territory (but see Chapter 4). Similarly, evidence for a maximum range exists only at one site in this study, and so inferences to other sites are made tentatively.

RANGE-USE PATTERNS AND DRIFTING TERRITORIALITY

Few studies have examined time budgets of female and male small mammals occurring at different population densities over a range of time periods. It was hitherto unknown whether female water voles actively defended entire territories on a *daily* basis, or whether they visited their entire ranges over much longer time periods. This distinction could determine the degree of "flexibility" of female territories, and therefore whether females exhibited drifting territoriality (Doncaster & Macdonald, 1991; Taber & Macdonald, 1992), as opposed to territories with defined and stable borders (Leuze, 1976). Such flexibility of females territories could also be determined by the population density, since Chapter 3 suggests that females competed for habitat at high but not lower densities.

Chapter 4 showed that *daily* ranges of both males and females were smaller than *weekly* ranges at both sites at which voles were radio-tracked. *Weekly* ranges in turn only represented a proportion of the *total* ranges for each individual. Females apparently did not defend an entire range over short time periods, and in fact neither

male nor female ranges reached an asymptote with increasing observations but continued to increase throughout the period of study for each individual, due to a continual process of gaining and losing territory.

A possible explanation for the discrepancy between *daily* and *weekly* ranges was that *weekly* ranges were determined by the extent of close interactions between males and females. When males and females overlapped ranges, they often spent a number of days confined discrete locations, presumably for mating purposes. These locations at both tracked sites were usually tussock sedges (*Carex paniculata*) (pers. obs), in which females are also known to raise litters (Leuze, 1976; pers. obs.). Therefore for both males and females, the patterns of ranging witnessed apparently related to mating behaviour. I concluded that females did not actively defend their territories on a *daily* basis but spent periods of time in discrete locations, presumably in order to mate with males or to wean young (e.g. Leuze, 1976), and males did not visit their entire range over short periods presumably due to selectively, and closely, mate-guarding females in oestrus (e.g. (Bond & Wolff, 1999).

Daily ranges were the same at both study sites for both sexes. The proportion of *weekly* ranges that the *daily* ranges represented, however, was larger at the high population density site, suggesting that *weekly* ranges were smaller at this site for both sexes. Similarly, *total* ranges of both males and females were smaller at the high population density site than at the low population density site. The association of increased population density and smaller *weekly* and *total* ranges led to speculation that the position of female territories could become entirely inflexible (and therefore static) except via dispersal or mortality at population densities higher than those found in this study.

Although the time periods over which ranges were estimated (*daily* / *weekly* / *total* ranges) were somewhat arbitrary, it seems plausible that *daily* ranges at least approximated a minimum territorial requirement, since the size of these ranges did not correlate with variations in population density. If so, we might expect the maximum possible population density of water voles to approximate one vole of a given sex every 30-40 metre length of habitat (the mean *daily* range for either study site or sex).

From trapping data, the mean female range length was 20m (standard deviation 20m) at the Wendover Canal. This is less than the predicted 30-40m from the *daily* ranges at the Bure Marshes and Little Bedwyn Canal. The emergent vegetation at the Wendover Canal was extremely broad (emergent vegetation width range from 0 – 15m in width, mean 3.8m; standard deviation 4.6m), and dense enough for water voles to feed upon at considerable distances from the bank (pers. obs.). Water vole ranges in such habitats may comprise an *area* rather than a *length*. Thus, although this does not substantially alter the relationships described between habitat quantity, population density and range lengths of male and female water voles in Chapters 2 and 3 (since this is the logical extreme of increasing the quantity of habitat per metre length of bank), it does suggest that ranges at the Wendover Canal were shorter than would be predicted from the densities seen if we assumed linearity of the water course.

The position of the ranges of males and females varied mainly through a process of range-shifting, punctuated by less frequent, larger scale breeding dispersal events (Chapter 4). The majority of dispersal distances recorded were under 1km but the two largest dispersal events recorded in this study were 2.7km and 1.4km, both recorded from trapping data and both at the Wendover Canal where a linear stretch of 4km of habitat was trapped. Telfer et al. (2003) demonstrated that Capture Mark

Recapture underestimated dispersal rates and distances of water voles in the Scottish highlands, but their results concur with those of this study that dispersal distances above 1km became increasingly rare in the population, but with occasional events of 4-5km being recorded. The balance of evidence seems to suggest, therefore, that populations separated by over a kilometre should experience reduced levels of exchange of individuals.

Implications for conservation

Chapter 3 suggested an ideal *maximum* spacing of release pens, at approximately 50-60m (see above). Chapter 4 suggests a *minimum* spacing should be 30-40m. In view of the inherent flexibility of female territories, and the ability of males to overlap ranges, I suggest that a spacing of release pens containing male-female pairs of water voles at 40-60m should be appropriate for the majority of linear water courses in the UK, dependent upon the width of the forage.

Habitat restoration or re-introduction projects should perhaps attempt to recreate water vole habitat or populations within dispersal distance of an extant population (see Chapter 1; Macdonald & Strachan, 1999). Increasing connectivity between lowland populations would increase the likelihood of those populations remaining viable (Brown & Kodric - Brown, 1977), and may possibly buffer the impacts of American mink. Based upon the breeding dispersal rates in Chapter 4, and the studies by Telfer et al. (2003), I suggest that this will generally require the restored habitat to be less than 1km away, and preferably within 600m, as most of the dispersal events recorded were less than this distance.

RADIO-COLLARS AND BIRTH SEX RATIO BIASES

Chapter 4 presented information concerning the range-use and dispersal of water voles derived from a large scale radio-collaring study. An important assumption of the use of radio-tags is that the tags themselves do not adversely affect the behaviour, survival or welfare of the study species (see Amlaner & Macdonald, 1980, and papers therein; Kenward, 2001). This is especially true if the species in question is already endangered and requiring conservation measures to preserve populations. It is, however, extremely difficult to detect adverse reactions of study species to radio-tags, and many studies of small mammals have either failed to find an effect or perceived the effects to be negligible (de Mendonca, 1999).

Chapter 5 dealt with observations only at the Bure Marshes. Although radio-collaring took place at the Little Bedwyn site, many fewer individuals (14 as opposed to 53) were collared, representing a much smaller proportion of the population, and over a much shorter time period (4 as opposed 12 months). The likelihood of discerning putative impacts of radio-collaring at the Little Bedwyn site, therefore, was substantially smaller, and not pursued.

Chapter 5 demonstrates that there was a decline in numbers of female, but not male water voles at the Bure Marshes during radio-tracking at this site. This decline did not occur when only trapping took place and did not occur at the Little Bedwyn site at the same time (during which period the Little Bedwyn site was not radio-tracked), and so was apparently unrelated to trapping or seasonal effects. The decline occurred not due to decreased survival or immigration, or increased emigration of females, but apparently from a reduction in the birth rate of females during this period. The decline in recruitment of females almost exactly reflected the proportion

of the female population that was radio-collared in a given month. The collaring of water voles at the Bure Marshes was therefore strongly correlated with a substantial male skew in birth sex ratios and associated with a dramatic decline in the numbers of females present on site. This suggested that the female decline resulted from direct effects of radio-collars upon the birth rate of females.

Sex ratio adjustment has been shown in a number of vertebrate species, including Arvicoline rodents (Bond et al., 2003; Wolff et al., 2002), and skewed sex ratios have been described for stressed and malnourished females of different species (Labov et al., 1986; McGinley, 1984). Female water voles exhibit decreased litter sizes, male-biased offspring sex ratios and stress responses in response to decreased food availability and body weight (Bazhan et al., 1996; Nazarova & Evsikov, 2000), suggesting that skewed sex-ratios in water voles are associated with female stress. This implies that effects of stress upon females due to the attachment of radio-collars could have resulted in the decline observed.

Implications for conservation

An important, and often overlooked, consideration when re-introducing a species is what would constitute a "success" (Macdonald et al., 2002; Chapter 1). A "success" should be defined prior to re-introduction, and will most likely comprise a target number of extant individuals, reflecting a perceived minimum population size that could be considered viable over a relatively long time period (Beck et al., 1994; Sarrazin & Barbault, 1996). Attributing "success" or "failure" to a restoration attempt, therefore, requires knowledge of the numbers of individuals extant at various times post-release, and therefore a carefully devised post-release monitoring strategy. In the

majority of cases for water voles, monitoring involves sign survey, trapping or radio-tracking.

The association between the decline in female recruitment and radio-collaring demonstrated in Chapter 4 is sufficiently convincing to call into question the usage of radio-tracking as a population monitoring tool for water voles, especially following a re-introduction attempt. It seems likely, given the severity of the female decline observed at the Bure Marshes, that there are few extant populations of water voles in Britain that would not be expected to suffer at least some deleterious consequences if monitored using radio-collars.

SUMMARY AND FURTHER STUDIES

Numbers of individuals within water vole populations was associated with the width of the habitat which they occupied: wider habitat margins correlated with higher population densities, larger growth rates, heavier individuals and smaller range lengths of both male and female water voles. This suggested that population densities may have responded to increased food resources.

Whilst males apparently remained non-territorial, irrespective of population density, the size of their ranges was apparently bounded by social limitations, potentially deriving from aggressive interactions with other males and females. The positions of female territories were not geographically fixed, and constantly drifted. This possibly resulted from mating behaviour with males occurring in discrete locations, meaning that entire female ranges were visited over relatively long time periods. The degree to female territories drifted was larger at the low population density site. This is in keeping with the observation that female territory sizes

apparently reached a maximum size at low population densities at which intrasexual competition for resources was reduced. These data suggest that female territories have both a maximum and a minimum size, at the latter of which, the position of territories may become stable.

A decline in the number of females at one study site was associated with male-skewed birth sex ratios and the occurrence of radio-collaring at that site. A suggested mechanism for action was that radio-collars caused the stress to pregnant females and thereby resulted in maternal sex ratio adjustment, producing male-skewed litters.

All of the studies in this thesis were observational studies of wild populations. As such, testing of hypotheses as to the exact causes of the patterns observed was not possible, and the majority of these conclusions were derived from associations of factors at, and between, study sites.

Experimentally studying the relationship between radio-collars and stress in water voles is necessary to support our hypothesis concerning maternal sex ratio adjustment. Since radio-collaring is prevalent in the study of so many mammalian species, and indeed of other taxa, such a study would have many wider implications.

Separation of the *offspring-defence* and *food-defence* hypotheses for female territoriality should be possible unless both apply, in which case their separation would logically be impossible. In this study, I was unable to separate the effects of food resources and population density upon the size of female territories. Similarly, female territory sizes may also depend upon numbers of nesting sites available (see above). This could lead to predictions similar to those for the FDH (see Ostfeld, 1990) since if numbers of nesting sites co-varied with food resources, both would increase with increasing territory length at each site, and both would potentially be defensible. Removal experiments, artificially lowering the population density at high density

sites, coupled with experimental manipulation of numbers of nesting sites should feasibly be able to disentangle the factors influencing female range sizes in water voles. Whether such a study would be permissible with such an endangered species is, however, highly debateable.

Males overlapped with other males as frequently as they overlapped females, and, from two observations of radio-tracked males, could potentially spend extended periods within 10-20m of one another. Requiring a pragmatic approach to discerning territoriality, or the lack of it, I assumed this was sufficient evidence for male non-territoriality in water voles. I acknowledge that in reality, however, territoriality may encompass a continuum from nearly full overlap of ranges to complete range exclusion. The reasons for, and behavioural expression of, male spacing systems in small mammals warrants further investigation to discern if males are truly non-territorial when females are territorial, or whether their ranges are non-random with respect to female territories (implying a degree of territoriality).

In summary, this thesis provides original information, potentially of use in the restoration of habitat, and the restoration of water vole populations *to* habitat, for conservation purposes. These studies also address, and hopefully compliment, ecological theory concerning maternal sex ratio adjustment, and the spacing behaviour and population demography of both male and female small mammals.

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Appendix I

Reintroducing 'Ratty'

Reprinted with permission from the *New Scientist*, 11th October 2003, page 51; winning essay from the *New Scientist* / Wellcome Trust New Millennial Science Essay Competition 2003.

It's early and it's raining. The record sheet on the clipboard is soaked and slowly turning to mush. In my hand is the 20th occupied trap of the morning. I open it up, carefully, and find "Ratty" staring back, nearly motionless. The whiskers are vibrating, the chest rises and falls, and the vole is desperately attempting to insinuate that *I'm really not here at all, so if you could see your way clear to going away soon, that would be good. Thank you.*

Just for a second - and it doesn't matter how often I have done this before - I find a smile on my face. And then my body kicks into the usual routine: gently empty vole into net; scan vole's scruff for the minute transponder containing the identification number (00 0603 DD42); sex (F); weigh (305g) and release. The vole scampers away and takes a running dive into the water; a plop, a twist, a cloud of sediment and she's gone.

Back in the office, the water vole in question is making a small but valuable contribution to its own conservation. We now have data from a number of different habitat types about water voles' survival rates, birth rates, sex ratios, ranging behaviour and dispersal, how they establish and defend their territories. It is a good thing that we have such detailed information, because what we are trying to do is not easy.

Water voles are going extinct in the UK at colossal rate. During the 1990s there were two national surveys of water voles. By the second survey, 88% of the populations recorded in the first had disappeared. This decline continues unabated, despite the fact that the causes are well known.

Since the second world war, Britain's agriculture has become intensified beyond recognition. The consequences for water voles have been immense. Much of the vegetation that they use in their diet and shelter, and many of the waterway banks

in which they burrow have been destroyed by livestock-trampling or drainage. The remaining populations are mostly small, isolated, and vulnerable to predation, especially by American mink.

American mink have been escaping from fur-farms since the 1920s and are now found in nearly every river catchment in Britain. It is almost impossible to overstate how much damage they do: a single mink is capable of consuming every water vole in several kilometres of waterway in a few months. So Ratty suddenly has more than just weasels to contend with. His home is a wreck and he is being hunted to extinction by a voracious alien predator.

Water vole habitat is now legally protected and mink trapping is increasingly prevalent. These measures alone, however, can only slow the decline. To reverse it we need to increase the number of populations in the UK. In the present situation this means reintroducing captive-bred voles to vacant areas.

Reintroduction is a great opportunity for constructive conservation but is also very difficult to get right. All animals need the correct habitat and if the habitat is even subtly wrong it can prove disastrous. This is why I have spent my time trapping, tagging and radio-tracking water voles in existing populations: I am attempting to ensure that our knowledge is exactly right so that when we reintroduce them, we know what the correct habitat looks like, how much of it we need, how many water voles are needed to fill it and, crucially, at what point we can say that we have been successful.

The underlying reasons for this research are necessarily ethical. There are many arguments for wildlife conservation, but possibly the most honest and compelling is that a world in which water voles exist is simply a better place to live than one in which we have allowed them to become extinct.

Water voles are robust, breed quickly, and cope well with reintroduction. In conservation terms they have everything going for them. Failure to keep water voles in existence would be a reflection of an apathetic attitude rather than an unavoidable fate. Besides, who wants to sit, book in hand, explaining to their children that Ratty is dead, and it's all our fault?

Appendix II

Model Selection and Parameters for MARK Analyses

Robust Design models

Four separate Robust Design Models were fitted, Bure Males, Bure Females, Bedwyn Males and Bedwyn Females.

Robust design models combine data from *primary sampling periods* and *secondary sampling periods*. Following (Kendall & Nichols, 1995; Kendall et al., 1997) *primary sampling periods* are the intervals between trapping sessions within which gains (birth and immigration) and losses (death and emigration) to the population can occur. In the case of this study, the *primary sampling periods* were capture sessions, or weeks of captures, in separate months. *Secondary sampling periods* are within-capture-session periods, during which the population is assumed to be closed to gains and losses. In this study the *secondary sampling periods* were days of capture within each capture session week.

The survival estimates presented in Chapter 5 derived from between sessions (*primary periods*) estimates, whereas population size estimates derived from within sessions (*secondary periods*) closed capture population estimates, both implemented via Robust Design models.

Survival rate estimation

There were 8 relevant capture sessions (September 01 – April 03) for the Bure Marshes and 6 for the Little Bedwyn site (June 02 – May 03).

I fitted models in which Phi (the survival parameter) was held as Phi(t) (survival rates may vary between sessions), without considering Phi(.) models (survival rates constant over time). This was because all the evidence for water voles

suggests large over-winter mortality rates, but lower rates of loss during summer months. It is biologically unlikely that models that incorporate both one-month between-session periods during the summer when vegetation is abundant, and six month between-session periods over the winter, during which vegetation is scarce, should contain survival rates at a constant value.

Emigration estimation

Two types of models were considered: with, and without temporary emigration. Two parameters define emigration; gamma', the probability of an animal emigrating to outside of the trapped area, and gamma'', the probability of the animal returning having emigrated (Kendall et al., 1997). The no-emigration model was fitted by setting both gamma' and gamma'' to 0 (Kendall et al., 1997). In this no-emigration model any animal leaving the site counts as having deceased, and consequently affects the survival parameter. In the case of this study (Chapter 5) this was advantageous in demonstrating that female survival / emigration was not responsible for the female decline witnessed. The best fitting models were all no-emigration models (the minimum AIC difference between a no-emigration model and it's equivalent containing emigration was 6 in any analysis). Had any animals permanently emigrated, this would have lowered the survival rates for females in the no-emigration model. Female survival rates at the Bure Marshes were high, suggesting that neither female mortality nor emigration were responsible for the female decline. Time dependence in emigration variables was not manipulated since in all cases no-emigration models fitted substantially better than models incorporating emigration.

Population size estimation

Population size (N) for a give session was estimated from p (the probability of first capture) and c (probability of recapture) of individuals in each session. For each capture session, p and c were either able to vary between days of capture, noted as p(t) and c(t), or not vary between days, noted as p(.) and c(.).

Synthesis and candidate list

A fully parameterised model containing temporary immigration, survival able to vary between primary sampling periods, and both p and c able to vary for each secondary period for an 8 sampling periods design (e.g. Bure Marshes) would be notated thus:

g'(t)g''(t)Phi(t)p1(t)(p2(t)p3(t)p4(t)p5(t)p6(t)p7(t)p8(t)c1(t)c2(t)c3(t)c4(t)c5(t)c6(t)c7(t)c8(t)

Each of the p and c parameters were able to be made constant - i.e. p(.) and c(.), meaning that the probability of first capture and recapture would be held constant for all *secondary periods* within a trapping session, and both emigration and non-emigration models were fitted. A model with no emigration (g' and g'' = 0) and with no variation in probability of first capture in the 3rd and 4th sessions and no variation in probability of recapture in the 7th session would be notated thus:

nePhi(t)p1(t)(p2(t)p3(.)p4(.)p5(t)p6(t)p7(t)p8(t)c1(t)c2(t)c3(t)c4(t)c5(t)c6(t)c7(.)c8(t)

MARK analysis and model selection

The candidate list of models for each Robust Design analysis contained each combination of p(t), p(.), c(t), c(.) and of emigration / no emigration.

Model fit

Best fitting models for the Robust Design are presented in Table 1. Goodness of fit tests of the most parameterised model were unavailable for the Robust Design in MARK, but the similarity of the survival rates to those form Pradel's model (see below for GoF testing for Pradel's model) and population estimates to numbers captured suggest that the models were good fits to the data.

In all cases, the differences between the best fitting models and the next best were slight, such that the models were equivalent (models with an AIC with 1-2 are usually considered identical: Anderson & Burnham (1999). Estimated survival rates and population estimates from equivalent fitting models were similar, usually to at least 3 decimal places. The AIC difference between the best fitting and worst fitting models, however, was a minimum of 80 in each case. Parameter estimates from the best fitting models are presented on pages 199-204.

Table 1: Best fitting Robust Design models, selected on the basis of AICc. AIC difference gives the difference in AICc between the best fitting model and the next best.

Site	Sex	Model	AICc	AIC difference
Bure	Male	nePhi(t)p1(.)(p2(t)p3(t)p4(.)p5(.)p6(.)p7(.)p8(.)c1(.)c2(.)c3(.)c4(.)c5(.)c6(.)c7(.)c8(.)	836.73	0.93
Bure	Female	nePhi(t)p1(.)(p2(.)p3(.)p4(.)p5(t)p6(.)p7(.)p8(.)c1(.)c2(.)c3(.)c4(.)c5(.)c6(.)c7(.)c8(t)	565.68	0.81
Bedwyn	Male	nePhi(t)p1(t)(p2(t)p3(.)p4(.)p5(.)p6(.)c1(.)c2(.)c3(.)c4(.)c5(.)c6(.)	568.39	0.63
Bedwyn	Female	nePhi(t)p1(t)(p2(t)p3(.)p4(.)p5(.)p6(.)c1(.)c2(.)c3(.)c4(.)c5(.)c6(t)	530.11	0.46

Pradel's Recruitment Models

These models allow recruitment rates of each gender to be estimated using Pradel's model for survival and recruitment estimation (Pradel, 1996).

These models are open population models, and do not make use of closed captures (i.e. *they use only primary sampling periods*). The models fitted estimated survival rates (Phi), probability of recapture (p) and recruitment rates (f), defined as the number of new individuals captured at time t+1 per extant individual at time t. For the candidate list it was biologically infeasible that either survival rate or recruitment rates should be constant across time periods, since these periods incorporated periods both between successive summer captures and over-winter. Therefore only recapture probability was permitted to be constant or vary, denoted at p(t) or p(.). Bootstrap goodness of fit tests for each analysis revealed that the most parameterised model was a good fit to the data (models within bottom 60% of theoretical deviances in each case). Parameter estimates from these models are given in pages x-y.

Table 2: Best fitting Pradel recruitment models, selected on the basis of AICc. AIC difference gives the difference in AICc between the best fitting model and the next best.

Site	Sex	Model	AICc	AIC difference
Bure	Male	Phi(t)p(.)f(t)	718.80	7.37
Bure	Female	Phi(t)p(.)f(t)	392.30	5.41
Bedwyn	Male	Phi(t)p(.)f(t)	707.17	2.51
Bedwyn	Female	Phi(t)p(.)f(t)	532.20	9.82

Literature Cited

Anderson, D.R. & Burnham, K.P. (1999) Understanding information criteria for selection among capture-recapture or ring recovery models. Bird Study, 46, 14-21.

Kendall, W.L. & Nichols, J.D. (1995) On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. Journal of Applied Statistics, 22, 751-762.

Kendall, W.L., Nichols, J.D., & Hines, J.E. (1997) Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology, 78, 563-578.

Pradel, R. (1996) Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics, 52, 703-709.

Parameter Estimates

N.B. gamma parameters not shown since set to 0.

Bure Male Robust Design

Real Function Parameters of:

NEPhi(t)p1(.)p2(t)p3(t)p4(.)p5(.)p6(.)p7(.)p8(.)c1(.)c2(.)c3(.)c4(.)c5(.)c6(.)c7(.)c8(.)}

Parameter	Estimate	Standard Error	Lower	Upper
1:S	0.3913046	0.1017639	0.2176804	0.5976233
2:S	0.4285714	0.0935220	0.2618897	0.6132053
3:S	0.5017691	0.1024394	0.3108693	0.6921545
4:S	0.6757513	0.1049489	0.4490582	0.8419894
5:S	0.7777718	0.0735318	0.6032185	0.8895903
6:S	0.7815657	0.0869561	0.5686864	0.9066275
7:S	0.2368661	0.0746889	0.1213406	0.4109399
21:p Session 1	0.7187500	0.0794805	0.5418119	0.8466935
22:p Session 2	0.1785714	0.0723789	0.0763370	0.3637966
23:p Session 2	0.3043476	0.0959439	0.1525318	0.5153754
24:p Session 2	0.2499999	0.1082531	0.0970694	0.5082476
25:p Session 2	0.4166664	0.1423186	0.1848043	0.6923618
26:p Session 2	0.5714289	0.1870439	0.2298264	0.8562711
27:p Session 2	1.0000000	0.2224881E-05	0.9999956	1.0000044
28:p Session 3	0.5416666	0.1017071	0.3461726	0.7251222
29:p Session 3	0.3636371	0.1450408	0.1433049	0.6612528
30:p Session 3	0.4686796E-12	0.3659349E-06	-0.7172320E-06	0.7172329E-06
31:p Session 3	0.4285726	0.1870439	0.1437298	0.7701744
32:p Session 3	0.7500019	0.2165053	0.2378340	0.9664903
33:p Session 3	1.0000000	0.8894173E-05	0.9999826	1.0000174
34:p Session 4	0.5318037	0.0760786	0.3842630	0.6739854
35:p Session 5	0.3640736	0.0630370	0.2513594	0.4939808
36:p Session 6	0.4421546	0.0660793	0.3191867	0.5726490
37:p Session 7	0.3462065	0.0704268	0.2234628	0.4935221
38:p Session 8	0.6000003	0.0979796	0.4025863	0.7695254
39:c Session 1	0.7000001	0.0591608	0.5732518	0.8020991
40:c Session 2	0.4050632	0.0552311	0.3028805	0.5161929
41:c Session 3	0.4555555	0.0524960	0.3559250	0.5588751
42:c Session 4	0.5232559	0.0538580	0.4182232	0.6262712
43:c Session 5	0.5619835	0.0451039	0.4725482	0.6475643
44:c Session 6	0.4509804	0.0492689	0.3573862	0.5481767
45:c Session 7	0.3965516	0.0454194	0.3117680	0.4880418
46:c Session 8	0.8571430	0.0591485	0.6995151	0.9392623
47:N Session 1	23.000000	0.6740217E-03	23.000000	23.000844
48:N Session 2	28.000000	0.0000000	28.000000	28.000000
49:N Session 3	24.000000	0.0000000	24.000000	24.000000
50:N Session 4	21.000000	0.0000000	21.000000	21.000000
51:N Session 5	36.961077	2.2794688	35.320233	47.009459
52:N Session 6	34.361863	1.8537035	33.183067	43.131093
53:N Session 7	34.194537	2.5706386	32.354992	45.566461
54:N Session 8	15.000000	0.0000000	15.000000	15.000000

Bure Female Robust Design

Real Function Parameters of:

{NEPhi(t)p1(.)p2(.)p3(.)p4(.)p5(t)p6(.)p7(.)p8(.)c1(.)c2(.)c3(.)c4(.)c5(.)c6(.)c7(.)c8(t)}

		95% Confidence Interval		
Parameter	Estimate	Standard Error	Lower	Upper
1:S	0.3288090	0.0992557	0.1686710	0.5418821
2:S	0.5734363	0.1317765	0.3186419	0.7944222
3:S	0.6704718	0.1124957	0.4285784	0.8466148
4:S	0.6869985	0.1293136	0.4031008	0.8770525
5:S	0.8387958	0.1149328	0.4958312	0.9649489
6:S	0.5660552	0.1494917	0.2835217	0.8113196
7:S	0.4414388	0.1665649	0.1737390	0.7481380
21:p Session 1	0.6808511	0.0679945	0.5360299	0.7975420
22:p Session 2	0.1658249	0.0665357	0.0718724	0.3378825
23:p Session 3	0.5081274	0.0800000	0.3555220	0.6592330
24:p Session 4	0.4538957	0.0834344	0.3005506	0.6165174
25:p Session 5	0.2000001	0.1032796	0.0658986	0.4697571
26:p Session 5	0.5000002	0.1443376	0.2438649	0.7561354
27:p Session 5	0.6666668	0.1924498	0.2681048	0.9161042
28:p Session 5	1.0000000	0.2186125E-05	0.9999957	1.0000043
29:p Session 5	0.8193542	0.0000000	0.8193542	0.8193542
30:p Session 5	0.8193542	0.0000000	0.8193542	0.8193542
31:p Session 6	0.3637642	0.1062418	0.1886516	0.5843531
32:p Session 7	0.4409602	0.1028571	0.2582531	0.6411908
33:p Session 8	0.7142856	0.1707471	0.3266085	0.9279852
34:c Session 1	0.7160494	0.0501015	0.6087303	0.8034376
35:c Session 2	0.4615384	0.0798268	0.3135190	0.6166651
36:c Session 3	0.5555555	0.0585607	0.4398647	0.6655215
37:c Session 4	0.5624999	0.0716028	0.4209287	0.6945738
38:c Session 5	0.5090909	0.0674088	0.3793537	0.6376151
39:c Session 6	0.3666667	0.0879815	0.2160011	0.5488529
40:c Session 7	0.4848484	0.0869989	0.3222779	0.6506899
41:c Session 8	1.0000000	0.1344466E-05	0.9999974	1.0000026
42:c Session 8	0.2000001	0.1788856	0.0271820	0.6910545
43:c Session 8	0.7999998	0.1788855	0.3089456	0.9728179
44:N Session 1	32.000000	0.6860392E-13	32.000000	32.000000
45:N Session 2	20.606184	6.0951302	15.418855	44.758358
46:N Session 3	18.000000	0.3386454E-04	18.000000	18.000023
47:N Session 4	13.000000	0.6170677E-03	13.000000	13.000535
48:N Session 5	15.000000	0.1548511E-23	15.000000	15.000000
49:N Session 6	11.746198	1.7169653	11.052277	21.651079
50:N Session 7	9.0000005	0.8101081E-03	9.0000000	9.0008975
51:N Session 8	5.0000000	0.8753786E-04	5.0000000	5.0000664

Bedwyn Male Robust Design

Real Function Parameters of :
{NEPhi(t)p1(t)(p2(t)p3(.)p4(.)p5(.)p6(.)c1(.)c2(.)c3(.)c4(.)c5(.)c6(.)}

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:S	0.5000008	0.0980581	0.3167448	0.6832566
2:S	0.7693577	0.0809508	0.5712327	0.8842588
3:S	0.6889736	0.0790089	0.5122104	0.8140981
4:S	0.2657994	0.0775324	0.1424923	0.4409421
5:S	0.5710439	0.1262685	0.3109928	0.7694593
19:p Session 1	0.8682329E-13	0.8172341E-07	-0.1601778E-06	0.1601780E-06
20:p Session 1	0.0384615	0.0377146	0.0053906	0.2279258
21:p Session 1	0.2800000	0.0897998	0.1397323	0.4821556
22:p Session 1	0.2222223	0.0979908	0.0859611	0.4646723
23:p Session 1	0.2857147	0.1207364	0.1114672	0.5605176
24:p Session 1	1.0000000	0.3092202E-04	0.9999394	1.0000606
25:p Session 2	0.3658537	0.0752240	0.2340564	0.5213505
26:p Session 2	0.4230771	0.0968907	0.2519588	0.6148828
27:p Session 2	0.7333336	0.1141798	0.4668507	0.8962278
28:p Session 2	0.2499997	0.2165065	0.0335099	0.7621679
29:p Session 2	1.0000000	0.5685150E-05	0.9999889	1.0000111
30:p Session 3	0.3184455	0.0594341	0.2145600	0.4441848
31:p Session 4	0.5362160	0.0732918	0.3935247	0.6732137
32:p Session 5	0.3684298	0.0992298	0.2018461	0.5736793
33:p Session 6	0.6862249	0.0965264	0.4759875	0.8403966
34:c Session 1	0.4864866	0.0821695	0.3320903	0.6435057
35:c Session 2	0.5344827	0.0463133	0.4435710	0.6231597
36:c Session 3	0.4788728	0.0592861	0.3658195	0.5941324
37:c Session 4	0.4454550	0.0473886	0.3554762	0.5391570
38:c Session 5	0.5499997	0.0786607	0.3959762	0.6949997
39:c Session 6	0.4210523	0.0800932	0.2763897	0.5806716
40:N Session 1	26.000000	0.4464556E-04	26.000000	26.000055
41:N Session 2	41.000000	0.9586306E-18	41.000000	41.000000
42:N Session 3	45.400130	5.6625039	39.158700	63.974306
43:N Session 4	35.218393	1.1175773	35.006199	42.694651
44:N Session 5	17.262514	2.1228830	16.130341	28.228971
45:N Session 6	15.000000	0.2359189E-03	15.000000	15.000181

Bedwyn Female Robust Design

Real Function Parameters of:
{NEPhi(t)p1(t)(p2(t)p3(.)p4(.)p5(.)p6(.)c1(.)c2(.)c3(.)c4(.)c5(.)c6(t)}

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:S	0.3888891	0.1149044	0.1978746	0.6214397
2:S	0.6586077	0.1050850	0.4278149	0.8200404
3:S	0.9198154	0.1026447	0.0018512	0.9999992
4:S	0.4487104	0.1093738	0.2549295	0.6594237
5:S	0.7258633	0.1218800	0.4739014	0.9614937
19:p Session 1	0.0555556	0.0539903	0.0077673	0.3065306
20:p Session 1	0.2352942	0.1028794	0.0911787	0.4855087
21:p Session 1	0.1538462	0.1000683	0.0387385	0.4506404
22:p Session 1	0.1818184	0.1162914	0.0458136	0.5070312
23:p Session 1	0.3333335	0.1571349	0.1111472	0.6665858
24:p Session 1	1.0000000	0.1144112E-04	0.9999776	1.0000224
25:p Session 2	0.1818182	0.0822304	0.0699467	0.3963621
26:p Session 2	0.3333335	0.1111111	0.1580052	0.5712255
27:p Session 2	0.4166670	0.1423188	0.1848045	0.6923626
28:p Session 2	0.1428573	0.1322600	0.0196699	0.5806110
29:p Session 2	1.0000000	0.3378976E-04	0.9999338	1.0000662
30:p Session 3	0.3592055	0.0789891	0.2224542	0.5234312
31:p Session 4	0.3042742	0.0763011	0.1774850	0.4698934
32:p Session 5	0.2484761	0.0752394	0.1305076	0.4213986
33:p Session 6	0.3915053	0.1035513	0.2153547	0.6013197
34:c Session 1	0.4411765	0.0851538	0.2863119	0.6083989
35:c Session 2	0.3333334	0.0702728	0.2119931	0.4816731
36:c Session 3	0.3225806	0.0839590	0.1831734	0.5027795
37:c Session 4	0.4035088	0.0649817	0.2849518	0.5345194
38:c Session 5	0.5312501	0.0882155	0.3614310	0.6941271
39:c Session 6	0.2369638E-12	0.2810479E-06	-0.5508537E-06	0.5508541E-06
40:c Session 6	0.4166667	0.1423187	0.1848044	0.6923621
41:c Session 6	0.2666668	0.1141799	0.1037725	0.5331496
42:N Session 1	18.000000	0.8133768E-05	18.000000	18.000006
43:N Session 2	22.000000	0.3599164E-04	22.000000	22.000040
44:N Session 3	22.340663	3.1463287	19.700679	34.927441
45:N Session 4	26.968370	3.7429882	23.830930	41.952204
46:N Session 5	17.902761	3.7821479	14.791887	33.234486
47:N Session 6	16.863648	2.5230641	15.252204	28.771305
48:N Session 7	28.650139	5.6046411	23.582169	49.951715
49:N Session 8	20.091798	2.1884070	19.090589	32.158565

Bure Males Pradel Recruitment Model

Real Function Parameters of {Phi(t) p(.) f(t) PIM}

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:Phi	0.4037035	0.1052563	0.2232104	0.6146592
2:Phi	0.4360402	0.0960071	0.2645474	0.6243301
3:Phi	0.5022658	0.1039860	0.3087000	0.6951548
4:Phi	0.6679790	0.1052695	0.4424421	0.8360838
5:Phi	0.7785921	0.0730406	0.6051626	0.8897252
6:Phi	0.7647372	0.0795625	0.5773901	0.8855012
7:Phi	0.2791118	0.0803581	0.1503764	0.4585722
8:p	0.9466551	0.0298482	0.8478289	0.9826155
9:f	0.8045514	0.2564629	0.1440987	0.9901621
10:f	0.4159090	0.1492216	0.1760210	0.7035711
11:f	0.3665590	0.1487206	0.1415600	0.6700426
12:f	1.0053178	0.3151746	0.3875756	1.6230599
13:f	0.2070855	0.0920365	0.0800856	0.4393053
14:f	0.1967083	0.0855273	0.0781413	0.4143239
15:f	0.2114065	0.0893119	0.0857648	0.4337771

Bure Females Pradel Recruitment Model

Real Function Parameters of {Phi(t) p(.) f(t) PIM}

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:Phi	0.2892706	0.0819250	0.1571017	0.4705577
2:Phi	0.6316514	0.1257366	0.3728756	0.8318108
3:Phi	0.6520907	0.1203573	0.3985359	0.8413160
4:Phi	0.6892274	0.1332077	0.3959369	0.8824090
5:Phi	0.8134298	0.1119530	0.5066448	0.9487448
6:Phi	0.5897801	0.1502562	0.2985528	0.8292487
7:Phi	0.4635148	0.1775664	0.1756976	0.7778830
8:p	0.9279569	0.0401382	0.7988214	0.9766264
9:f	0.1979101	0.0922434	0.0732133	0.4352484
10:f	0.4285792	0.2037184	0.1280770	0.7929449
11:f	0.1011056	0.0912334	0.0154808	0.4458512
12:f	0.4472941	0.2249898	0.1196920	0.8280872
13:f	0.7179329E-08	0.2371228E-04	-0.4646889E-04	0.4648325E-04
14:f	0.1725475	0.1327574	0.0326044	0.5633583
15:f	0.1063636	0.1203045	0.0098616	0.5871800

Bedwyn Males Pradel Recruitment Model

Real Function Parameters of: {Phi(t) p(.) f(t) PIM}

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:Phi	0.5197867	0.1023715	0.3263670	0.7074517
2:Phi	0.7272673	0.0760781	0.5570092	0.8497409
3:Phi	0.7629541	0.0855260	0.5602224	0.8904966
4:Phi	0.2291292	0.0728803	0.1169158	0.4002309
5:Phi	0.5569300	0.1404423	0.2917670	0.7931865
6:p	0.8737189	0.0476810	0.7478603	0.9416549
7:f	1.0112827	0.2947165	0.4336383	1.5889271
8:f	0.2368499	0.1019756	0.0931464	0.4839438
9:f	0.1001537	0.0630315	0.0274827	0.3047659
10:f	0.2069497	0.0877371	0.0838462	0.4266282
11:f	0.3812777	0.2012705	0.1037375	0.7664034

Bedwyn Females Pradel Recruitment Model

Real Function Parameters of: {Phi(t) p(.) f(t) PIM}

Parameter	Estimate	Standard Error	95% Confidence Interval Lower	Upper
1:Phi	0.4085541	0.1210799	0.2055332	0.6484362
2:Phi	0.6351939	0.1054286	0.4164918	0.8094314
3:Phi	0.9340231	0.0779784	0.5424055	0.9941204
4:Phi	0.6789338	0.1054475	0.4503495	0.8451440
5:Phi	0.6244186	0.1144070	0.3898814	0.8122203
6:p	0.8712020	0.0450999	0.7547024	0.9369915
7:f	0.7807124	0.2923944	0.1112860	0.9902174
8:f	0.2229583	0.1309973	0.0611965	0.5581107
9:f	0.2873225	0.1530956	0.0851907	0.6357525
10:f	0.1994666	0.1100659	0.0606172	0.4903465
11:f	0.1825574	0.1111779	0.0492971	0.4902770

Ode to Fieldwork

When the rain's persisting down from a leaden sky
And you're wading up a river when you could be warm and dry
When everybody that you meet just has to ask you "Why?"
Shout "Oh f'curiosity, you gormless passers-by!"

When the day is hot and still a buzzing fills the air
The sky is black with horse-flies, your heart black with despair
And when the weather's dank and chill you'll hear a high-pitched whine
That'll be mosquitoes trying to suck blood from your spine.

[If not your back, then it's your head, your chest, your knees, your arms
In fact, they'll skewer anything, it's all part of their "charm".]

Your tent at night is cold and wet, you sleep in starts and fits
Because your skin is itching, full of mosquito spit.
Your head is frozen to the ground, your roll-mat won't stop rucking
The pheasants wake you up at five with mindless bloody clucking.

You may catch a water vole, a fieldvole, shrew or rat
Unless they've all been eaten by fox, heron, mink or cat
And when you scruff a water vole, be sure to have him mastered
Or he'll turn and bite you on the thumb, ungrateful little rodent.

And when it is all over, you return to office work
And dream of insects, dirt and damp, you really are a berk.
So this, my friend, is fieldwork, you chose it for your job
Sometimes it seems delight sublime…sometimes a total sod!