The dynamics of wild woodland rodents

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by

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Abstract

This thesis investigates the variation of life history traits within species, how they underpin population dynamics in woodland rodent populations and how they are effected by interactions between species. We ask how do life history traits differ between populations of the same species in similar habitats? We then go on to ask how two different species living in sympatry differ and the possible effects of interactions. We used data collected against three populations of Columbian ground squirrels (*Urocitellus columbianus*) in Canada and two species of woodland rodents from a site in the UK. Integral Projection Models or IPMs were used to compare the three populations of Columbain ground squirrels and identify differences between them. By using a form of perturbation analysis on the IPMs it was possible to identify the driving demographic and trait transition functions for the differences between the three populations. We then looked at interactions between wood mice (*Apodemus sylvaticus*) and the bank vole (*Myodes glareolus*) in the UK, and the possible effect on trapping bias. As data was limited for the two UK species, we could not construct a full IPM, but instead looked at the differences in growth rates of both species to determine what was the most important factors.

Comparing the population level estimates from the IPMs for the Columbian ground squirrels, revealed significant differences between the populations. In particular the populations differed in growth rate (λ), generation length and R_0. Per-

turbation analysis of the three IPMs revealed the adult survival function to be the major contributor to the differences between the three population. The inheritance function also had a large impact on the offspring estimates.

For the two UK rodent species we found a large impact on the trapping bias due to interactions between the two species. With a significant increase in the chance of the same species being caught within a trap as previously caught. When analysing growth rates, we found that environmental factors only impacted growth for some groups, and we suggest that this may be due to the mitigation by the woodland of impacts of the environmental conditions. We did find that the density of a third species, the yellow necked mouse (*Apodemus flavicollis*), did have a large negative impact on growth rates on the other two species.

In summary species population dynamics can very considerably between populations, even when the populations exist in potentially similar habitats. It is also possible for species living in sympatry to also have an impact on each other's population dynamics. Extreme care should then be taken when making comparisons between species based solely on single population data.

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1

Introduction

The aim of this thesis is to extend our knowledge of woodland small mammal life histories and population dynamics, with a particular emphasis on the differences between populations and the interactions between species. We wanted to ask if and how populations of the same species differ when located in potentially similar habitats. And if they do differ, what is the major contributing factors to the differences. This is important as it is rare to find studies that monitor more than one population of a species, yet the findings from these studies are often used to make predictions about the differences between species. Building on this we then population dynamics. To achieve our aim we first considered three populations of a rodent species common in regions of Canada and the North-Western United States and then we looked at two common species of woodland rodents in the United Kingdom.

In this introduction I will discuss the population dynamics and life histories strategies of the three rodent species, considering the environmental differences and what we currently do not know about them. I will then briefly outline two theories that have been proposed to explain the population dynamics differences

observed between species, before considering the possible interactions between individuals. Finally I will detail a class of model that has been gaining in popularity in recent years that offers many advantages over previous methods of analysing individual captures to determine population level estimates, such as population growth rate, mean size, mean survival rate and trait distribution.

Columbian ground squirrels

Columbian ground squirrels (*Urocitellus columbianus*) are burrow-dwelling rodents that are found in Canada and the North-Western United States. At maturity they have a total length of 325-410mm (Elliott and Flinders, 1991) with males generally being larger and individuals not reaching maturity until 3 years of age. The squirrels spend most of the year in hibernation being active for only 90-100 days (Dobson and Murie, 1987). The length of active period varies with climate and the environment and longer periods have been observed in some studies (Neuhaus, 2000a, table 1). During the active period the squirrels have to mate, give birth to offspring and fatten for the subsequent hibernation period. The mating season occurs following the emergence of the females from hibernation, the mature males having emerged earlier, and last for for approximately 3 weeks (Elliott and Flinders, 1991). It is believed that most females of 2 years of age and older will attempt to breed (Rubach et al., 2016). It is not unknown for yearlings to breed but this is rare and is associated with good habitat quality and favourable climate (Festa-Bianchet, 1981), food supplementation has also be found to cause yearlings to reproduce (Dobson and Kjelgaard, 1985a,b). Reproductive success is classified in many studies as the number of offspring that survive to emerge from their first hibernation (King et al., 1991). Columbian ground squirrels are considered to be

income breeders (Broussard et al., 2005), meaning that the resources they use to produce and raise offspring come from the resources they gather during the active period. This is in contrast to capital breeders that use their fat stores to produce and raise young, possibly replacing the fat stores at a later date. This means that females are dependant on available food resources for their reproductive success. The offspring emerge 51±2 days after mating (Neuhaus, 2017; Skibiel et al., 2009), consequently they have a very short period to gain the weight required to survive their first hibernation. The emergence from the natal burrow coincides with the timing of weaning (Neuhaus et al., 2004). The mass of the female has been found to influence the litter size: bigger females have larger litters (Dobson and Kjelgaard, 1985a,b; Murie and Dobson, 1987), with the mean litter size in wild populations ranging from 2.1 to 4.2 (Murie and Dobson, 1987). Some studies have found that litter size changes with elevation, being smaller at higher altitudes (Murie et al., 1980), whilst others have found no influence (Zammuto and Millar, 1985). Females are believed to manipulate their litter sizes, both before birth and during lactation, based on their ability to wean young (Neuhaus, 2000b). Columbian ground squirrels consume a variety of food resources which vary with the environment, but tend to prefer higher quality forage (Elliott and Flinders, 1991; Shaw, 1925). Offspring have been found to prefer highly digestible food stuffs, and this is more important than the energy or protein content (Bennett, 1999). Both males and females establish territories, with the female territory being near the nesting burrow (Festa-Bianchet and Boag, 1982; Murie and Harris, 1984). Individuals will tolerate overlap with kin, and the presence of the mother can improve the survival of offspring after weaning (King et al., 1991). Density-dependent mechanisms have been suggested to regulate Columbian ground squirrels, with an increase in density causing a decline in litter sizes and offspring survival (Boag and Murie, 1981).

The main cause of mortality in Columbian ground squirrels is thought to be predation (Michener, 1977), with a range of factors influencing the chance of being predated. A lack of food or the increased need for resources during lactation and to a lesser extent gestation, will cause individuals to forage further from burrows and for longer periods, increasing the chance of being predated (Neuhaus and Pelletier, 2001). Weight at immergence into the hibernacle is more important for juveniles than it is for mature animals, this is possibly related to the poor construction of the hibernacle by the offspring (Murie and Boag, 1984). Mortality is lowest during the period of hibernation, although visits from badgers (Murie, 1992) can cause high mortality in some years. Finally altitude has been found to be important in determining life history (Dobson and Murie, 1987) with individuals at higher elevations living longer and maturing later (Murie and Harris, 1982; Murie, 1985; Murie and Dobson, 1987; Risch et al., 1995). But how variable are the population dynamics and life histories of individuals in different populations at similar elevations? Understanding intra-species variation will allow for a better understanding of inter-species variation. Variations in life histories between populations of the same species may be driven largely by differences in the environment, a phenotypic plastic response to the environmental differences (Dobson and Murie, 1987) and possibly genetic differences. By quantifying this variation we see within a species, we can correctly understand the variation between species.

Bank voles

Bank voles (*Myodes glareolus*) are a burrow-dwelling species common in Great Britain, occurring north of the Arctic circle down to the Pyrenees and across to central Siberia (Harris and Yalden, 2008; Stenseth, 1985). They show habitat preference for woodlands (Flowerdew et al., 2004) and hedgerows but are rarely found

in fields (Klaa et al., 2005; Kotzageorgis and Mason, 1997; Tkadlec and Zejda, 1998), in all cases dense ground cover has been found to be important (Kotzageorgis and Mason, 1997; Mazurkiewicz, 1994) to habitat choice. Individuals range in size from 90.8mm in August to November to 100.7mm in April (combined head and body length) (Corbet, 1964; Harris and Yalden, 2008). They increase in weight considerably in April with males (26.1g) being heavier than females (21.9g) compared to the previous August-November weights (17.7g) (Corbet, 1964; Harris and Yalden, 2008). It should be noted that there is large variation in weight for females in April which can possibly be explained by pregnant individuals. Unlike Columbian ground squirrels, bank voles do not hibernate during the winter period, staying active, with their activity peaks at dusk and dawn during the summer but are less nocturnal during the winter months (Ashby, 1972; Greenwood, 1978; Kikkawa, 1964). Reproduction is detailed in Alibhai and Gipps (1985), Bujalska (1983), Clarke (1985), and Harris and Yalden (2008) but is summarised here for convenience. The breeding season normally starts in March-April and continues to September-October, but breeding can continue through the winter months, given a mild winter and an abundance of food. A high population density is known to reduce the breeding season. Offspring that are born at the beginning of the breeding season, mature fast and can breed in the same year, whilst offspring that are born nearer the end of the breeding season will not mature until the following spring. Multiple litters can be produced during the breeding season at 3-4 week intervals. Individuals normally only breed in one season. Mean litter sizes range from 3.53 to 4.11 (Alibhai and Gipps, 1985) for the UK. Reproductive success is determined by time of year, food availability, mother's body weight and age, population density and environment (Clarke, 1985; Jonsson et al., 2002). Home ranges of both females and males overlap during the non-breeding season, but during the breeding season

female home ranges are exclusive (Wolton and Flowerdew, 1985), although non-breeding female kin are tolerated (Mappes et al., 1995). Bank voles are classified as herbivores, but will also consume fruit, seeds, fungi and animal matter, with dead leaves being consumed during the winter months (Watts, 1968). Diet is believed to be mainly determined by available food stuffs (Harris and Yalden, 2008). Population density fluctuates both within year and between years. Multi-annual cycles of 3 to 5 years (Hansson, 1996; Norrdahl and Korpimäki, 2002) have been observed in Northern populations but no multi-annual cycles have been observed in Great Britian (Alibhai and Gipps, 1985; Harris and Yalden, 2008). Multi-annual cycles consist of a large scale increase in numbers and a subsequent decline, followed by at least one year of low numbers. Annual cycles are variable but generally numbers increase during the summer period, peak in the autumn and early winter and then decline in winter and spring (Flowerdew et al., 2004; Mallorie and Flowerdew, 1994).

Wood mice

Wood mice (*Apodemus sylvaticus*) are designated as a woodland species, but being highly opportunistic and adaptable they can be found in nearly any habitat (Harris and Yalden, 2008). Similar to bank voles they are a burrow dwelling species, being very common in Great Britain and possibly Britain's most abundant mammal. Dense cover is not as important for wood mice as it is for bank voles; deer grazing and the decrease of mid-storey and ground cover during a 50 year period in Wytham Woods showed no changes in the density of wood mice (Buesching et al., 2011; Flowerdew and Ellwood, 2001). During the summer, juveniles are less than 15g whilst adults are usually greater than 20g. Pregnant females can exceed 40g (Harris and Yalden, 2008), however during the winter the median weight is nor-

mally 17 to 19g. Combined head and body length ranges from 86-103mm for males and 81-103mm for females (Harris and Yalden, 2008). Like bank voles, wood mice do not hibernate during the winter months, but unlike bank voles they are considered mainly nocturnal with two activity peaks during long nights and one during short nights (Flowerdew, 2000; Montgomery and Gurnell, 1985). Some diurnal activity had been observed during the summer months (Corp et al., 1997; Gorman et al., 1993). Reproduction normally runs from March to October, with multiple litters during the breeding season (Clarke, 1985). Mean litter size normally ranges from 4 to 7 (Clarke, 1985; Harris and Yalden, 2008). Like bank voles it is possible for the breeding season to continue through the winter period (Montgomery, 1980a), although this is normally associated with a large mast crop (Flowerdew, 1973; Gurnell, 1981; Jensen, 1982; Newson, 1960; Smal and Fairley, 1982; Smyth, 1966; Watts, 1970). Although early starts to breeding have been observed without any obvious increase in food (Fairley and Comerton, 1972), in the absence of yellow necked mice (*Apodemus flavicollis*)(Montgomery, 1980b). Litters born during the winter months tend to be small in numbers (Montgomery et al., 1991). Again, like bank voles offspring born in the spring and summer mature quickly and can breed in the same year, whilst those born in the autumn do not mature until the following spring (Green, 1979; Montgomery, 1980a). There is an increased chance of juveniles breeding in the same year with low population densities (Montgomery, 1982). Up to six litters have been observed in the wild (Harris, 1995) although most females only have one or two pregnancies before no longer being caught in the trapped population (Flowerdew, 1985). Home ranges increase with maturity (Randolph, 1977; Smal and Fairley, 1982), male home ranges will increase significantly during the breeding season to overlap multiple female home ranges, whilst female home ranges increase less and are exclusive of other females (Corp et al., 1997).

Offspring recruitment is low during the spring but increases in the autumn (Flowerdew, 1985). Two hypotheses have been suggested to explain this, the Adult Aggression Hypothesis and the Habitat Saturation Hypothesis (Plesner-Jensen, 1996). The first relates the low recruitment due to aggression by adults, which decreases in the autumn as the older individuals are removed from the population (Flowerdew, 1985; Montgomery and Gurnell, 1985; Wilson et al., 1993). And the second to juveniles dispersing from parents habitat until surrounding areas reach saturation point, and the saturation then causes increase in the original habitat (Wolff et al., 1988). Winter survival seems to be positively related to the mast crop in the autumn (Flowerdew, 1985). Wood mice are classified as granivores, although they have similar diets to bank voles, without seeming to compete for food (Clarke, 1985; Gurnell, 1985; Watts, 1968). Identified as scatter hoarders (Vander Wall, 1990) they gather seeds in the Autumn and store them in multiple caches throughout their home range. Although they are seed predators, they are also an important seed vector, as not all seed caches are consumed (Takahashi et al., 2007). It is possible that changes in seed preferences of wood mice, can therefore impact the native tree species composition of the woodland, although this would occur over a long time scale. Studies have found that arboreality in wood mice is greater than first thought, with male wood mice utilising trees to a greater extent than females (Buesching et al., 2008). Buesching et al. (2008) believe that this behaviour is due to a number of factors including predator avoidance, intra- and inter-specific competitor avoidance, exploration and food acquisition. Density of wood mouse populations fluctuates annually (Flowerdew, 1985; Flowerdew and Ellwood, 2001), with no evidence of multi-annual cycles. There is normally autumn-winter peaks with spring summer troughs (Mallorie and Flowerdew, 1994), although density varies considerably between habitats and years and has been linked to the avail-

ability of food and the masting of native trees (Montgomery and Montgomery, 1990).

The habitats of Columbian ground squirrels are quite different from that of the other two species. The Columbian ground squirrel has to endure periods of extreme cold with no access to food. It is then no surprise that the life histories of Columbian ground squirrel differs considerably from the other two species. We would assume that bank voles and wood mice would have similar population dynamics as they share the same habitats, and this does seem to be mostly the case. But historic studies of bank voles and wood mice have mostly concentrated on studying population density and have not considered life histories. Two studies have considered the changes in growth of woodland rodents, but they only trapped during the breeding season and therefore did not consider the complete life history of individuals (Amori and Luiselli, 2011a,b).

Theories used to explain rodent population dynamics

A number of theories have been suggested to describe the differences between species. r-K first purposed by Wilson and MacArthur (1967), suggests that all species exist on a continuum running from r to K. With species that are nearer to r having a smaller size, an earlier age at maturity, lower survival, larger litter sizes and higher genetic variability. Whilst those species that exist nearer to K on the continuum have a larger size, a later age at maturity, a higher survival, small litter sizes and lower genetic variability. In contrast bet-hedging theory (Cohen, 1966) makes predictions that are contra to r-K theory, with individuals producing offspring with trait values that optimise long-term reproduction in a varying en-

vironment. Three categories of bet-hedging have been proposed (Olofsson et al., 2009). **Conservative bet-hedging** is where an individual will produce offspring with a low variation in the trait value, that are not optimal for any particular environment, but will provide the highest chance across all possible environments. The example that Olofsson et al. (2009) give is a clutch of eggs, where all the eggs are of similar size with little variation, within and between clutches. **Diversified bet-hedging** is where an individual will produce offspring with a high variation in trait values within a batch of offspring, but a low variation in trait values across years. This gives the highest chance that at least some individuals will survive from each batch of offspring. **Adaptive Coin Flipping** is where the individual makes a prediction of what the environment will be for a particular year and produces offspring with trait values optimised for that year. This means a low variation in the trait values within a batch but a high variation between years. But identifying bet-hedging strategies using trait means and variances can be very difficult (Rees et al., 2010), due to the confounding effects of shifts in mean demographic rates or mean fitness.

Species interactions in rodents

It is important to note that interactions are not between species, but rather between individuals of a species; either of the same species (intra-specific) or different species (inter-specific). Interactions range in their effects from being beneficial for all individuals (mutualism), to detrimental for one or more of the individuals (e.g. predation). The effects from interactions between individuals can be divided into categories (for review see Lang and Benbow, 2013). **Facilitation** is where one or more of the individuals involved is benefited by the interaction (Davies et al., 2012), mutualism and symbiosis are both examples of facilitation between individ-

uals. **Amensalism** is where one or more of the individuals detrimentally affect other individuals, without gaining any perceivable benefit. One possible example of this would be bark stripping by grey squirrels (*Sciurus carolinensis*) from young trees (Kenward and Parish, 1986). **Antagonism** is where one or more individuals benefits at the expense of other individuals. The classic example of this is predation or herbivory. **Competition** is where all individuals are detrimentally affected by the interaction. Competition can be further subdivided into three major types, interference competition which is a direct form of interaction and exploitation and apparent competition which are both indirect. Interference competition is where individuals directly restrict access of other individuals to a resource, for example dominant males stopping subordinates from mating (Kutsukake and Clutton-Brock, 2008). Exploitation competition is where individuals compete for a resource, such as food or nesting sites. If one group of individuals is better at accessing the resource, then this could lead to the exclusion of the other individuals (Hardin et al., 1960). Apparent competition is where two individuals may not compete directly for a resource but instead can be consumed by another individual of a predator species, effectively the first two individuals are competing to reduce their chance of being consumed. An example of apparent competition has been found by Malo et al. (2013) between native British tree species and the invasive shrub rhododendron (*Rhododendron ponticum*), where the presence of rhododendron was found to modify the behaviour and density of wood mice, increasing the predation rate on native tree seeds.

Intra-specific and inter-specific interactions can both generate population-level signatures. Inter-specific competition can also lead to niche differentiation or resource partitioning (Schoener, 1974), where species use the same resource but in

different ways, at different times or in different areas. Resource partitioning may result in the coevolution of the species, but this can be hard to prove (Connell, 1980). An example of resource partitioning has been observed in bank voles (*Myodes glareolus*) and wood mice (*Apodemus sylvaticus*), where each species selects different micro-habitats and has different activity times (Canova, 1993). At extremes inter-specific competition can cause the exclusion of one or more species (Hardin et al., 1960) and even local extinction. Interactions between individuals can lead to changes in individual fitness (Eccard and Ylönen, 2002) with a decrease in body mass and a reduction in fecundity (Gurnell et al., 2004), and changes in behaviour, such as territoriality (Krebs, 1971) and caching behaviour (Heinrich and Pepper, 1998).

Individual phenotypic characteristics can be important in determining the outcomes of interactions and the distribution of characteristics within a population can be changed by interactions. For example, a small body size, in most cases, is preferable under exploitative competition, as less resources are needed by the individual, but under interference competition a larger body size is favourable, as larger individuals tend to be superior at competing against other individuals. Where both types of competition are in affect, it is possible for the preference for a particular body size due to one type of competition to be overridden by the preference of the other type of competition (Le Bourlot et al., 2014).

It is possible that the mere presence of unknown individuals or other species can elicit changes in individuals, including changes in reproductive condition, puberty and behaviour. For example, in house mice (*Mus musculus*), olfactory cues left in the environment by strange males can cause fighting among the resident males

(Rowe, 1970). Interactions between individuals can also cause a trophic cascade; if the interaction changes the abundance or behaviour of a particular species then this can impact species above or below this species in the food web. One of the most famous examples of a trophic cascade is the reintroduction of wolves in Yellowstone National Park (Ripple and Beschta, 2012). Finally understanding interactions between species can be important in predicting how an ecosystem will respond to change, including climate change (Suttle et al., 2007).

Population models

A number of models have been used over the years to understand the dynamics and life histories of different species. From the simple exponential model through to the more complex Leslie matrix (Leslie, 1945). But the difficulty with all these models comes from parametrising them. It is hard to calculate the required parameter values using data that is commonly collected by ecologists. Additionally the simpler models only consider density and do not take into account individual heterogeneity. Differences in phenotypic characteristics of individuals can have a large impact of population dynamics and interactions between species. One solution to these problems is Integral Projection Models or IPMs; the parameters for these models are easily calculated from standard tests that ecologists are familiar with e.g. growth and survival. The advantages and construction of IPMs are described by Coulson (2012) and Easterling et al. (2000) and are summarised here.

IPMs allow the distribution of phenotypic traits to be tracked through time and can be used to scrutinise life history evolution and population dynamics. The population structure in IPMs is defined both by continuous and discrete traits and does not have the limitation of matrix models where variables need to be broken

into discrete categories (Rees and Ellner, 2009). The four main functions of an IPM are *1*) survival, *2*) development, *3*) recruitment and *4*) inheritance rates (Easterling et al., 2000). A simple example of an IPM is given by

$$n(x, t+1) = \int [G(x|y,t) \cdot S(y,t) + D(x|y,t) \cdot R(y,t)] \cdot n(y,t) dy \tag{1.1}$$

where $n(y,t)$ is the distribution of trait at time t, $n(x,t+1)$ is the distribution of trait at time $t+1$, $G(x|y,t)$ is the growth function, $S(y,t)$ is the survival function, $D(x|y,t)$ is the inheritance function and $R(y,t)$ is the recruitment function. There are also two optional functions that can be included, one each for immigration and emigration. The parameters for the various IPM functions can be estimated using a wide variety of statistical models. From simple linear and generalised linear models to more complex models using Bayesian techniques. The advantage that IPMs have over matrix models, apart from being easily parameterised, is that they allow for the modelling of continuous traits, such as weight or size, in addition to categorical values. That is not to say that matrix models can not be size structured, rather they require the trait to be divided up into a defined number of classes. A matrix model that has a large number of classes is going to be indistinguishable from an IPM, but is going to be very hard to parameterise. On the other hand the kernel that is produced from the functions of the IPM, can be easily used to generate a matrix with a high number of classes. This allows for eigenanalysis that ecologist are familiar with, to be easily carried out for the IPM.

Thesis structure

The first chapter will cover the construction of IPMs for three populations of Columbian ground squirrels. Although it is known that populations dynamics

of this species differ due to changes in altitude (Dobson and Murie, 1987), little is known of the variation between population in similar habitats. The second chapter will build on the first and using perturbation analysis to estimate changes in population level estimates such as population growth rate, mean weight and mean survival rate due to the differences between the demographic rates and trait-transition rates in the three populations. This will provide an understanding of the contribution of each demographic and trait-transition rate to the differences between the three populations. The third chapter will then concentrate on the interactions between two species of rodent in Britain and impact that this has on the methods used to study small mammals. This chapter will also provide support for the protocols we used to study small mammals. The final chapter will look at differences in growth rate between the same two species living in sympatry. We had intended to use data from both an existing site at Silwood Park, Imperial College and a new site setup in Wytham Woods. Due to low capture and recapture rates use of the new site proved to not be possible. The reasons for this will be discussed and possible solutions explored.

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2

The comparative dynamics of three populations of Columbian ground squirrels (*Urocitellus columbianus*)

Running head

Comparison of three populations of ground squirrels

Title

The comparative dynamics of three populations of Columbian ground squirrels (*Urocitellus columbianus*)

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Abstract

Collecting data on marked individuals can be expensive in regards to both time and resources. Therefore rarely is more than one population of a species studied. But the information from these single population studies is often used to make predictions about the difference between species. In this chapter we wanted to understand if there was any differences in the population dynamics of a species living across different populations. We used individual capture data collected on three populations of Columbian ground squirrels (*Urocitellus columbianus*) living in similar habitats within 3km of each other at similar elevations. Due to the similar habitats we would expect to find similar population dynamics. To check this assumption, we used the individual data to populate Integral Projection Models (IPMs). The IPM highlighted differences between each of the three populations, in the population growth rate (λ), generation length and R_0. There was also differences in the stable size distribution and relative reproductive value, suggesting differences in the population dynamics and breeding strategies between the three populations. The results of this chapter suggest that within species variation can be substantial and care needs to be taken when making comparisons between species based solely on single population data.

Introduction

The logistical challenges of collecting data from populations of marked individuals can be substantial. A consequence of this is that most individual based studies are only able to monitor a single population (Clutton-Brock and Huchard, 2013). It can then often be assumed that the dynamics observed from a single focal population are representative of those of other populations of the same species living in different locations (Froy et al., 2016). However, given the strength of species

interactions, spatial variation in the weather, and differences in resource availability between locations, there is no *a priori* reason that two populations of the same species in different locations exhibit different dynamics (Gaillard et al., 1998). A key question, is how might demography and population dynamics differ between populations of the same species in different locations?

There are cases where different groups have studied the same species using similar protocols in different locations and compared their population dynamics. A notable example comes from great tits (*Paris major*) in Europe. Husby et al. (2010) found that although the response of laying date and clutch size to temperature were similar across sites, the between individual variation in plasticity differed markedly and given this they suggest therefore that making generalisations about the impact of changing environmental conditions across populations will be difficult. But not all studies have found differences, Perrins (1965) found that population density of great tits fluctuated similarly in three populations, located in Marley Woods in Wytham Oxfordshire, Forest of Dean in Gloucestershire and Hoghe Veluwe, near Arnhem, Holland, during the period 1947-63. Another example comes from two populations of bighorn sheep (*Ovis canadensis*) in Canada (Sheep River and Ram Mountain) (Coulson et al., 2005; Jorgenson et al., 1993). Although the two populations exhibited similar variation in population growth, the direct contributions from the demographic rates was different. The pooled mortality at Sheep River explained more variation in the growth rate, whilst the lamb winter survival at Ram Mountain had a greater contribution. Coulson et al. (2005) also found that although the contributions from covariation between the demographic rates was similar, the contributions from the individual covariances did vary significantly between the two studies. A study of two populations of roe

deer (*Capreolus capreolus*) in France found stark differences between the populations. The population in Trois Fontaines, that faced severe winters, was highly productive and the population density remained constant during the study period. In contrast the population at Chizé, with mild winters, showed density dependance in both reproduction and body weight (Jean-Michel et al., 1993). Finally rodent populations, including but not limited to *Apodemus sylvaticus*, *Myodes glareolus* and *Microtus agrestis*, are known to vary greatly in size in both time and space. The multi-annual oscillations in density on which Chitty (1952) based his hypothesis (the "Chitty effect") is absent in some areas of the Great Britain (Richards, 1985) but present in others.

When population dynamics do differ between populations, the next question is why? The proximate reason is because survival, recruitment or dispersal rates vary between the populations. But a more interesting question is why do these rates vary? Demographic rates are determined by an interaction between the distribution of individual phenotypes within a population, and the ecological environment (Coulson, 2012). Consequently, one way to compare populations is to compare phenotype-demographic rate maps across populations, and to combine these associations into Integral Projection Models (IPMs) – a tool that is now widely used to study population dynamics, life history and phenotypic trait dynamics (Easterling et al., 2000; Rees and Ellner, 2009).

IPMs have been used to investigate a wide variety of questions for many species. From Ellner and Rees (2006) use of IPMs to investigate complex demographic attributes of species, to Bassar et al. (2016) showing how asymmetric competition effects the life history of Trinidadian guppies. The basic IPM has been extended

to investigate a number of biological applications, including age structure, multi-species interactions, density dependence and environmental stochasticity (Ellner et al., 2016). Species covered have included, but are not limited to terrestrial plant species (Adler et al., 2010; Childs et al., 2003; Dahlgren and Ehrlén, 2011), mammals (Coulson et al., 2011; Simmonds and Coulson, 2015), birds (Childs et al., 2016), marine organisms (Bruno et al., 2011), freshwater organisms (Bassar et al., 2016, 2017) invertebrates (Smallegange et al., 2014) and reptiles (Jaffré and Le Galliard, 2016; Wallace et al., 2013). IPMs have not been used to compare dynamics across more than one population of the same species, and to understand how these populations may be similar or may differ.

Here we apply IPMs to three sub-populations of the same species to understand if there are any differences between populations of the same species living in similar habitat. We would expect the IPMs to predict similar population level estimates, given the similar habitat of the three populations. To check this, we compared the predictions for populations' average growth rate (dominant eigenvalue λ), the stable size distribution and relative reproductive value (the dominant right and left eigenvectors respectively), which allowed comparison of the population dynamics and breeding strategies across the three populations.

The study investigated three populations of the Columbian ground squirrel (*Urocitellus columbianus*) located in alpine and subalpine meadows of the Rocky Moutains, South Western Alberta. Previous research has identified some differences between attributes of these populations living in different isolated meadows. Elevation is an important factor in determining population structure (Dobson and Murie, 1987). Females in higher elevation sites are likely to live longer and ma-

ture later (Murie and Harris, 1982; Murie, 1985; Murie and Dobson, 1987; Risch et al., 1995). Zammuto and Millar (1985) attributed this to the more predictable weather but scarcer resources at higher elevations compared to lower elevations where resource availability is more variable. Other studies have suggested that *U. columbianus* are exhibiting plastic responses in their life history traits in response to the unpredictable environment (Dobson and Kjelgaard, 1985a; Dobson and Murie, 1987; King et al., 1991; Neuhaus, 2000a). Altitude has also been found to be negatively correlated with litter size, with Murie et al. (1980) suggesting that this was due to the timing of the snow melt and the growth of the vegetation varying with altitude. Both body weight and reproduction of *U. columbianus* have been found to increase in response to increased supply of food (Dobson and Kjelgaard, 1985a,b). In studies that included the recruitment to 1 year of age as a measure of reproductive success, the over-winter survival of the offspring has been found to be the most important factor (King et al., 1991). Survival of juveniles over their first winter is correlated with their prehibernation body weight, which in turn is mostly determined by their growth rate after emergence from the natal burrow. Growth rate of juveniles after emergence has been found to be enhanced by the digestibility of the food stuff and is more important than the energy or protein it provides (Bennett, 1999).

Methods

Integral projection model

The Integral projection model (IPM) used was a univariate, deterministic model of the form

$$n(z', t+1) = \int [G_a(z'|z)S_a(z) + G_j(z'|z^*)Pr(z^*)C(z^*|z)B(z)Pb(z)]n(z,t)dzdz^* \tag{2.1}$$

Equation 2.1 describes how the distribution of body weights in the population at time $t+1$ is determined by the body weights at time t given the survival, development and reproduction of the population. The distribution of body weights at time $t+1$ is represented by $n(z', t+1)$. The effect of body weight on survival for the adults is represented by $S_a(z)$, probability of reproducing by $Pb(z)$ and litter size by $B(z)$. The growth rate (development) is represented by $G(z'|z)$, the offspring's size given the mother's weight is $C(z^*|z)$. Because the offspring are censused at a later time than the adults, additional functions are required to calculate their development and chance of recruitment into the adult population, represented by $G_j(z'|z^*)$ and $Pr(z^*)$ respectively. Finally $n(z,t)$ is the distribution of body weights at time t. In the functions z represents the possible adult weights at time t, z' the possible adult weights at time $t+1$ and z^* the possible weights of the offspring at the offspring census. A life cycle diagram for the Columbian ground squirrels is shown in figure 2.1.

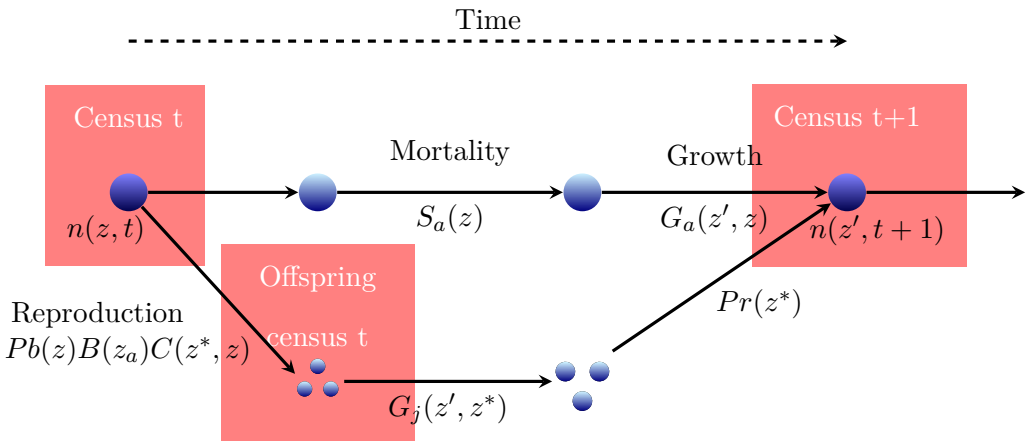


Figure 2.1. Life cycle diagram and census points for the Columbian ground squirrels. The shade red areas denote the times that the censuses were conducted, for both the adults (individuals of 1 year old or above) and the offspring.The adults are represented by the single blue dots and the offspring by the three dots. Reproduction is split into three different functions, probability of reproduction ($Pb(z)$), the litter size ($B(z)$) and offspring size ($C(z^*,z)$). Due to the offspring being censused later than the adults, separate functions are required for growth and survival/probability of recruitment. $G_a(z',z)$ for adult development, $G_j(z',z^*)$ for offspring development, $S_a(z)$ for adult survival and $Pr(z^*)$ for probability of offspring recruitment into the adult population.

The IPM was approximated using a high dimensional matrix (iteration matrix), with weight being split into 250 equal sized classes ranging from -20% below the minimum weight observed to +20% above the maximum weight observed for the population. The Survival, Probability of Reproducing, Litter Size and Probability of recruitment kernels were approximated using the functions $\boldsymbol{S}$, $\boldsymbol{Pb}$, $\boldsymbol{B}$ and $\boldsymbol{Pr}$ respectively. The Adult Development, Offspring Weight and Offspring Development transitional kernels were approximated as functions $\boldsymbol{G_a}$, $\boldsymbol{C}$ and $\boldsymbol{G_j}$ respectively. The distributions of weight at time t and time $t+1$ were represented as vectors $\boldsymbol{n}(t)$ and $\boldsymbol{n}(t+1)$ respectively and the matrix model was

$$\boldsymbol{n}(t+1) = \boldsymbol{A}\boldsymbol{n}(t) = [\boldsymbol{G_a S} + \boldsymbol{G_j PrCBPb}]\boldsymbol{n}(t) \tag{2.2}$$

Interrogation of the IPMs

The Eigen function was applied to the iteration matrices approximated from the IPM functions to determine the dominant eigenvalue which is the estimated population growth rate or λ. Using the Eigen function it was also possible to determine the stable weight ($w(z)$) and reproductive distributions (Caswell, 2001). By summing the multiplication of the stable weight distribution and the meshpoints (z) it was possible to determine the mean weight of the population (equation 2.3). The meshpoints are the centre points of each of size classes of the iteration matrix. The mean reproductive weight was calculated in a similar way using the stable reproductive distribution. The mean survival rate, reproductive probability and litter size was calculated by summing the stable size distribution multiplied by the output from the survival, reproduction and litter size functions respectively. Similarly by applying the Eigen function to the iteration matrix generated from the reproductive kernel it was possible to estimate the offspring mean size and mean recruitment rate.

$$\overline{z} = \frac{\int w(z)\, z\, dz}{\int w(z)\, dz} \tag{2.3}$$

It was possible to calculate the variance of the distributions using equation 2.4.

$$\sigma_z^2 = E(z^2) - \overline{z}^2 = \frac{\int w(z)\, z^2\, dz}{\int w(z)\, dz} - \overline{z}^2 \tag{2.4}$$

To calculate the variance due to the accuracy of the model, for all the estimates, it was necessary to bootstrap the data and rerun the statistical analysis and IPM; this was then iterated 1,000 times to get the variance. Finally to assess the sensitivity of each of the IPM parameters, the IPMs were rerun with each parameter being increased by 1% in isolation. The percentage increase or decrease was then

calculated for each of the IPM estimates for each parameter increase. This was repeated for each of the IPMs parameterised from the single statistical population models and the IPMs parameterised from the combined population statistical model.

Site and data collection details

The Colombian ground squirrel (*Urocitellus columbianus*) is a burrow-dwelling rodent common in regions of Canada and the North-Western United States. They spend most of their time hibernating and are only active for around 103 days each year (Neuhaus, 2000a, table 1), the time varying with local climate. The data were collected from the Sheep River Provincial Park in South Western Alberta, Canada at elevations between 1490-1550 m. The three locations are within 3km from each other, situated in the same valley, at 114° W and 50° N. Each of the three sites are surrounded by trees on three sides and a canyon on the forth side, with the impact of the wind is similar at the three sites. Population A study site was approximately 2.5ha at an elevation of 1,550m, with data being collected between 1994 and 1998 and 2007 and 2015. Population B was located in a 1.25ha meadow and differs from the other two sites in that it has a steep hill that leads to earlier snow melt. Data was collected between 1992 and 1997 for population B. Finally population C was located in a 1.0 hectare meadow with data being collected between 2004 and 2015. Population C is situated further East than the other two sites, which leads to more snow cover in some years. The sites for populations B and C were grazed by cattle from the end of June to October each year. During the 1990s the meadow for population A was not grazed until October, when it was used to gather the livestock until mid October, when the livestock was removed from the park. From 2000, the meadow for population A was grazed in a similar manner to the meadows for populations B and C.

All three study sites consist of subalpine meadows surrounded on one side by the sheep river canyon, on the other sides by aspen stands and coniferous woodlands and road for A and C. Animals in these breeding colonies have been permanently marked with metal ear tags at emergence from their natal den or, when immigrating at first sight. Because the surrounding terrain and aspen stands do not provide suitable habitat for the squirrels, we are able to say with a high degree of certainty that all animals alive are known. Animals not emerging in the following year are considered dead with the exception of 2 year old males which may have dispersed away from their natal colony the previous summer.

Each spring animals were trapped at emergence from hibernation with National and Tomahawk (15x15x48 and 13x13x40 cm) live traps baited with peanut butter. For each animal sex and reproductive status were noted and a weight taken with a Pesola spring scale to the nearest 5g. The animals were observed through the mating season to determine the day of conception for each female. Natal burrows were found through observation and the offspring caught, marked, counted and weight at first emergence from the natal den 51 ± 2 days after mating.

This study only considers females of the populations, because maternity can be more easily and accurately determined compared to paternity. Additionally, significantly more male offspring disperse from the population compared to females (Neuhaus, 2006). Including males would require the models to incorporate immigration and emigration and increase its complexity.

Ethical statement

The research, capture and handling of animals was conducted under guidelines on care and use of wildlife provided by the Canadian Council on Animal Care. The protocol was approved by the "Live and Environmental Sciences Animal Resource Center" LESARC at the University of Calgary.

Statistical models

All statistical analysis was conducted using **R** version 3.3.1 (R Core Team, 2016). To check if the variance of the weight traits was similar across the three populations for both adults and offspring, an analysis of variance test was used with a Tukey multiple comparisons of means as the post hoc test if required. As the data was not always sampled in the same years, across the three populations, we checked for the weight traits measured in the same year, for offspring and adults, to see if they varied or not, using again an analysis of variance test.

Linear (LM) and general(ised) linear (GLM) regression models were used to calculate the parameters required by the various functions in the IPM. The statistical models for the survival, probability of recruitment and probability of reproducing that were used to parameterise the respective functions ($\boldsymbol{S}$, $\boldsymbol{Pr}$, $\boldsymbol{Pb}$) were GLMs with a binomial error structure and a logit link. The response for all was a binary variable with 0=died, 1=survived for survival, 0=not recruited, 1=recruited for recruitment and 0=no reproduction, 1=reproduced for reproduction. The three statistical models included weight as a quadratic term. The litter size function ($\boldsymbol{B}$) was parameterised by a GLM with a Poisson error structure and a log link. The response was the female litter size and the predictor was set to mother's weight at time t with a quadratic term. Development ($\boldsymbol{G_a}$), offspring development ($\boldsymbol{G_j}$) and offspring weight ($\boldsymbol{C}$) functions were parameterised by linear models with a

Gaussian error structure and an identity link. The response for the development and offspring development models was weight at time $t+1$ with the predictor being weight at time t for the development model and offspring weight for the offspring development model, both with a quadratic term. For the offspring size model the response was the offspring weight and the predictor was the mother's weight at time t again with a quadratic term. The fits of the models were checked by examining the plots of standard deviance and residuals against predicted values. Model reduction was conducted and the best model chosen by comparing the AIC values. Outliers were checked for using the Bonferroni Outlier Test from the `car` package (Fox and Weisberg, 2011). If outliers were detected then a robust form of the statistical models with Mallows or Huber type robust estimators (Cantoni and Ronchetti, 2001) was used, from the `robustbase` R package (Maechler et al., 2016). Dispersion was checked for the GLMs with binomial or Poisson distributions; for Poisson the dispersion test from the `AER` package (Kleiber and Zeileis, 2008) was used, for binomial the residual deviance was compared to the residual degrees of freedoms. If over-dispersion was detected then the quasi form of the distribution was used.

To construct the functions for growth and offspring growth the variance around the regressions of weight at time $t+1$ as a function of weight at time t and offspring weight was needed. For the offspring size model the variance around the regression of offspring weight as a function of mother's weight was needed. This was achieved by using the R `dnorm` function with the mean and standard deviation taken from the linear models.

Separate statistical analyses were conducted for each of the three populations.

Additionally the data for the three populations were combined and the statistical analysis was repeated against this dataset, with categorical covariates added to the models to denote which population each record was from. An interaction effect between population and weight was also included. The combined models allowed for statistical comparisons to be made between populations. As with the single population models, terms were removed and fit compared using the AIC values following the method described by Crawley (2013). The estimates from the statistical analyses were used to parameterise the IPM functions. Two sets of IPMs were produced, one for the single population statistical analysis and the other for the combined population statistical analysis.

Results

For population A there was a total of 1,204 captures of 675 unique individuals, for population B there were 260 captures of 121 unique individuals and population C there were 466 captures of 248 unique individuals. The mean(±standard deviation) capture weight for population A was 274.0±141.0g, population B 268.2±151.7g and population C 247.2±146.4g. The mean litter size for population A was 2.8±1.0, population B 3.1±0.9 and population C 3.4±1.1; these values included both male and female offspring. The mean offspring weight for population A was 104.5±21.4g, population B 102.6±15.7g and population C 101.8±18.8g. It was found that reproduction did not occur below a certain weight for each of the populations (A 200g, B 250g, C 250g). The mean female density of the populations was A 86.0±43.1, B 43.3±16.9 and C 38.8±12.5. Unless otherwise noted these values refer to just the females of the population.

For adults in the three populations there was a significant effect of the popula-

tion on the weight trait at the p<.05 level for [F(2,1919) = 5.801, p = 0.003]. Post hoc comparisons using the Tukey HSD test indicated that the adult mean weight trait for population C (M = 247.200, SD = 146.377) was significantly different than population A (M = 274.040, SD = 140.994). From the analysis of variance test of trait values measured in the same year across populations, there was a significant difference for offspring between population A and B in 1997 at the p<.05 level for [F(1,43) = 6.454, p = 0.015] and for offspring between population A and C in 2011 at the p<.05 level fpr [F(1,25) = 4.812, p = 0.038]. Years checked were 1994, 1995, 1996 and 1997 for population A and B and years 2007 to 2015 for population A and C.

Statistical models

Model reduction indicated the most parsimonious statistical models from which the functions of the IPMs were parameterised. Tables 2.1 and 2.2 provide the list of the statistical models used to parameterise the IPMs for both the single and multiple population models respectively. The fit of both the multi and single population statistical models is shown in figures S2.1 and S2.2 and model choice in tables S2.1 to S2.4. A brief overview of the results from the statistical models is included here.

Single population models

Weight did not have a significant impact on survival for population A, whilst for population B and C weight had a positive effect with the best fitting models including a negative quadratic term, indicating that survival was highest at the median weights compared to the extremes. Offspring weight was positively correlated with

offspring recruitment for the three populations with population A and B having negative quadratic terms. For adult development there was a positive effect of weight at time t on weight at time $t+1$ for population A, whilst weight at time t for population B and C had a negative effect on weight at time $t+1$ but with a positive quadratic term. For offspring development weight at time t had a positive effect on weight at time $t+1$ for the three populations, but with population A having a negative quadratic term. The chance of reproducing was positively correlated with weight but for population A and C there was a negative quadratic term that indicated a drop off of reproductive chance at the highest weights. Weight had no impact on the litter size for any of the populations. Finally for inheritance mother's weight had a negative effect on offspring weight with a positive quadratic term for populations A and C, whilst for population B mother's weight had a positive effect on offspring weight. Outliers were detected in the inheritance models for three populations, the development model for population A and the offspring development model for population C, to account for this robust versions of the models were used. Over dispersion was detected in the survival model for populations A and C, offspring recruitment models for the three populations, reproduction model for population A and the litter size model for population A, to account for this a quasi form of the error distribution was used.

Table 2.1. For the single population models, parameter estimates taken from the most parsimonious model, describing the relationship between body mass and demographic and trait transition rates. The predicted values are survival (recruitment) probablity (S), development (G), reproduction probablity (Pr), litter size (B) and inheritance (C). The subscripts a and j refer to the adult (yearlings and older) and offspring individuals that the functions apply to. The subscript values represent the standard error of the estimates. Logit(Y) indicates a Binomial regression link and Log(Y) a Poisson regression. x denotes the possible weights at time t for survival, development and reproduction probablity. For litter size and inheritance x denotes the possible weights of the mother at time t. For offspring recruitment and offspring development, x denotes the offspring's weight at time of emergence from the natal burrow.

Function	Model	Pop.	Fitted LM / GLM	n
Survival probability	Logit(S_a)	A	$0.9839_{(0.0823)}$	746
		B	$-7.3606_{(3.3747)} + 0.0478_{(0.0197)}x - 0.0001_{(0.0000)}x^2$	157
		C	$-5.1570_{(2.2445)} + 0.0303_{(0.0131)}x - 0.0000_{(0.0000)}x^2$	255
Offspring recruitment	Logit(S_j)	A	$-4.8789_{(1.8289)} + 0.0755_{(0.0323)}x - 0.0003_{(0.0001)}x^2$	413
		B	$-11.6411_{(6.9492)} + 0.2068_{(0.1313)}x - 0.0009_{(0.0006)}x^2$	103
		C	$-1.2020_{(0.8128)} + 0.0122_{(0.0079)}x$	204
Development	G_a	A	$303.2889_{(9.7117)} + 0.2772_{(0.0256)}x$	543
		B	$398.8696_{(62.4590)} - 0.2382_{(0.3505)}x + 0.0008_{(0.0005)}x^2$	129
		C	$428.2129_{(60.5053)} - 0.3409_{(0.3495)}x + 0.0009_{(0.0005)}x^2$	144
Offspring development	G_j	A	$62.2264_{(53.4814)} + 2.7721_{(0.9076)}x - 0.0084_{(0.0038)}x^2$	205
		B	$208.1540_{(36.1223)} + 0.5243_{(0.3426)}x$	50
		C	$237.7550_{(12.1328)} + 0.2369_{(0.1081)}x$	102
Reproduction probablity	Logit(Pr)	A	$-11.4389_{(2.5977)} + 0.0421_{(0.0137)}x - 0.0000_{(0.0000)}x^2$	738
		B	$-8.1771_{(1.3050)} + 0.0215_{(0.0033)}x$	157
		C	$-24.9746_{(5.5211)} + 0.1118_{(0.0282)}x - 0.0001_{(0.0000)}x^2$	255
Litter size	Log(B)	A	$-0.1876_{(0.0678)}$	304
		B	$0.2429_{(0.0990)}$	80
		C	$0.4680_{(0.0711)}$	124
Inheritance	C	A	$266.2348_{(47.1748)} - 0.7991_{(0.2363)}x + 0.0010_{(0.0003)}x^2$	251
		B	$78.3111_{(14.7747)} + 0.0545_{(0.0331)}x$	102
		C	$203.2650_{(19.3690)} - 0.5232_{(0.1095)}x + 0.0006_{(0.0002)}x^2$	199

Combined population model

For the combined models, weight was found to have a positive effect on survival with a negative quadratic term. There was a significant difference in survival between population A and B, but not between populations A and C or populations B and C. There was an interaction effect between weight and population, with population B showing a positive increase over population A and population C being significantly lower than population B. For offspring recruitment there was no significant difference between the populations and no significant interaction effect between weight and population. Weight was found to have a positive effect on recruitment with a negative quadratic term. Weight at time t had a positive correlation with weight at time $t+1$ for development and although there was no difference between the populations, there was an interaction effect between weight and population with population B being significantly higher than population A. For Offspring development no difference was detected between the populations, weight at time t was positively correlated with weight at time $t+1$ with a negative quadratic term. There was an interaction effect between weight and population for reproduction with population C showing a positive increase over population A. There was no significant difference in reproduction between populations, although the terms were retained due to the interaction terms being significant. Weight at time t had a positive effect on reproduction with a negative quadratic term. Weight had no effect on litter size but there was a difference between the populations, with population C being the highest followed by population B and finally population A being the lowest. Finally for inheritance no difference was found between the populations. Mother's weight at time t had a negative effect on offspring weight but with a positive quadratic term. Over-dispersion was detected in the survival and recruitment models, to counteract this a quasi-binomial error distribution was

used. For the development, offspring development and inheritance models outliers were detected, so a robust form of the models were used.

Table 2.2. For the multi population model, parameter estimates taken from the most parsimonious model, describing the relationship between body mass and demographic and trait transition rates. The predicted values are survival (recruitment) probablity (S), development (G), reproduction probablity (Pr), litter size (B) and inheritance (C). The subscripts a and j refer to the adult (yearlings and older) and offspring individuals that the functions apply to. The subscript values represent the standard error of the estimates. Logit(Y) indicates a Binomial regression link and Log(Y) a Poisson regression. x denotes the possible weights at time t for survival, development and reproduction probablity. For litter size and inheritance x denotes the possible weights of the mother at time t. For offspring recruitment and offspring development x denotes the offsprings weight at time of emergence from the natal burrow.

Function	Model	Pop.	Fitted LM / GLM	n
Survival probability	Logit(S_a)	A	$-0.3055_{(0.7185)} + 0.0085_{(0.0039)}x - 0.0000_{(0.0000)}x^2$	1295
		B	$-0.3055_{(0.7185)} + 0.0085_{(0.0039)}x - 0.0000_{(0.0000)}x^2 - 1.1116_{(0.6067)} + 0.0049_{(0.0018)}x$	1295
		C	$-0.3055_{(0.7185)} + 0.0085_{(0.0039)}x - 0.0000_{(0.0000)}x^2 - 0.6074_{(0.5471)} - 0.0000_{(0.0015)}x$	1295
Offspring recruitment	Logit(S_j)	A	$-3.4660_{(1.3866)} + 0.0510_{(0.0247)}x - 0.0002_{(0.0001)}x^2$	720
		B	$-3.4660_{(1.3866)} + 0.0510_{(0.0247)}x - 0.0002_{(0.0001)}x^2$	720
		C	$-3.4660_{(1.3866)} + 0.0510_{(0.0247)}x - 0.0002_{(0.0001)}x^2$	720
Development	G_a	A	$302.9277_{(9.7818)} + 0.2781_{(0.0257)}x$	816
		B	$302.9277_{(9.7818)} + 0.2781_{(0.0257)}x - 7.2551_{(17.8164)} + 0.0838_{(0.0460)}x$	816
		C	$302.9277_{(9.7818)} + 0.2781_{(0.0257)}x + 21.2740_{(16.8805)} - 0.0091_{(0.0444)}x$	816
Offspring development	G_j	A	$130.8069_{(44.8079)} + 1.7754_{(0.7904)}x - 0.0051_{(0.0034)}x^2$	357
		B	$130.8069_{(44.8079)} + 1.7754_{(0.7904)}x - 0.0051_{(0.0034)}x^2$	357
		C	$130.8069_{(44.8079)} + 1.7754_{(0.7904)}x - 0.0051_{(0.0034)}x^2$	357
Reproduction probablity	Logit(Pr)	A	$-12.9714_{(2.2225)} + 0.0503_{(0.0114)}x - 0.0000_{(0.0000)}x^2$	1150
		B	$-12.9714_{(2.2225)} + 0.0503_{(0.0114)}x - 0.0000_{(0.0000)}x^2 - 1.2134_{(1.5103)} + 0.0043_{(0.0038)}x$	1150
		C	$-12.9714_{(2.2225)} + 0.0503_{(0.0114)}x - 0.0000_{(0.0000)}x^2 - 1.5615_{(1.2907)} + 0.0055_{(0.0033)}x$	1150
Litter size	Log(B)	A	$-0.1876_{(0.0630)}$	508
		B	$-0.1876_{(0.0630)} + 0.4305_{(0.1174)}$	508
		C	$-0.1876_{(0.0630)} + 0.6556_{(0.0950)}$	508
Inheritance	C	A	$203.9398_{(20.4441)} - 0.5107_{(0.1009)}x + 0.0006_{(0.0001)}x^2$	552
		B	$203.9398_{(20.4441)} - 0.5107_{(0.1009)}x + 0.0006_{(0.0001)}x^2$	552
		C	$203.9398_{(20.4441)} - 0.5107_{(0.1009)}x + 0.0006_{(0.0001)}x^2$	552

IPM

The estimates obtained from the IPMs, parameterised from both the single population and multiple population statistical models for each population are shown in table 2.3. The table also includes the standard deviation calculated from the IPM due to the spread of the weights, the standard error due to the accuracy of the IPM and the means and standard deviation of the raw data. A graphical representation of the estimates are shown in figures S2.3 to S2.10. The most interesting results from the tables and figures are detailed here.

For population growth rate both the single and multi population sourced IPMs estimated λ near to the raw value for the three populations. The mean adult (yearlings and older) weight estimates from the IPMs where very similar to the values calculated from the raw data as was the mean reproductive weight and survival rate estimates. Because weight was found to not be significant for survival in the single population model for population A, the standard deviation from the IPM was zero. For all populations the estimates for reproductive probability from both IPMs were similar to the raw data although the standard deviation from the IPM suggested the reproductive probability varied considerably. For litter size because mother's weight was found to not be a significant predictor, the litter size did not vary with mother's weight, therefore the estimate from the IPM is the same as the mean value of the raw data. Finally the offspring recruitment rate estimates for population A were higher than those suggested by the raw data. For population B the single population model estimate was much lower than the raw data estimate but within the variation suggested by the standard deviation of the IPM, the multiple population model on the other hand produced an estimate higher than what would be expected from the data. For population C both IPMs estimated a

reproductive probability higher than the raw data mean.

Taking the stable weight distribution estimated using the eigenanalysis, it is possible to construct graphs showing the proportional density of individuals in each weight class. Figures 2.2 and 2.3) show the stable weight Z distributions for the single and multi population sourced IPMs respectively, for the three populations. The IPMs estimate two peaks of density: one at around 200 to 300 grams and another at around 400 to 500 grams. The single population sourced models estimates much higher densities in the first peak for populations B and C, but this is not evident in the multi population sourced IPMs. In both the single and multi population sourced models population A has its highest peak in densities at a lower weight than the other two populations.

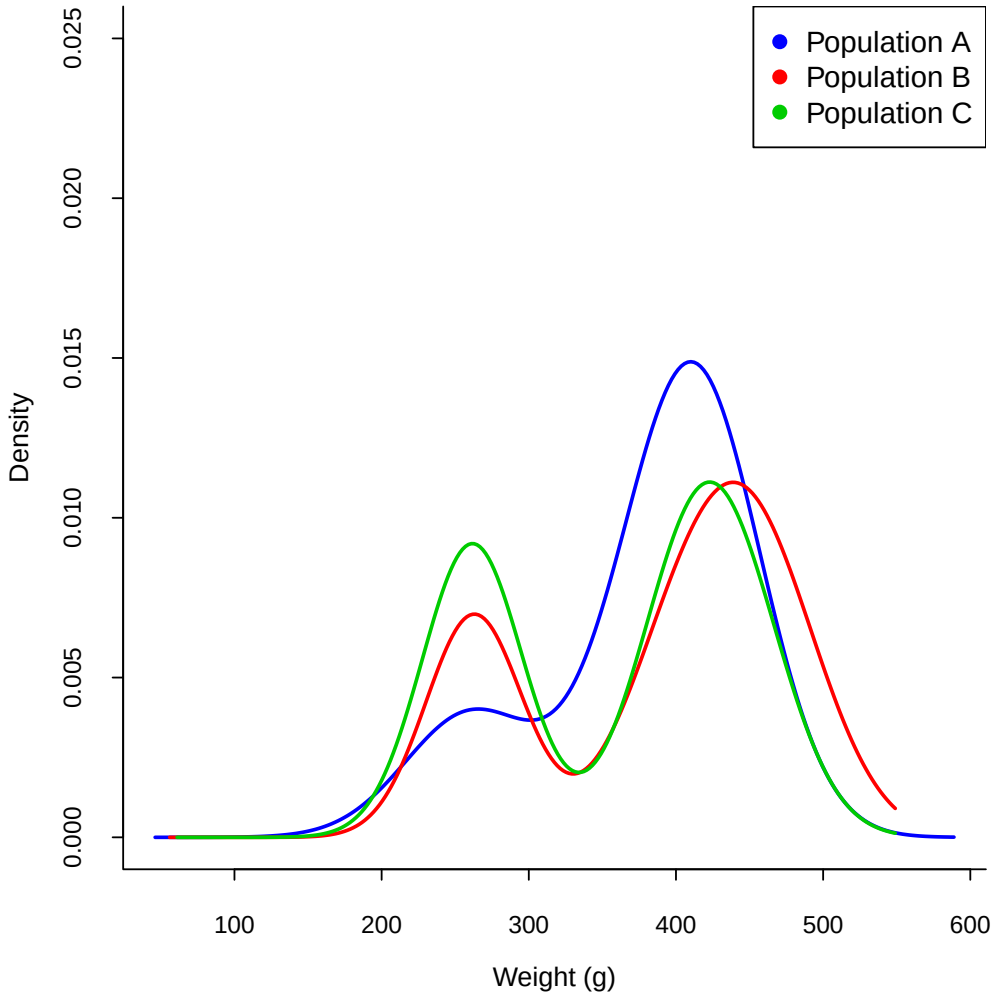


Figure 2.2. Stable weight distribution calculated from the IPMs for populations A, B and C, parameterised from the statistical models that include a single population.

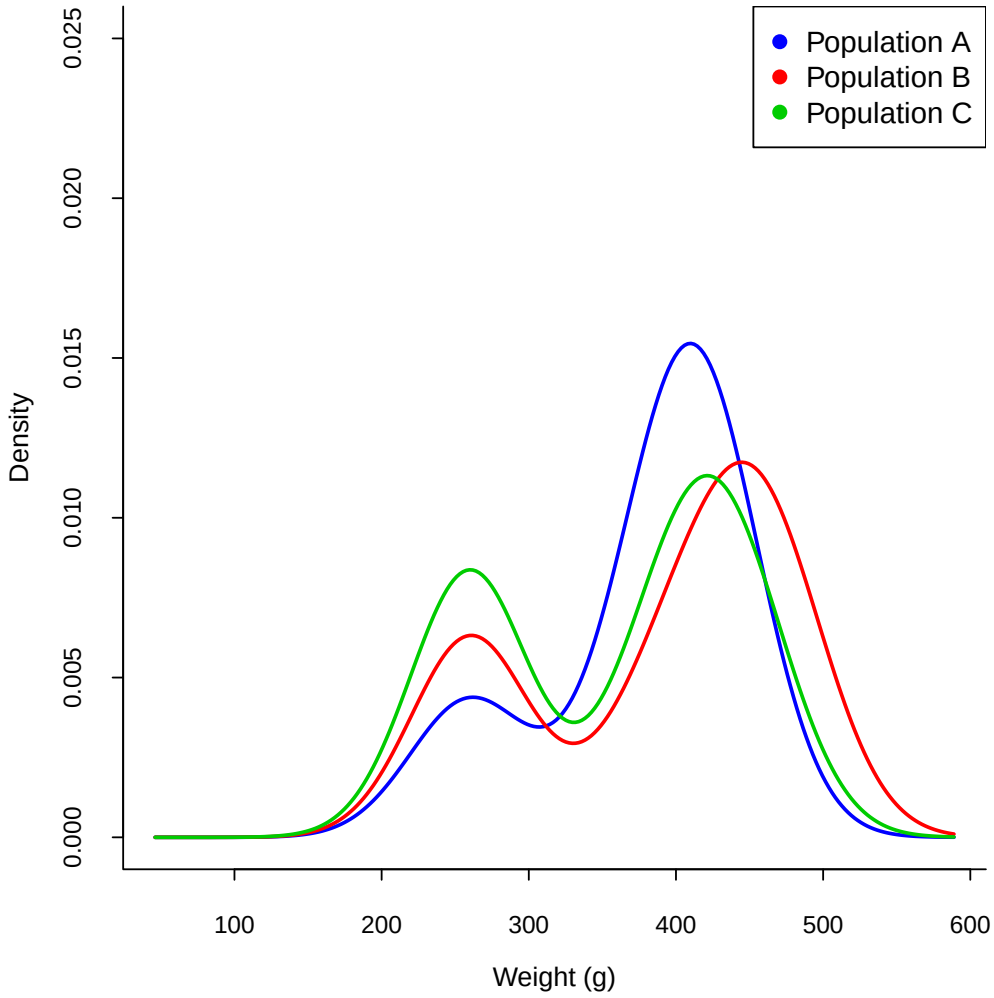


Figure 2.3. Stable weight distribution calculated from the IPMs for populations A, B and C, parameterised from the statisical models that include all populations

The results from the sensitivity analysis are shown in Tables 2.4 for the single population sourced IPMs and Table 2.5 for the multi-population sourced IPMs. We detail here the most interesting results from the analysis. For the single population sourced IPMs, increasing the reproduction terms for the three populations caused an increase in the mean reproductive rate and λ but a decrease in the mean litter size and mean recruitment rate, the strongest effect being from an increase in the weight term on the mean reproductive weight. The effect of increasing the repro-

ductive terms was strongest for populations A and C. An increase in the offspring recruitment terms caused an increase in the mean weight and a slight increase in λ but a decrease in mean reproductive rate, mean litter size, mean offspring weight and mean recruitment rate, the strongest effect being on the mean weight from an increase in the weight term. The strongest impact of increasing the offspring recruitment terms was on population B. An increase in the survival terms caused an increase in λ, mean reproductive rate, mean litter size, mean offspring weight and mean recruitment rate for populations B and C, but the effect was very weak for population A. For the IPMs sourced from the multi population models, increasing the reproduction terms affected the same estimates as the single population IPMs, except that the strength of the effect was the same for the three populations. Increasing the offspring recruitment terms also affected the same estimates as the single population sourced IPMs but the strength of the effect was lower across the three populations. The estimates affected by an increase in the survival terms was also similar to the single population sourced IPMs but again the strength of the effect was much lower.

Table 2.3. Population estimates calculated from the raw data and the IPMs parameterised from the one and multiple population statistical models. For the IPMs, the mean and σ calculated using the eigen function. The SE is calculated by bootstrapping the data and re-running the statistical analysis and IPMs through 1,000 iterations.

		One population model			Multi population model			Raw data	
	Pop.	$\overline{x}$	σ	SE	$\overline{x}$	σ	SE	$\overline{x}$	σ
Growth rate λ	A	0.91		0.001	0.91		0.001	0.96	0.44
	B	1.16		0.002	1.18		0.001	1.17	0.28
	C	0.94		0.002	0.96		0.001	1.01	0.35
Weight (g)	A	379.18	75.29	0.095	378.66	73.91	0.093	362.32	83.94
	B	385.96	90.16	0.223	386.41	94.13	0.162	376.78	89.99
	C	358.94	88.33	0.141	358.63	89.85	0.122	363.41	88.61
Reproductive weight (g)	A	417.78	49.04	0.100	416.36	47.12	0.095	414.95	53.42
	B	441.25	53.44	0.200	442.64	55.48	0.215	433.81	58.73
	C	423.88	46.10	0.154	422.56	53.35	0.155	424.60	49.37
Survival rate	A	0.73	0.00	0.001	0.73	0.02	0.001	0.73	0.02
	B	0.83	0.10	0.001	0.84	0.06	0.001	0.83	0.03
	C	0.57	0.08	0.001	0.59	0.03	0.001	0.57	0.03
Reproduction probability	A	0.45	0.23	0.001	0.45	0.23	0.001	0.41	0.02
	B	0.54	0.34	0.001	0.54	0.33	0.001	0.51	0.04
	C	0.47	0.36	0.001	0.47	0.34	0.001	0.48	0.03
Litter size (females)	A	0.83	0.00	0.002	0.83	0.00	0.002	0.83	0.98
	B	1.28	0.00	0.004	1.28	0.00	0.003	1.27	0.99
	C	1.60	0.00	0.003	1.60	0.00	0.003	1.60	1.14
Offspring recruitment rate	A	0.57	0.03	0.004	0.56	0.04	0.002	0.48	0.02
	B	0.41	0.12	0.004	0.56	0.04	0.002	0.48	0.05
	C	0.54	0.04	0.002	0.56	0.04	0.002	0.52	0.03

Table 2.4. Sensitivity analysis of the single population sourced IPMs. The percentage increase in the IPM estimates when increasing each parameter by 1% in isolation. The parameter heading abbreviations are 'I' for the intercept, 'W' for the weight term and 'W^2' for the quadratic term. Blank values in the table are due to the parameter not being significant in the statistical models.

		Survival			Recruitment			Development			Off. Development			Reproduction			Litter size	Inheritance		
Estimate	Pop.	I	W	W^2	I	W	W^2	I	W	W^2	I	W	W^2	I	W	W^2	I	I	W	W^2
Growth rate λ	A	0.22			0.40	0.63	0.24	0.38	0.13		0.01	0.06	0.02	0.80	1.16	0.38	0.03	0.45	0.56	0.29
	B	0.90	2.05	1.04	1.15	2.09	0.97	−0.06	−0.03	−0.07	0.23	0.06		0.40	0.42		0.05	0.20	0.06	
	C	1.58	3.31	1.66	0.16	0.16		−0.01	−0.02	−0.04	0.40	0.04		1.65	2.77	1.24	0.13	0.43	0.47	0.25
Weight (g)	A	0.02			−0.16	−0.25	−0.10	0.67	0.23		0.04	0.17	0.06	−0.32	−0.46	−0.15	−0.01	−0.03	−0.03	−0.02
	B	0.09	0.24	0.14	−0.53	−0.93	−0.43	0.65	0.15	0.21	0.16	0.04		−0.18	−0.19		−0.02	−0.05	−0.01	
	C	0.20	0.45	0.25	−0.06	−0.06		0.68	0.20	0.20	0.26	0.03		−0.57	−0.94	−0.43	−0.04	−0.07	−0.08	−0.04
Reproductive weight (g)	A	0.01			−0.05	−0.08	−0.03	0.77	0.28		0.00	−0.02	−0.01	−0.32	−0.36	−0.08	0.00	−0.07	−0.09	−0.05
	B	0.02	0.10	0.08	−0.18	−0.33	−0.16	0.93	0.23	0.33	−0.07	−0.02		−0.25	−0.22		−0.01	−0.04	−0.01	
	C	0.05	0.16	0.11	−0.02	−0.02		1.03	0.31	0.31	−0.10	−0.01		−0.55	−0.76	−0.24	−0.01	−0.05	−0.06	−0.03
Survival Rate	A	0.27			0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	B	1.17	2.65	1.33	−0.15	−0.25	−0.11	−0.34	−0.08	−0.13	0.24	0.06		−0.05	−0.05		−0.01	0.02	0.01	
	C	2.23	4.64	2.32	−0.02	−0.02		−0.58	−0.18	−0.18	0.39	0.04		−0.17	−0.28	−0.13	−0.01	0.04	0.04	0.02
Reproduction Probablity	A	0.05			−0.43	−0.68	−0.26	1.90	0.66		0.06	0.29	0.10	4.07	5.92	1.91	−0.03	−0.22	−0.27	−0.14
	B	0.23	0.62	0.37	−1.40	−2.49	−1.16	1.52	0.34	0.43	0.25	0.06		1.54	1.61		−0.06	−0.16	−0.05	
	C	0.61	1.31	0.69	−0.17	−0.17		0.85	0.23	0.19	0.41	0.04		4.36	7.31	3.27	−0.13	−0.30	−0.33	−0.18
Litter Size (Female)	A	0.00			0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00
	B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00		0.24	0.00	0.00	
	C	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.47	0.00	0.00	0.00
Offspring weight (g)	A	0.00			0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.80	1.11	0.28
	B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00		0.00	0.83	0.14	
	C	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	1.80	1.16	0.36
Recruitment rate	A	0.00			2.10	4.63	2.43	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	−0.32	−0.18	−0.04
	B	0.00	0.00	0.00	6.47	10.75	4.44	0.00	0.00	0.00	0.00	0.00		0.00	0.00		0.00	1.59	0.28	
	C	0.00	0.00	0.00	0.55	0.62		0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	1.12	0.73	0.23

Table 2.5. Sensitivity analysis of the multi population sourced IPMs. The percentage increase in the IPM estimates when increasing each parameter by 1% in isolation. The parameter heading abbreviations are 'I' for the intercept, 'W' for the weight term and 'W^2' for the quadratic term. Blank values in the table are due to the parameter not being significant in the statistical models.

		Survival			Recruitment			Development			Off. Development			Reproduction			Litter size	Inheritance		
Estimate	Pop.	I	W	W^2	I	W	W^2	I	W	W^2	I	W	W^2	I	W	W^2	I	I	W	W^2
Growth rate λ	A	0.07	0.73	0.44	0.29	0.43	0.15	0.23	0.08		0.03	0.05	0.01	0.93	1.42	0.51	0.03	0.32	0.33	0.17
	B	0.04	0.38	0.23	0.34	0.52	0.18	0.37	0.13		0.09	0.13	0.04	0.65	0.99	0.36	0.04	0.42	0.47	0.26
	C	0.09	0.89	0.52	0.49	0.74	0.26	0.31	0.09		0.11	0.15	0.05	1.03	1.50	0.52	0.05	0.59	0.63	0.33
Weight (g)	A	0.01	0.07	0.04	−0.12	−0.17	−0.06	0.66	0.23		0.08	0.11	0.03	−0.36	−0.55	−0.20	−0.01	−0.03	−0.03	−0.02
	B	0.00	0.04	0.03	−0.17	−0.25	−0.09	0.61	0.22		0.11	0.15	0.05	−0.31	−0.47	−0.18	−0.02	−0.05	−0.05	−0.03
	C	0.01	0.12	0.08	−0.16	−0.23	−0.08	0.45	0.15		0.14	0.20	0.06	−0.32	−0.47	−0.17	−0.02	0.00	0.00	0.00
Reproductive weight (g)	A	0.00	0.03	0.02	−0.04	−0.05	−0.02	0.76	0.28		−0.01	−0.02	0.00	−0.34	−0.39	−0.10	0.00	−0.05	−0.05	−0.03
	B	0.00	0.01	0.01	−0.06	−0.09	−0.03	0.75	0.29		−0.02	−0.03	−0.01	−0.39	−0.49	−0.14	−0.01	−0.08	−0.09	−0.05
	C	0.00	0.06	0.04	−0.05	−0.08	−0.03	0.66	0.23		−0.03	−0.05	−0.01	−0.43	−0.52	−0.14	−0.01	−0.08	−0.09	−0.05
Survival Rate	A	0.08	0.86	0.52	0.01	0.01	0.00	−0.17	−0.06		0.01	0.01	0.00	0.02	0.03	0.01	0.00	0.02	0.02	0.01
	B	0.05	0.48	0.29	−0.04	−0.06	−0.02	0.05	0.01		0.06	0.08	0.02	−0.08	−0.12	−0.04	0.00	0.02	0.02	0.01
	C	0.12	1.22	0.71	0.01	0.02	0.01	−0.20	−0.07		0.03	0.04	0.01	0.03	0.04	0.02	0.00	0.05	0.05	0.03
Reproduction Probablity	A	0.01	0.18	0.12	−0.31	−0.46	−0.16	1.79	0.62		0.13	0.18	0.05	4.62	7.07	2.54	−0.03	−0.17	−0.18	−0.09
	B	0.01	0.11	0.08	−0.43	−0.64	−0.22	1.08	0.37		0.17	0.24	0.07	2.44	3.73	1.38	−0.05	−0.24	−0.26	−0.15
	C	0.03	0.36	0.22	−0.47	−0.70	−0.24	1.05	0.33		0.22	0.32	0.10	2.61	3.82	1.34	−0.05	−0.23	−0.24	−0.13
Litter Size (Female)	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00
	B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00
	C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.00	0.00	0.00
Offspring weight (g)	A	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.60	0.82	0.20
	B	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.60	0.82	0.20
	C	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.60	0.82	0.20
Recruitment rate	A	0.00	0.00	0.00	1.50	2.77	1.17	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.74	0.39	0.10
	B	0.00	0.00	0.00	1.50	2.77	1.17	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.74	0.39	0.10
	C	0.00	0.00	0.00	1.50	2.77	1.17	0.00	0.00		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.74	0.39	0.10

Discussion

Comparison of population dynamics and demographic rates are often made between different species, but comparing two or more populations of the same species, can be informative in assessing the role of the environment, phenotypic variation, and genetic variation of the species (Murie, 1985). Understanding the ecological differences between populations of the same species is important as it gives us an idea how accurate our estimates will be when comparing between species, particularly when conducting comparative analyses and meta-analyses across multiple species. In this paper we constructed Integral Projection Models (IPMs) to compare three populations of ground squirrels to determine if there were any differences between populations living in similar habitats, at similar altitudes. Previous work has found differences in the life histories of ground squirrel populations living at different altitudes (Murie, 1985), but very little information exists on the differences at similar altitudes. Of course, differences in life histories can also be caused by annual variation in climate, in addition to differences due to the habitat. Previous studies have shown that rainfall can affect the food resources that are available to squirrels. Due to their short annual active period, this can have a large impact on their ability to build resources to survive hibernation (Dobson et al., 2016). Additionally the depth of the snow pack can impact the microclimate of the hibernacula, with deeper snow decreasing the energetic costs of hibernation (Dobson and Murie, 1987). As the data for the three populations were collected at different times, our estimates are going to encapsulate temporal effects in addition to spatial effects on population dynamics and demographic rates.

The basic IPM is constructed from functions that estimate the survival, development and reproduction of a population. In this case we have used linear and

generalised linear models to parameterise these functions, but other models can and have been used. The very act of constructing the statistical models for the IPM functions can offer insight into the population dynamics of the species under analysis. So we will consider the statistical models in addition to the estimates from the IPMs.

Both sets of IPMs (single and mulit-population sourced) provide estimates that are very close to the estimates from the raw data. In the following sections we will consider the estimates for survival, development and reproduction by comparing the three populations and what is already known about Columbian ground squirrels from previous studies.

Survival

Survival of the population is split into two functions in the IPM due to the offspring being censused at a later time than the rest of the population. This gives us two estimates, the survival rate and the recruitment (offspring survival) rate. Comparing these two rates across the three populations, the recruitment rate was lower compared to the survival rate across the three populations. This is in accordance with what has been found in previous studies (Boag and Murie, 1981b; Dobson and Murie, 1987; Neuhaus and Pelletier, 2001; Zammuto, 1987), with mortality being higher in the first year of life compared to older individuals. Looking at the differences between the populations, population B had a higher survival rate but a lower recruitment rate than the other two populations. This could suggest that the environment and climate favoured the survival of adults over the recruitment of offspring to a greater extent than the other two populations. The site for population B has a big sun-exposed slope which may beneficial for adults in spring, the snow clearing earlier, but this does not explain the low offspring survival. Other studies

have suggested that late breeding females still had access to high-quality forage up to the weaning date (Bennett, 1999), but after the emergence of the offspring from the natal burrow the quality of the forage would have diminished. As offspring have a shorter time to build up fat reserves for hibernation they are much more reliant on the availability and quality of food resources (Dobson and Kjelgaard, 1985a). Timing of rains and snowstorms can influence when females breed; late breeding can mean that offspring have less time to accumulate resources (Neuhaus et al., 1999). Recruitment rate can also be affected by the presence of the mother after weaning, offspring that suffer the loss of the mother after weaning (emergence from natal burrow) have a much lower chance of survival (King et al., 1991). Additionally infanticide has been observed in populations of Columbian ground squirrels (Stevens, 1998). Whilst the presence of kin has been suggested to increase the survival of offspring in mammals (Clutton-Brock, 1988) and Columbian ground squirrels do allow daughters to share home ranges, King et al. (1991) found no evidence for increased survival of offspring in their study due to kin grouping, whilst other studies have found an increase in reproductive success when kin are present (Dobson et al., 2012; Neuhaus et al., 2004; Viblanc et al., 2010). Any or all these factors could be responsible for the differences the models are exhibiting, but there are also a number of additional drivers that can affect survival rate. Reproduction is often considered to have a survival cost associated with it, but for Columbian ground squirrels conflicting results have been found, with a number of studies finding no evidence (Hare and Murie, 1992; Murie and Dobson, 1987), whilst later studies have found a cost (Neuhaus, 2000a,b). Neuhaus and Pelletier (2001) found that mothers that weaned young had a higher mortality than those that lost their litter during lactation, they also suggested that mothers may forage further away from their burrows to offset the costs of reproduction, but in doing so,

may increase the chance of predation. Additionally population density has been found to effect maternal survival (Froy et al., 2016) and possibly offspring survival (Boag and Murie, 1981a; Elliott and Flinders, 1991). Michener (1977) found for Richardson's ground squirrels (*Urocitellus richardsonii*) that breeding success is associated with a later time of entry into hibernation, with squirrels foraging longer to increase their resources, leading to an increased chance of predation, it may be possible that this also applies to Columbian ground squirrels. Survival during hibernation is the safest time for adult Columbian ground squirrels, the one exception is in years when a badger visits in the winter, this happened in 2008 and 2009 and had a large impact on population C and a to lesser extent population A and B (Neuhaus, 2017).

The non-significant effect of weight on survival for the single population A model requires consideration. Squirrels have been found to be heavier at lower elevations at a younger age, but with higher adult survival at higher elevations (Zammuto and Millar, 1985), indicating that an increased survival is not necessarily linked to an increased weight for Columbian ground squirrels. As there is little difference in altitude between the sites we would normally expect the three sites to exhibit similar survival trends but this is clearly not the case. Populations A's site had a different cattle grazing management strategy at the beginning of the study and this could be an explanation for the differences. Cattle grazing of grasslands can promote increased growth and improve the quality of the forage (Burton et al., 1964), but at higher intensity it can severely reduce the amount of forage available (Huntly, 1991). Without additional data on the plant composition and biomass it is not possible to draw any conclusions but is a possible area of further study.

From the sensitivity analysis, population C was the most sensitive to an increase in the parameters for survival on the survival rate and the population growth rate λ, possibly indicating that survival of the adults (yearlings and above) is a limiting factor for population C. The sensitivity analysis for recruitment confirms what we have already discussed, with population B showing the largest increase in λ and recruitment rate when increasing the parameters for recruitment, indicating that recruitment of offspring may be the limiting factor for this population.

Reproduction

Reproduction is represented in the IPM by three functions, reproductive probability: the chance that a mother will wean at least one offspring, litter size: the number of female offspring weaned and inheritance: how mother's weight determines the weight of the weaned offspring. Possibly the most the striking result for reproduction from the statistical analysis is the lack of affect that mother's weight had on the litter size for the three populations. This is contrary to what has been observed in many other studies (Dobson and Kjelgaard, 1985a,b; Murie and Dobson, 1987). Our contradictory results may be due to us looking at only female litter size, not including males in the analysis. Columbian ground squirrels have smaller litter sizes and mature later than other species of ground squirrel (Murie et al., 1980). Litter size may, at least in part, be driven by the quality of the forage available (Murie et al., 1980). The mother's weight we are using as a predictor for litter size is the weight at emergence from hibernation and does not represent the weight that the females are able to obtain during the breeding season. This may offer perhaps one explanation why weight is not a significant predictor for litter size in this case. Another explanation is that weight at emergence from hibernation may not be a good indicator of body condition, as weight also encapsulates structural size of the individual in addition to the body condition (Skibiel et al.,

2009). Although other studies have found a significant effect of spring weight on litter size (Dobson et al., 1999; Risch et al., 1995; Rubach et al., 2016; Skibiel et al., 2009), it has been suggested that the energy requirements for gestation and lactation comes mainly from the resources that the mother obtains on a daily basis (income breeder) (Broussard et al., 2005; Dobson et al., 1999; Risch et al., 1995; Rubach et al., 2016). There is quite a difference in litter sizes between the three populations, possibly suggesting that the resources available to the breeding females differed. The lack of changes observed in the sensitivity analysis, for litter size, to anything other than the litter size intercept parameter, is due to weight not being significant in the statistical models. A change in the weight distribution in the population will therefore not impact the litter size estimate from the IPMs. There were only small changes to the population growth rate λ in the sensitivity analysis, when increasing the litter size parameters, for the three populations, indicating that other factors were more important.

Care has to be taken when comparing the estimates for reproductive probability with the reproductive success mentioned in other studies. Previous studies have measured reproductive success as being the number of offspring to emerge from hibernation in the spring after birth (King et al., 1991). But in our study the period after weaning (emergence from natal burrow) to the next spring is represented by the recruitment rate, with the litter size also being separated. It should be noted, in previous studies the period after weaning is found to account for much of the variance observed in their reported reproductive success (King et al., 1991). So the reproductive probability in this study is the chance the female will mate, gestate and wean at least one offspring that will emerge from the natal burrow. As mentioned in the methods section we included a cut-off point for reproduction

probability, below which a female would not reproduce. This cut-off has been observed in a number of previous studies (Neuhaus et al., 2004; Neuhaus, 2000b), also indicating that the age of primiparity is highly influenced by body mass. Population B had the highest reproduction probability of the three populations, but the other two populations showed a greater sensitivity to increase in the reproduction parameters to reproduction and population growth λ. There are a number of possible reasons for the difference observed between the three populations in the reproductive probability; the most obvious would be the differences in the environmental factors that affect the weight of individuals and available resources (King et al., 1991), including temporal effects such as adverse weather conditions (Neuhaus et al., 2004; Neuhaus et al., 1999). It has been suggested that nearly all females of breeding age will attempt to breed (Rubach et al., 2016), as the highest cost of reproduction is during the period of lactation (Clutton-Brock et al., 1989). Females could then alter their reproductive output during the lactation phase of breeding by adjusting the nourishment given to the offspring (Neuhaus, 2000b). It has been suggested that total litter loss during the lactation phase, may be a consequence of female body condition (Neuhaus, 2000b). Finally increasing population density has been shown to negatively impact reproduction, although density affects Columbian ground squirrels to a much lesser extent than environmental factors (Neuhaus et al., 2004; Neuhaus et al., 1999).

For the inheritance statistical models, population A, C and the multi population models showed a higher offspring weight for the extremes of mother's spring weight. Although this could be explained by mothers of lower weight having smaller litters, the lack of significance of mother's weight on litter size does not support this. Previous studies have found a strong positive influence of a mother's spring

body mass on the quality of the offspring (Dobson et al., 1999; Risch et al., 1995). Skibiel et al. (2009) found that mothers in better condition raised offspring that were heavier at weaning and grow faster during lactation. They also found that litter size had a negative impact on the weight at weaning, growth during lactation and weight at birth. As already discussed, Columbian ground squirrels have been considered income breeders (Rubach et al., 2016), therefore the affects of the environment and climate are going to have an impact on the ability of the mother to provide nourishment to her offspring during gestation and lactation. When comparing the three populations, the single population sourced IPMs suggested that population B had a higher mean reproductive weight but a lower mean offspring weight than the other two populations. But the multi-population statistical model for inheritance found no significant difference between the three populations. It is therefore possible that the inclusion of other factors such as total litter size (including males) and environmental measurements in the inheritance statistical models and function is needed. It should be noted that the estimates from the single population source IPM for offspring weight for population B, was significantly lower than the estimates for population A. This could indicate that population B females were investing less in reproduction and more in their own body mass compared to population A.

Development

Development is split into two functions in the IPM, one covering the development of offspring from first emergence from the natal burrow to first emergence after hibernation in the year after birth. And the other covering the development of yearlings and older, from one emergence from hibernation to the next emergence in the following year. From the IPM estimates, females tend to be heavier and reproduced at a heavier weight in population B compared to the two other popu-

lations although the variation in these estimates meant they were not significantly different. Columbian ground squirrels are not considered fully grown in terms of structure and body mass until at least age three (Boag and Murie, 1981b). From previous studies we know that Columbian ground squirrels have only a short period to acquire the resources needed to grow, reproduce and survive hibernation to the following year (Dobson et al., 1992; Murie and Harris, 1982). It has been shown that females that failed to breed or had smaller litters in one year were in better body condition at spring emergence the following year (Rubach et al., 2016). As already mentioned, Columbian ground squirrels are income breeders, but for surviving hibernation they rely on stored fat resources acquired before hibernation (Boag and Murie, 1981b; Broussard et al., 2005; Murie and Harris, 1982). The availability and quality of food resources therefore has a large impact on the development of both offspring and mature individuals (Dobson and Kjelgaard, 1985a). With the availability and quality being driven by the environment and climate (Dobson and Murie, 1987).

IPM construction

When constructing the IPMs it was important to have a good understanding of the sampling methodologies used (Ellner et al., 2016). For example, the different timing of the census of the offspring in this study necessitated the use of separate survival and development functions for the offspring. When constructing the IPMs for this study we kept them as simple as the biology of the species allowed. There is a number of possible additions that could be made to the models on what we know about the ecology of Columbian ground squirrels. From previous studies we know that climate could play a large role in observed population dynamics; including a random effect for year in the statistical models would allow

for the variation between years, for each population, to be taken into account. But this would increase the complexity of the analysis considerably, as eigenanalysis could not be used directly and the population would need to be simulated (Ellner et al., 2016). As we have mentioned survival, development and reproduction can all be affected by reproductive success. Including an additional covariant, breed successfully in previous year, in the statistical models would allow for this effect to be investigated. For reproduction, the size of the litter is known to impact the quality of the offspring (Neuhaus, 2000b), so including this as a covariant in the offspring development model would allow for the effect to be investigated. Finally, as we know there is difference in reproduction and development of individuals due to their age, with individuals not reaching maturity until at least three years old (Boag and Murie, 1981b). Including age as a covariant in the models would provide information on the impact of age on survival, development and reproduction of the populations.

In conclusion IPMs provide a useful tool to compare populations, with even a basic IPM, as we have produced here, providing useful insights into the population dynamics of a species and the differences between populations. Although the estimates produced from an IPM can be extracted from the raw data, the IPM has the advantage of taking into account the interconnected nature of the functions. For example, as can be seen from the sensitivity analysis, an increase in the reproduction function causes a decrease in the survival rate of the population, due to a higher proportion of individuals in the population being of a lower weight and therefore a lower survival. Although in this study some of the estimates from the IPMs are not significantly different between the populations, there does seem to be a difference between population A and B in terms of reproduction, although care is

needed as the multi-population statistical models found no difference between the populations for offspring development. It possible that differences in predation, richness of habitat, population density, kin structure, infanticide, availability of resource and the interacting effect of climate between sites can lead to the differences in survival, reproduction and development (Dobson and Kjelgaard, 1985a). In the end we can not really tell for sure why these three populations differ, the most likely explanation as we have already alluded to, is the temporal, environmental and micro climatic differences between the populations, directly affecting the squirrels or indirectly via the availability and quality of food resources. Most life history studies use 'average' demographic rates for a population when examining differences between species, but the work here suggests that (sub)populations of the same species can and do differ in time and space, with associations between the demographic rates and phenotypes. Therefore any analysis based on one population or short term study can provide mis-leading information.

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Supporting Information

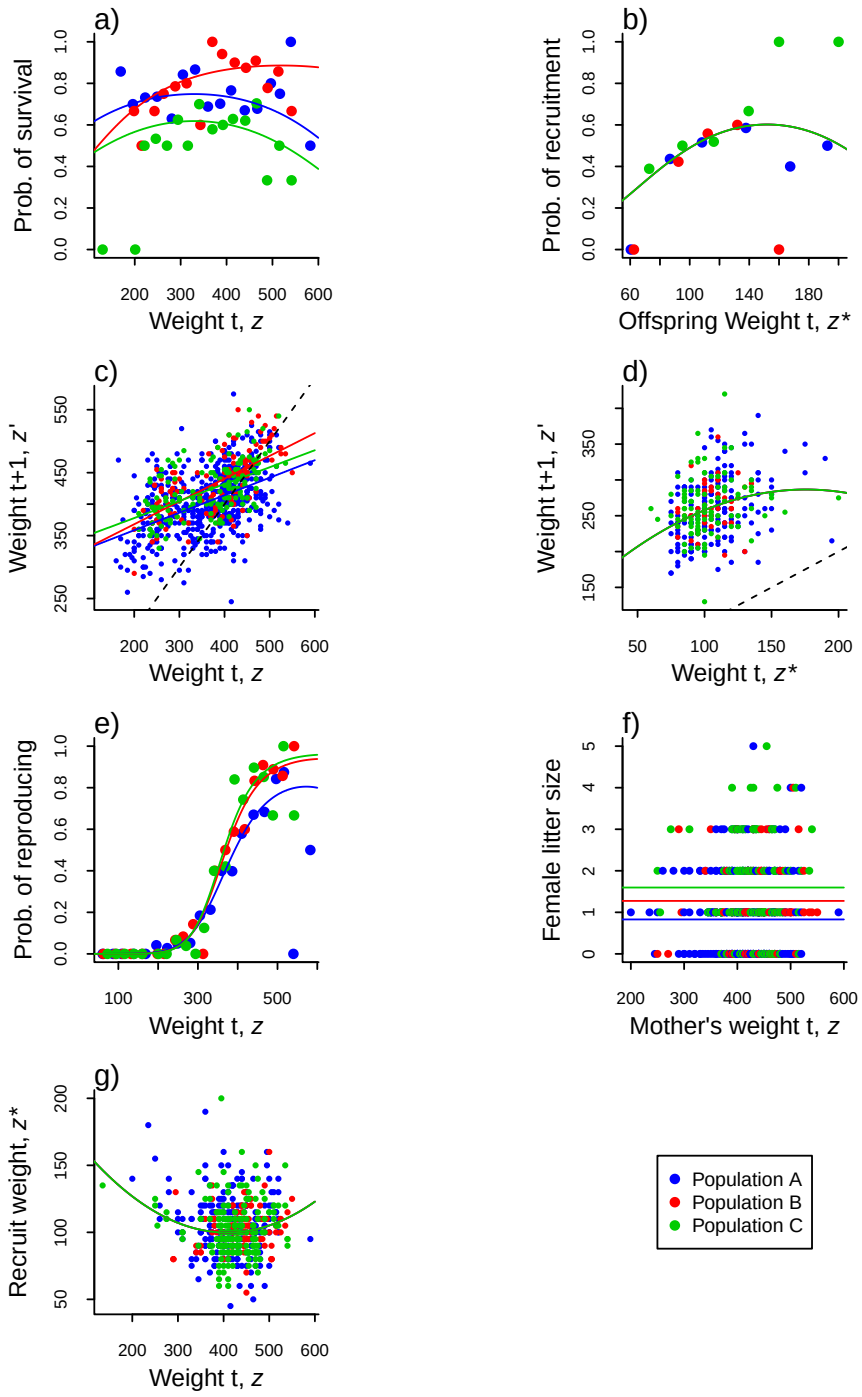


Figure S2.1. Plots of the all populations models against the data. a) survival, b) offspring recruitment c) growth, d) offspring growth, e) reproduction, f) female litter size and g) recruit weight. For survival, offspring recruitment and reproduction the data represented by the dots is the proportion summarised into 20 weight classess for each population. For growth and offspring growth the black dashed line represents the point of zero growth.

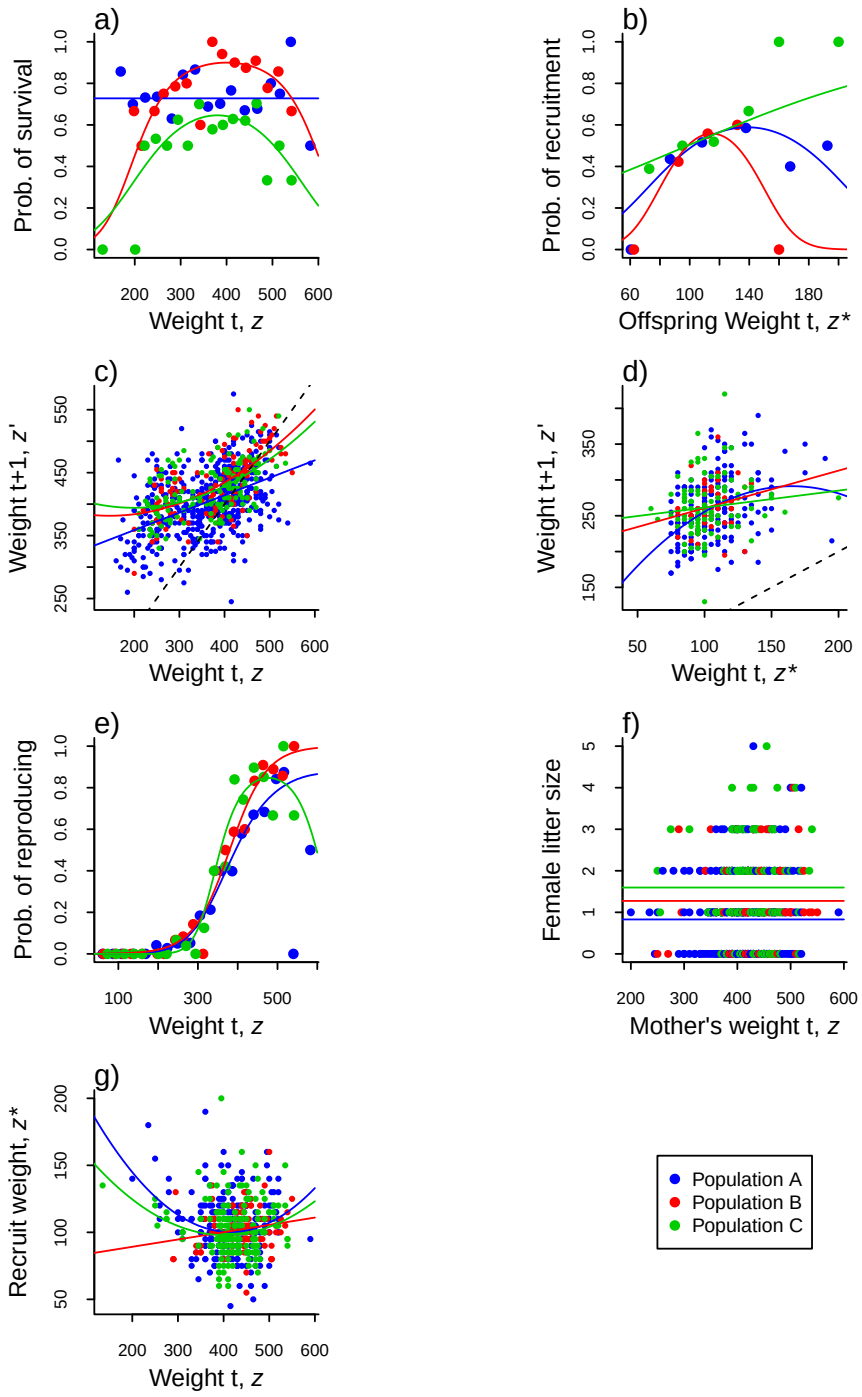


Figure S2.2. Plots of the separate population models against the data. a) survival, b) offspring recruitment c) growth, d) offspring growth, e) reproduction, f) female litter size and g) recruit weight. For survival, offspring recruitment and reproduction the data represented by the dots is the proportion summarised into 20 weight classess for each population. For growth and offspring growth the black dashed line represents the point of zero growth.

Table S2.1. Comparision of the statisical models for population A

Model	df	AIC	DAIC
Survival			
survived ∼ 1	1.00	875.35	0.00
survived ∼ weight	2.00	877.12	1.77
survived ∼ weight + weight2	3.00	878.98	3.63
Offspring recruitment			
survived ∼ weight + weight2	3.00	566.01	0.00
survived ∼ weight	2.00	567.90	1.90
survived ∼ 1	1.00	575.45	9.45
Growth			
weightt1 ∼ weight	2.00	4086.96	0.00
weightt1 ∼ weight + weight2	3.00	4088.95	1.99
weightt1 ∼ 1	1.00	4210.98	124.02
Offspring Growth			
weightt1 ∼ weight + weight2	3.00	1520.13	0.00
weightt1 ∼ weight	2.00	1523.13	3.00
weightt1 ∼ 1	1.00	1562.58	42.45
Reproduction			
Repr ∼ weight + weight2	3.00	784.60	0.00
Repr ∼ weight	2.00	786.30	1.70
Repr ∼ 1	1.00	998.37	213.77
Litter size			
ltsizeF ∼ 1	1.00	754.46	0.00
ltsizeF ∼ weight + weight2	3.00	756.35	1.89
ltsizeF ∼ weight	2.00	756.42	1.96
Recruit weight			
wtoff ∼ wtmother + wtmother2	3.00	1524.20	0.00
wtoff ∼ wtmother	2.00	1537.76	13.56
wtoff ∼ 1	1.00	1538.32	14.12

Table S2.2. Comparision of the statisical models for population B

Model	df	AIC	DAIC
Survival			
survived ∼ weight + weight2	3.00	141.02	0.00
survived ∼ weight	2.00	143.68	2.66
survived ∼ 1	1.00	146.13	5.10
Offspring recruitment			
survived ∼ weight + weight2	3.00	144.23	0.00
survived ∼ 1	1.00	144.55	0.32
survived ∼ weight	2.00	145.03	0.81
Growth			
weightt1 ∼ weight + weight2	3.00	944.17	0.00
weightt1 ∼ weight	2.00	945.19	1.02
weightt1 ∼ 1	1.00	1007.48	63.31
Offspring Growth			
weightt1 ∼ weight	2.00	348.92	0.00
weightt1 ∼ 1	1.00	349.30	0.38
weightt1 ∼ weight + weight2	3.00	349.83	0.91
Reproduction			
Repr ∼ weight	2.00	142.96	0.00
Repr ∼ weight + weight2	3.00	144.93	1.98
Repr ∼ 1	1.00	219.59	76.63
Litter size			
ltsizeF ∼ 1	1.00	222.77	0.00
ltsizeF ∼ weight	2.00	224.35	1.58
ltsizeF ∼ weight + weight2	3.00	226.13	3.35
Recruit weight			
wtoff ∼ wtmother	2.00	562.09	0.00
wtoff ∼ 1	1.00	562.90	0.82
wtoff ∼ wtmother + wtmother2	3.00	563.56	1.47

Table S2.3. Comparision of the statisical models for population C

Model	df	AIC	DAIC
Survival			
survived ∼ weight + weight2	3.00	347.63	0.00
survived ∼ weight	2.00	350.62	2.99
survived ∼ 1	1.00	354.05	6.41
Offspring recruitment			
survived ∼ weight	2.00	284.22	0.00
survived ∼ weight + weight2	3.00	285.38	1.17
survived ∼ 1	1.00	290.04	5.83
Growth			
weightt1 ∼ weight + weight2	3.00	1028.73	0.00
weightt1 ∼ weight	2.00	1029.86	1.13
weightt1 ∼ 1	1.00	1098.77	70.04
Offspring Growth			
weightt1 ∼ weight	2.00	751.84	0.00
weightt1 ∼ weight + weight2	3.00	753.26	1.42
weightt1 ∼ 1	1.00	774.74	22.89
Reproduction			
Repr ∼ weight + weight2	3.00	208.11	0.00
Repr ∼ weight	2.00	216.94	8.84
Repr ∼ 1	1.00	359.28	151.17
Litter size			
ltsizeF ∼ 1	1.00	378.62	0.00
ltsizeF ∼ weight	2.00	380.55	1.93
ltsizeF ∼ weight + weight2	3.00	382.37	3.75
Recruit weight			
wtoff ∼ wtmother + wtmother2	3.00	1162.62	0.00
wtoff ∼ 1	1.00	1169.17	6.55
wtoff ∼ wtmother	2.00	1170.77	8.15

Table S2.4. Comparision of the statisical models that includes the three populations.

Model	df	AIC	DAIC
Survival			
survived ∼ weight + pop + weight2 + weight:pop	7.00	1575.90	0.00
survived ∼ weight + pop + weight:pop	6.00	1579.57	3.67
survived ∼ weight + weight2	3.00	1597.61	21.71
survived ∼ weight	2.00	1614.46	38.56
survived ∼ pop	3.00	1616.46	40.56
survived ∼ 1	1.00	1653.68	77.78
Offspring recruitment			
survived ∼ weight + weight2	3.00	989.61	0.00
survived ∼ weight	2.00	989.97	0.36
survived ∼ weight + pop + weight2 + weight:pop	7.00	996.77	7.16
survived ∼ weight + pop + weight:pop	6.00	997.15	7.54
survived ∼ 1	1.00	1006.90	17.29
survived ∼ pop	3.00	1010.04	20.43
Growth			
weightt1 ∼ weight + pop + weight:pop	6.00	6071.43	0.00
weightt1 ∼ weight + pop + weight2 + weight:pop	7.00	6071.90	0.46
weightt1 ∼ weight + weight2	3.00	6113.99	42.55
weightt1 ∼ weight	2.00	6115.27	43.84
weightt1 ∼ pop	3.00	6322.36	250.93
Offspring Growth			
weightt1 ∼ weight + weight2	3.00	2624.56	0.00
weightt1 ∼ weight + pop + weight2 + weight:pop	7.00	2624.94	0.39
weightt1 ∼ weight	2.00	2627.40	2.85
weightt1 ∼ weight + pop + weight:pop	6.00	2628.62	4.07
weightt1 ∼ pop	3.00	2694.13	69.58
Reproduction			
Repr ∼ weight + pop + weight2 + weight:pop	7.00	1139.15	0.00
Repr ∼ weight + pop + weight:pop	6.00	1146.20	7.06
Repr ∼ weight + weight2	3.00	1147.64	8.50
Repr ∼ weight	2.00	1153.46	14.32
Repr ∼ pop	3.00	1577.23	438.09
Litter size			
ltsizeF ∼ pop	3.00	1355.85	0.00
ltsizeF ∼ weight + pop + weight:pop	6.00	1361.32	5.47
ltsizeF ∼ weight + pop + weight2 + weight:pop	7.00	1362.22	6.38
ltsizeF ∼ weight	2.00	1401.46	45.61
ltsizeF ∼ weight + weight2	3.00	1402.16	46.31
Recruit weight			
wtoff ∼ wtmother + wtmother2	3.00	3261.54	0.00
wtoff ∼ wtmother + pop + wtmother2 + wtmother:pop	7.00	3264.75	3.21
wtoff ∼ wtmother	2.00	3282.82	21.28
wtoff ∼ pop	3.00	3283.90	22.36
wtoff ∼ wtmother + pop + wtmother:pop	6.00	3284.65	23.11

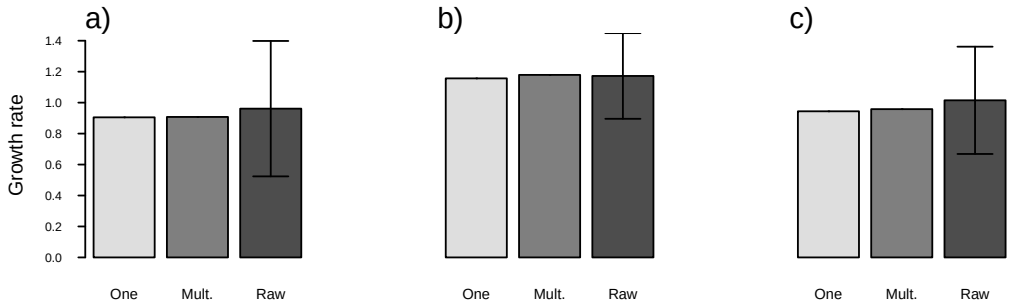


Figure S2.3. Population growth rate estimates from the IPM parameterised from both the single and the multiple population statistical models, compared against the raw values from the data. The error bars for the raw data represent the standard deviation. It is not possible to calculate the standard deviation of the growth rate for the IPMs as it is a population level estimate.

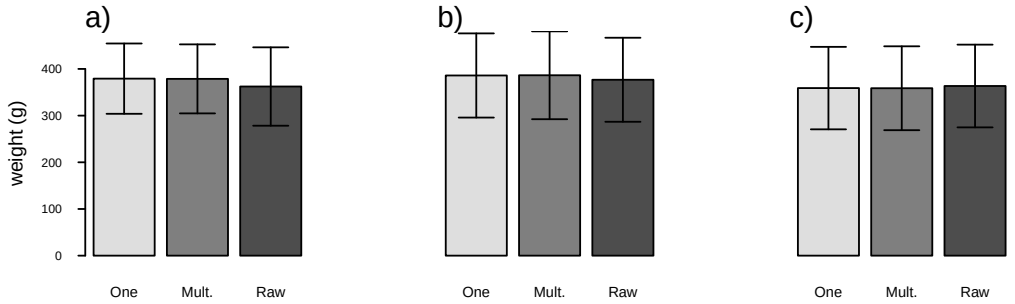


Figure S2.4. Weight estimates from the IPM parameterised from both the single and the multiple population statistical models, compared against the raw values from the data. The error bars represent the standard deviation.



Figure S2.5. Reproductive weight estimates from the IPM parameterised from both the single and the multiple population statistical models, compared against the raw values from the data. The error bars represent the standard deviation.

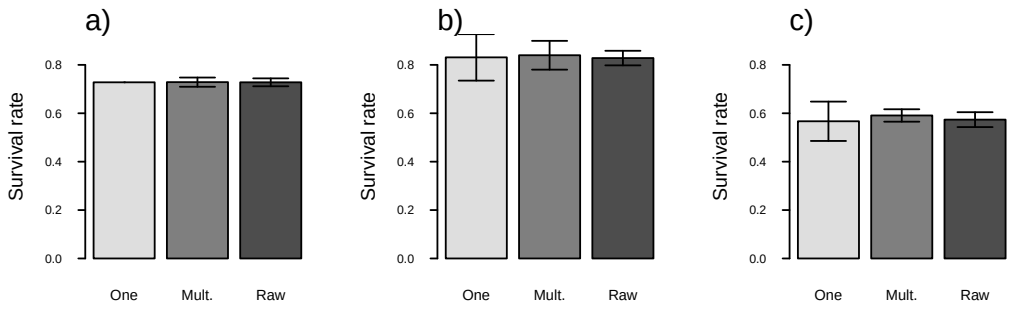


Figure S2.6. Survival rate estimates from the IPM parameterised from both the single and the multiple population statistical models, compared against the raw values from the data. The error bars represent the standard deviation.



Figure S2.7. Reproductive probablity estimates from the IPM parameterised from both the single and the multiple population statistical models, compared against the raw values from the data. The error bars represent the standard deviation.

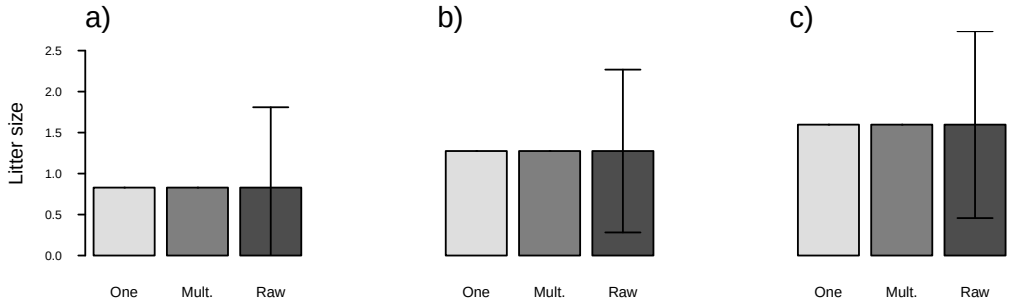


Figure S2.8. Litter size estimates from the IPM parameterised from both the single and the multiple population statistical models, compared against the raw values from the data. The error bars represent the standard deviation.

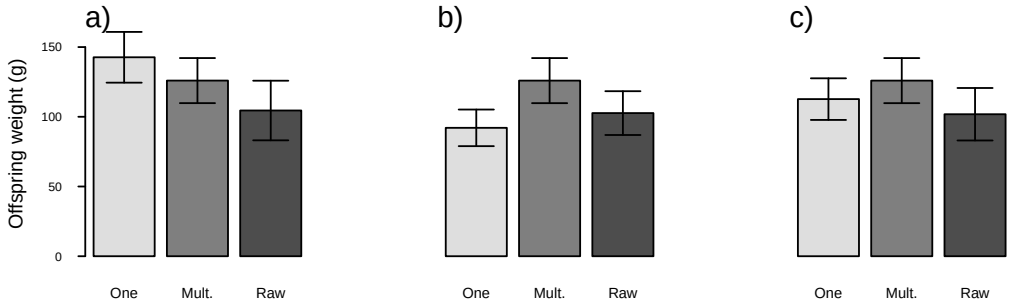


Figure S2.9. Offspring weight estimates from the IPM parameterised from both the single and the multiple population statistical models, compared against the raw values from the data. The error bars represent the standard deviation.

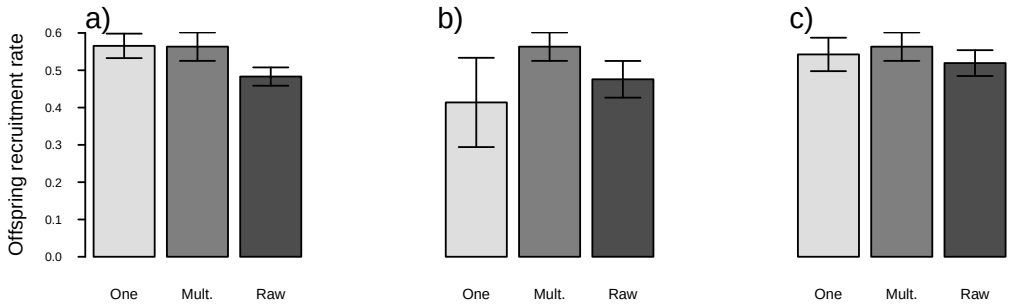


Figure S2.10. Offspring recruitment rate estimates from the IPM parameterised from both the single and the multiple population statistical models, compared against the raw values from the data. The error bars represent the standard deviation.

3

Life history variation among three populations of Columbian ground squirrels (*Urocitellus columbianus*)

Running head

Life history variation among three populations

Title

Life history variation among three populations of Columbian ground squirrels (*Urocitellus columbianus*)

Authors

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Abstract

We showed in the previous chapter that three populations of Columbian ground squirrel (*Urocitellus columbianus*) living in similar can differ in their population dynamics. In this chapter we ask what is driving these differences between the three populations. We took the Integral projection models (IPMs) constructed in the previous chapter, and used these to determine which demographic and trait transition functions are driving the differences between the three populations of Colombian ground squirrels. We used a form of perturbation analysis to quantify the changes in the population level estimates from the IPM when swapping the functions between the three population IPMs. The adult survival function was found to be the main contributor to majority of differences observed in the IPM estimates between the three populations, but with the inheritance function having a larger impact on the offspring estimates.

Introduction

A primary aim of population ecology is to understand why populations of animals fluctuate in size with time. Comparative demography addresses this question by taking methods developed to study single populations and using them to look for patterns across space (Adriaensen and Dhondt, 1990), time (Ozgul et al., 2010) or species (Armitage, 1981; Hansson, 1971). This work has revealed that species life history fall on a fast-slow continuum, with some species living for many years with low reproductive effort at each breeding attempt (e.g. African bush elephant (*Loxodonta africana*)), and others dying much younger but breeding much more frequently producing larger litter sizes (e.g. wood mice (*Apodemus sylvaticus*)). Phenotypic traits, like body mass, often correlate with a species' position on the slow-fast continuum.

One challenge that comparative demography faces is that different populations of the same species can also exhibit significantly different dynamics (Murie, 1985). Understanding how much variation can be observed between different populations of the same species is important as it helps set in relief the degree of differences observed between species. Unfortunately, the number of cases where multiple populations of the same species have been studied are relatively few and far between.

Several theories have been suggested to describe the differences observed between species, including r-K theory (Wilson and MacArthur, 1967). r-K theory suggests that animals exist along a continuum, running from r to K, with animals that are more r selected having smaller body size, early age at maturity, lower survival, larger litter sizes and higher genetic variability. The theory also suggest that animals living at higher altitudes will be more r selected due to the unpredictable, unstable food supply compared to those living at lower altitudes where the food supply is more stable and predictable. But this theory have been found to be inadequate in a number of cases. One such case is the Columbian ground squirrel (*Urocitellus columbianus*). Zammuto and Millar (1985) suggested that only proportions of r-K theory were useful for ground squirrels when all parameters are consistently measured. Columbian ground squirrels have been found to mature later, with a higher survival rate and possibly lower genetic diversity at higher altitudes, the opposite to what theory predicts. They associated this with higher altitudes having a more predictable environment, and although there was less food available on average it was also less variable. But they also found that body weight was not correlated with altitude.

Columbian ground squirrels are known to exhibit life histories that vary with altitude (Murie, 1985). Litter sizes have been found to be larger at lower elevations (Murie et al., 1980) in some studies, which has been attributed to the earlier snow melt and subsequent higher quality forage, but others (Murie, 1985) have found litter size not to be correlated with altitude. Zammuto and Millar (1985) reported that at higher elevations Columbian ground squirrels had later maturity and higher adult survival. But conversely reproductive success is lower at higher elevations (Murie and Harris, 1982).

The availability of food resources can impact the life history characteristics of Columbian ground squirrels. With supplemented food resources, spring body weight, litter size and survival of the young increased whilst age at maturity decreased (Dobson and Kjelgaard, 1985a). All this work suggests that the life history of ground squirrels can vary markedly across habitats, and this would result in the dynamics of their populations also varying across locations. In this paper we will examine the possible drivers for the variation of life history across squirrel populations. Although our analysis are specific to ground squirrels, we believe the insights our analysis provides are general.

In a previous chapter we showed how three populations of the Columbian ground squirrels, living in close proximity at similar altitudes can have different population dynamics and population growth rates. One question that arose from the estimates produced from the Integral Projection Models (IPMs) was what was driving the differences observed?.

IPMs have become increasingly popular over the last decade, allowing for an

understanding on how a phenotypic trait impact demographic rates, including survival, reproduction and litter size and trait-transition rates such as development (growth) and inheritance. Because an IPM can be used to approximate a high dimensional matrix (iteration matrix) using the midpoint rule (Ellner and Rees, 2006), eigenanalysis can be used to estimate population growth rates (λ) and mean trait and life history trajectories (Caswell, 2001).

We took the IPMs created in our previous study and conducted perturbation analysis, using a similar method to Ozgul et al. (2010) to estimate the changes in λ, mean weight, survival rate, reproductive weight, reproductive rate, litter size, offspring weight, recruitment rate, generation length and R_0, for the possible combination of changes between the three populations for the parameters used to populate the IPMs. This allowed us to understand which demographic or trait transition function had contributed most to the estimated differences between the populations. This kind of analysis is known as Life Table Response Experiment (LTRE) analyses (Caswell, 1989), where the effects on a dependent variable, usually λ, is decomposed into the contributions from the differences in the parameters that determine the variable (Caswell, 2010).

Methods

The study system

The Colombian ground squirrel (*Urocitellus columbianus*) is a burrow-dwelling rodent common in regions of Canada and the North-Western United States. They spend most of their time hibernating and are only active for around 103 days each year in our study sites. The three data sets were collected from the Sheep River Provincial Park in South Western Alberta, Canada (114° W and 50° N). The three

populations were within 3km of each other and at similar altitudes (1490-1550m). The sites for each population are described fully in our previous chapter.

Ethical statement

The research, capture and handling of animals was conducted under guidelines on care and use of wildlife provided by the Canadian Council on Animal Care. The protocol was approved by the "Live and Environmental Sciences Animal Resource Center" LESARC at the University of Calgary.

Construction of IPMs

The IPMs used in this study are the same as the ones used in our previous chapter. Their construction is summarised briefly here for convenience. The constructed IPMs are univariate, deterministic size-structured models with weight as a continuous variable. The kernel of the IPMs was described by functions that represented the survival, development and reproduction of the populations, with the functions being parameterised from statistical models built using individual capture data. Reproduction was split into three functions representing the chance of reproduction, the litter size and inheritance defined as, how a mother's weight determines an offspring's weight. Two additional functions were added to the IPM for offspring recruitment (offspring survival) and offspring development; this is to account for the offspring being censored at a different time to adults (yearlings and older). The IPM had the form

$$n(z', t+1) = \int [G_a(z'|z)S_a(z) + G_j(z'|z^*)Pr(z^*)C(z^*|z)B(z)Pb(z)]n(z,t)dzdz^* \tag{3.1}$$

Equation 3.1 describes how the distribution of body weights at time t changes to time $t+1$ given the survival, development and reproduction of the population. $n(z', t+1)$ describes the distribution of body weights at time $t+1$, whilst $n(z,t)$ describes the distribution of body weight at time t. $G_a(z'|z)$ is the development function, $S_a(z)$ is the survival function, $G_j(z'|z^*)$ is the offspring development function, $Pr(z^*)$ is the probability of offspring recruitment function, $C(z^*|z)$ is the inheritance function, $B(z)$ is the litter size function and $Pb(z)$ is the probability of reproducing function. Finally z is the possible distribution of weights at time t, z^* is the possible distribution of weights of offspring at emergence from the natal burrow and z' is the possible distribution of weights at time $t+1$.

An approximation of the IPM was constructed using a high dimensional matrix or iteration matrix with 250 weight classes. The matrix had the following form.

$$\boldsymbol{n}(t+1) = \boldsymbol{A}\boldsymbol{n}(t) = [\boldsymbol{G}_a\boldsymbol{S} + \boldsymbol{G}_j\boldsymbol{Pr}\boldsymbol{C}\boldsymbol{B}\boldsymbol{Pb}]\boldsymbol{n}(t) \tag{3.2}$$

With distributions of weights at time t and $t+1$ was represented by $\boldsymbol{n}(t)$ and $\boldsymbol{n}(t+1)$ respectively, $\boldsymbol{S}$, $\boldsymbol{Pb}$, $\boldsymbol{B}$ and $\boldsymbol{Pr}$ represented Survival, Probability of Reproducing, Litter Size and Probability of recruitment kernels respectively and $\boldsymbol{G}_a$, $\boldsymbol{C}$ and $\boldsymbol{G}_j$ represented Adult Development, Offspring Weight and Offspring Development transitional kernels respectively. The weight class range was determined by taking -20% below the minimum weight to +20% above the maximum weight observed in the population data. The value of each of the weight classes was determined using the mid-point rule (Ellner and Rees, 2006). From this iteration matrix it was possible to estimate, using eigenanlysis, the mean population growth rate or λ, the mean weight, survival rate, reproductive weight, reproductive rate, litter size,

offspring weight and recruitment rate. In addition to these population estimates we calculated R_0, the net replacement rate and G the generation time or the mean time between birth and the birth of the females median offspring. To calculate these two estimates we took the stable size distribution $w(z)$ calculated from the eigananalysis and multiplied it by the reproductive matrix ($\boldsymbol{M} = \boldsymbol{G_j PrCBPb}$) to get an initial cohort $\boldsymbol{n}_0$ on a proportional scale, equation 3.3.

$$\boldsymbol{n}_0 = \frac{\boldsymbol{M}w(z)}{\sum \boldsymbol{M}w(z)} \tag{3.3}$$

The next cohort was then calculated by multiplying the current cohort by the development and survival kernels, equation 3.4 where x is the cohort number or age, this was then repeated 100 times.

$$\boldsymbol{n}_x = \boldsymbol{GS}\boldsymbol{n}_{x-1} \tag{3.4}$$

The mean probability of surviving to age x ($\boldsymbol{l}_x$) was calculated by summing the results ($\boldsymbol{n}_x$) for each cohort. The per capita reproduction was calculated by taking $\boldsymbol{n}_x$ on a proportional scale and multiplied it by the reproductive kernel and then summing each cohort, equation 3.5.

$$\boldsymbol{m}_x = \sum_{x=1}^{100} \boldsymbol{M}\frac{\boldsymbol{n}_x}{\sum \boldsymbol{n}_x} \tag{3.5}$$

The values for $\boldsymbol{l}_0$ and $\boldsymbol{m}_0$ were set to 1 and 0 respectively as the initial cohort has 100% survival but no reproduction. Finally R_0 was calculated by $\sum(\boldsymbol{l}_x\boldsymbol{m}_x)$ and G was calculated by $\sum(x\boldsymbol{l}_x\boldsymbol{M}_x)$ divided by R_0

Perturbation analysis of the IPMs

We used a method first described by Ozgul et al. (2010) to identify the differences between the populations due to the demographic and trait transition rate functions. For each of the populations, we swapped one function from one of the other populations and reran then IPM and analysis. For example we took the development, offspring development, recruitment, inheritance, litter size and reproduction functions for population A and used the survival function from population B to create a new kernel. The new kernel was used to generate estimates for population growth rate λ, mean weight, reproductive weight, survival rate, reproductive probability, female litter size, offspring weight, offspring recruitment rate, net replacement rate (R_0) and generation length (G). This allowed us to quantify the differences between population A and B due to the survival function. Repeating this for each of the functions and each of the populations, allowed for a understanding of the differences between the three populations due to each of the demographic and trait transition functions.

Results

Full details of the statistical results, model choice and IPM results are included in our previous chapter. The IPM function parameters, extracted from the statistical models, are shown in table 3.1. The changes to the IPM estimates due to the perturbation analysis are shown in table 3.2, and figures S3.1 to S3.3. We detail below the most interesting results from the perturbation analysis.

Interpreting table 3.2 deserves some explanation, beyond what is included in the table caption. Each row of the table denotes a population estimate for one of the populations, with the Orig. column holding the unperturbed value. The rest of

the columns then holds the percentage increase or decrease due to the replacement of a demographic or trait transition function from one of the other populations. For example if we take the first row, which is the Growth Rate or λ for population A. The original value with no perturbation is 0.91. Looking along the row the replacement of the survival function (S) with the one from population B causes an increase in survival of 14.37 percent, the replacement of the recruitment function (R) with the one from population B, a -0.74 percentage decrease and so forth.

Table 3.1. Parameter estimates taken from the most parsimonious model, describing the relationship between body mass and demographic and trait transition rates. The predicted values are survival probablity (S), development (G), reproduction probablity (Pr), litter size (B) and inheritance (C). The subscripts a and j refer to the adult (yearlings and older) and offspring individuals that the functions apply to. The subscript values represent the stand error of the estimates. Logit(Y) indicates a Binomial regression link and Log(Y) a Poisson regression.

Function	Model	Pop.	Fitted LM / GLM	n
Survival probability	Logit(S_a)	A	$0.9839_{(0.0823)}$	746
		B	$-7.3606_{(3.3747)} + 0.0478_{(0.0197)}x - 0.0001_{(0.0000)}x^2$	157
		C	$-5.1570_{(2.2445)} + 0.0303_{(0.0131)}x - 0.0000_{(0.0000)}x^2$	255
Offspring recruitment	Logit(S_j)	A	$-4.8789_{(1.8289)} + 0.0755_{(0.0323)}x - 0.0003_{(0.0001)}x^2$	413
		B	$-11.6411_{(6.9492)} + 0.2068_{(0.1313)}x - 0.0009_{(0.0006)}x^2$	103
		C	$-1.2020_{(0.8128)} + 0.0122_{(0.0079)}x$	204
Development	G_a	A	$303.2889_{(9.7117)} + 0.2772_{(0.0256)}x$	543
		B	$398.8696_{(62.4590)} - 0.2382_{(0.3505)}x + 0.0008_{(0.0005)}x^2$	129
		C	$428.2129_{(60.5053)} - 0.3409_{(0.3495)}x + 0.0009_{(0.0005)}x^2$	144
Offspring development	G_j	A	$62.2264_{(53.4814)} + 2.7721_{(0.9076)}x - 0.0084_{(0.0038)}x^2$	205
		B	$208.1540_{(36.1223)} + 0.5243_{(0.3426)}x$	50
		C	$237.7550_{(12.1328)} + 0.2369_{(0.1081)}x$	102
Reproduction probablity	Logit(Pr)	A	$-11.4389_{(2.5977)} + 0.0421_{(0.0137)}x - 0.0000_{(0.0000)}x^2$	738
		B	$-8.1771_{(1.3050)} + 0.0215_{(0.0033)}x$	157
		C	$-24.9746_{(5.5211)} + 0.1118_{(0.0282)}x - 0.0001_{(0.0000)}x^2$	255
Litter size	Log(B)	A	$-0.1876_{(0.0678)}$	304
		B	$0.2429_{(0.0990)}$	80
		C	$0.4680_{(0.0711)}$	124
Inheritance	C	A	$266.2348_{(47.1748)} - 0.7991_{(0.2363)}x + 0.0010_{(0.0003)}x^2$	251
		B	$78.3111_{(14.7747)} + 0.0545_{(0.0331)}x$	102
		C	$203.2650_{(19.3690)} - 0.5232_{(0.1095)}x + 0.0006_{(0.0002)}x^2$	199

Population A

When replacing the functions in population A with those from population B, replacement of the survival function caused an increase in λ due to an increase in the adult survival rate and reproductive rate, with large increases in G and R_0. The development function replacement caused an increase in λ due to an increase in the reproductive rate and an increase in weight, R_0 also increased with a small increase in G. Replacement of the litter size function caused an increase in λ by increasing the litter size and consequently also R_0.

For population A being replaced with population C functions, there was a large decrease in λ with replacement of the survival function, due to a decrease in the survival rate and to a lesser extent a decrease in the reproductive rate, G and R_0 also decreased. The reproductive function replacement saw an increase in the reproductive rate but a decrease in the offspring weight and recruitment rate, R_0 increase but G decreased. There was an increase in λ when replacing the litter size function, although the litter size estimate increased the reproductive rate decreased, R_0 showed a similar increase as the reproductive weight.

Population B

The replacement of population B's functions by population A's caused the following changes. Replacement of the survival function caused a decrease in λ due to a decrease in the survival rate and the reproductive rate. Consequently both G and R_0 saw a decrease. With replacement of the reproduction probability function, λ and R_0 showed a decrease due to a decrease in the reproductive rate and recruitment rate. Litter size function replacement caused a decrease in λ and R_0 due to a decrease in the litter size. Interestingly, replacement of the offspring development

Table 3.2. Percentage change to the IPM estimates for each population when subsituting the demographic and trait transition rate functions from the other populations. Orig. is the original value of the estimate before any substitutions are made. Function abbreviations are S = Survival probablity, R = Offspring recruitment, D = Development, OD = Offspring Development, Rp = Reproduction probablity, LS = Litter Size and I = Inheritance.

		Population A							Population B							Population C						
Function	Orig.	S	R	D	OD	Rp	LS	I	S	R	D	OD	Rp	LS	I	S	R	D	OD	Rp	LS	I
Population A																						
Growth Rate λ	0.91								14.37	−0.74	3.08	0.02	2.54	8.18	0.03	−15.94	1.06	2.48	0.01	4.32	13.55	−0.33
Weight (g)	379.18								1.39	0.33	5.90	0.29	−1.01	−3.00	−0.13	−1.10	−0.53	4.31	0.24	−1.69	−4.67	−0.07
Survival rate	0.73								16.94	0.00	0.00	0.00	0.00	0.00	0.00	−19.16	0.00	0.00	0.00	0.00	0.00	0.00
Repr. Weight (g)	417.78								0.65	0.10	7.05	−0.04	0.16	−1.02	0.01	−0.19	−0.13	4.44	−0.03	−0.69	−1.64	0.06
Off. weight SD (g)	18.20								0.00	0.00	0.00	0.00	−0.55	0.00	−27.19	0.00	0.00	0.00	0.00	−0.54	0.00	−17.79
Recruit. rate	0.57								0.00	−37.24	0.00	0.00	−1.79	0.00	−26.52	0.00	11.38	0.00	0.00	−1.81	0.00	−1.18
Generation length (G)	3.92								129.65	−0.02	1.58	−0.20	0.46	−0.01	0.52	−28.63	0.07	−0.34	−0.16	−1.15	−0.01	0.27
R_0	0.55								138.89	−4.36	19.82	0.29	16.80	53.83	0.76	−53.27	6.76	16.40	0.23	30.52	92.66	−1.81
Population B																						
Growth Rate λ	1.16	−10.05	0.11	−1.89	−0.69	−3.05	−7.57	−0.86								−25.39	1.05	0.73	−0.07	0.56	4.87	−0.80
Weight (g)	385.96	−1.58	−0.06	−4.13	−0.31	1.45	3.86	0.55								−3.63	−0.54	−0.81	−0.03	−0.26	−2.09	0.31
Survival rate	0.83	−12.40	−0.03	1.44	−1.01	0.38	0.98	0.24								−31.86	−0.20	0.72	−0.11	−0.08	−0.58	0.04
Repr. Weight (g)	441.25	−0.89	−0.02	−5.51	0.15	0.08	1.31	0.12								−1.55	−0.16	−1.75	0.02	−0.70	−0.75	0.14
Repr. rate	0.54	−4.28	−0.16	−11.23	0.10	−11.29	10.30	1.38								−9.63	−1.39	−1.01	0.01	2.23	−5.59	0.88
Litter Size	1.28	0.00	0.00	0.00	0.00	0.00	−34.98	0.00								0.00	0.00	0.00	0.00	0.00	25.24	0.00
Off. weight (g)	92.07	0.00	0.00	0.00	0.00	−2.82	0.00	36.86								0.00	0.00	0.00	0.00	0.00	0.00	22.61
Off. weight SD (g)	13.13	0.00	0.00	0.00	0.00	−0.71	0.00	37.81								0.00	0.00	0.00	0.00	0.00	0.00	13.80
Recruit. rate	0.41	0.00	4.47	0.00	0.00	−5.65	0.00	12.27								0.00	16.06	0.00	0.00	0.00	0.00	22.85
Generation length (G)	6.88	−44.70	−0.03	30.54	−0.06	−0.20	0.00	−0.15								−61.79	−0.20	19.61	−0.01	−2.41	0.00	0.03
R_0	2.38	−51.60	0.45	3.37	−3.72	−15.42	−34.94	−5.10								−77.61	4.81	13.93	−0.40	1.78	25.19	−4.55
Population C																						
Growth Rate λ	0.94	19.61	−1.64	−2.04	−1.03	−5.14	−14.42	0.48	31.81	−2.16	−1.17	−0.10	−1.43	−5.64	0.41							
Weight (g)	358.94	2.05	0.63	−2.81	−0.88	1.94	6.14	−0.02	3.60	0.83	0.49	−0.05	0.53	2.12	−0.09							
Survival rate	0.57	28.40	0.22	1.40	−1.66	0.57	1.64	0.10	45.94	0.29	−0.91	−0.04	0.17	0.61	0.02							
Repr. Weight (g)	423.88	0.32	0.16	−3.54	0.07	0.07	1.61	−0.07	1.11	0.21	1.10	0.04	0.25	0.58	−0.05							
Repr. rate	0.47	6.48	1.88	−7.13	−0.05	−13.98	18.55	−0.20	10.67	2.49	−1.07	−0.20	−4.06	6.47	−0.33							
Litter Size	1.60	0.00	0.00	0.00	0.00	0.00	−48.09	0.00	0.00	0.00	0.00	0.00	0.00	−20.15	0.00							
Off. weight (g)	112.67	0.00	0.00	0.00	0.00	10.07	0.00	11.49	0.00	0.00	0.00	0.00	0.01	0.00	−18.07							
Off. weight SD (g)	14.92	0.00	0.00	0.00	0.00	0.23	0.00	21.16	0.00	0.00	0.00	0.00	0.00	0.00	−13.41							
Recruit. rate	0.54	0.00	−2.66	0.00	0.00	6.23	0.00	7.05	0.00	−6.32	0.00	0.00	0.01	0.00	−11.34							
Generation length (G)	2.61	44.42	0.14	5.79	−0.03	2.43	0.00	−0.05	209.19	0.19	−3.30	0.02	2.83	0.00	0.09							
R_0	0.77	110.52	−6.19	−9.08	−4.35	−21.93	−48.08	1.49	374.71	−8.08	−3.82	−0.15	−8.09	−20.15	1.84							

function caused a decrease in λ and R_0 whilst replacement of the development function also caused a decrease in λ but a increase in R_0 and G.

Replacement of the survival function from population C caused a decrease in λ, R_0 and G due to a decrease in the survival rate and reproductive rate. Whilst replacement of the recruitment function caused an increase in λ and R_0 by causing an increase in the recruitment rate. Finally replacement of the litter size function caused an increase in λ and R_0 due to an increase in the litter size, although both survival rate and reproductive rate saw slight decreases.

Population C

When replacing the survival function for population C with the one from population A, there was an increase in λ, R_0 and G mainly due to an increase in the survival rate, but the reproductive weight also increased. Replacement of the reproductive function saw a decrease in λ and R_0 due to a decrease in the reproductive rate, although there was an increase in the recruitment rate and offspring weight. Litter size function replacement caused a decrease in λ and R_0 due to a decrease in the litter size, although the reproductive rate saw an increase.

When using the functions from population B, the replacement of the survival function saw an increase in λ, G and R_0, due to an increase in the survival rate and reproductive rate. Finally replacement of the litter size function saw a decrease in λ and R_0 due to a decrease in the litter size, but with an increase in the reproductive rate.

Discussion

Comparing species' population dynamics and life histories is problematic because different (sub)populations of the same species can exhibit significantly different dynamics (Murie, 1985). Understanding the variation within a species is crucial to our understanding and our ability to quantify how different species vary. Taking the Integral Projection Models (IPMs) created for three (sub)populations of Columbian ground squirrels (*Urocitellus columbianus*) we constructed in a previous chapter, we used a method described by Ozgul et al. (2010) to understand the differences in the strength of the contributions from the various IPM functions to the estimates. Here we will detail these differences, how they relate to r-K theory and what is already known about the dynamics and life histories of Columbian ground squirrels. If r-K theory was operating then we would expect to see populations with lower mean weights to have an early age at maturity, lower survival and larger litter sizes, whilst populations with a heavy mean weight we would see the opposite, a later age at maturity, higher survival and smaller litter sizes.

Survival

Substitution of the survival function caused changes not only in λ and the survival rate but also in the mean weight, the mean reproductive weight and reproductive rate. As population C had the lowest survival rate, substituting its function caused a decrease in these estimates for the other two populations, whilst the survival function from population B caused an increase in the other two populations. Substitution of the survival function also had a large impact on the generation length, in particular population B survival function into population C caused over double the increase in generation length and over triple increase in R_0. When relating this to r-K theory we do see an increase in mean weight, reproductive

weight and increased generation length with increased survival, and a decrease in mean weight, reproductive weight and generation length with decreased survival. We do not see any change in the litter size though, which from a model perspective is due to the insignificant effect of mother's weight on female litter size.

So why does survival differ between the three populations? Survival of adult Columbian ground squirrels is believed to be driven by a number of factors. Predation is thought to be the major cause of mortality in many species (Neuhaus and Pelletier, 2001), but other interacting factors can increase the chance of predation. Unfavourable weather conditions can mean that squirrels are forced to forage for longer periods and move further away from the protection of their burrows in order to locate suitable forage (Neuhaus and Pelletier, 2001; Neuhaus et al., 1999). Population density can also impact adult survival, with an increase in density meaning more competition for resources but also a reduction in predation due to dilution (increased prey choice) (Neuhaus and Pelletier, 2001). Survival is not constant, with survival during hibernation being safest part of the year, unless a badger visits during the winter, which happened in 2008 and 2009 for the three populations, with the impact of this visit being the highest for population C (Murie, 1992; Neuhaus, 2017). Reproduction can impact adult survival with the period during lactation potentially having the highest mortality due to increased energetic costs (Neuhaus and Pelletier, 2001), although the costs of reproduction are not always observed in Columbian ground squirrel studies (Hare and Murie, 1992; Murie and Dobson, 1987). Habitat differences can also impact survival, as we mentioned in our previous paper, the grazing regime for population A differed from the other two sites at the start of the data collection period (Neuhaus, 2017). It is not possible to relate the differences between the populations to one or more

of these factors, and any or all of these could be in effect. What is certain is that the three populations differ greatly due to the survival of the adults; in the case of population C substitution of the survival function from population B caused over a 30% increase in λ.

Recruitment

Before substitution, population A had the highest recruitment rate, followed by population C, with population B having the lowest. In general when substituting the recruitment function, if there was decrease in the recruitment rate, then there was also a decrease in λ and R_0 and small increases in mean weight, survival rate, reproductive weight, reproductive rate and generation length. With an increase in reproductive rate the opposite was estimated. There were two exceptions to this; replacement of population A's recruitment functions saw the generation length change in the opposite direction, although the change was small. Additionally replacing the recruitment function in population C with the one from population A saw a decrease in λ. This is the opposite from what we may expect, as population A has a higher recruitment rate than population C before substitution.

Differences in recruitment between the three populations could be driven by a number of factors. Mortality of offspring in their first year is known to be higher than older individuals (Boag and Murie, 1981; Dobson and Murie, 1987; Neuhaus and Pelletier, 2001; Zammuto, 1987). In our models the recruitment rate represents the period from emergence from the natal burrow, approximately the same time as weaning, to emergence from the hibernacle the following year. Offspring only have a short period of time to build the resources required to survive hibernation and therefore are more sensitive to changes in the availability and quality of resources (Dobson and Kjelgaard, 1985a). The timing of the rains and snowstorms not only

effects the availability and quality of resources but also the timing of reproduction, with late breeding, offspring are going to have even less time to build their fat stores (Neuhaus et al., 1999). The presence of the mother after emergence from the natal burrow is known to have a positive effect on the survival of her offspring (King et al., 1991). These interacting effects may explain the observed differences between the three populations, although it is not possible to identify from our models the factor that has the greatest effect.

Development

No particular pattern is evident when substituting the development function. Before substitution, population B had the highest mean weight, followed by population A, with population C having the lowest mean weight. Interestingly, substitution of population A's development function into population B caused a greater change than substitution of population C's development function into population B. λ, mean weight, reproductive weight and reproductive rate all decreased but there was an increase in survival rate, generation length and R_0. From a model perspective, population A's development function does not have a quadratic term, whilst the development function for population C has a positive quadratic term. This is what is causing population A's development function to estimate a lower mean weight when substituted into population B.

Many factors can effect the development of individuals in a population and may contribute to the differences observed between the populations. As individuals are weighed at emergence from the hibernacle in the spring, the development function in our model represents the change in spring weight from one year to the next. Columbian ground squirrels are capital hibernators, relying on fat stores built up during their active period (Boag and Murie, 1981; Broussard et al., 2005; Murie

and Harris, 1982). The amount of resources they can accumulate during the active period depends not only on the local environment but also on the climate, with rain and snow storms impacting not only the quantity but also the quality of the available food resources (Dobson and Kjelgaard, 1985a; Neuhaus et al., 1999). The amount of fat reserves expanded during hibernation can also be impacted by the climate with a deeper snow pact providing an insulating effect (Dobson et al., 2016; Dobson and Murie, 1987; Murie and Boag, 1984). Weight of course does not just encapsulates the amount of fat reserves that an individual has but also includes structural size (Skibiel et al., 2009). At a population level, the mean weight estimate is not only going to encapsulate the fitness level of individuals due to the environment and climate, but also the differences in weight due to age structure of the population. Columbian ground squirrels do not reach full maturity to at least 3 years of age (Boag and Murie, 1981), with yearlings being significantly smaller.

Offspring development

When substituting the offspring development function, three estimates did not change significantly, these where litter size, offspring weight and recruitment rate. This may seem strange but the offspring development function represents the development of offspring into the adult population as yearlings, so a change in the development function is going to impact the adult weight, survival and reproduction estimates instead. The substitution of the offspring development function in most cases caused only slight changes to the estimates. The possible exception being the substitution of population A's function into the other two populations, even then there was only a small change to R_0 mainly due to a slight reduction in the survival rate.

The lack of difference between the three populations in the offspring development is supported by previous findings. Neuhaus (2000) found that the weight at emergence from the natal burrow is highly correlated with the weight at immergence into the hibernacle for the first hibernation and they suggest that offspring are not able to make up for a small mass at emergence from the natal burrow during the short period they have before hibernation. But in contrast to this, other studies (Bennett, 1999) have found that offspring growth and survival is enhanced by a higher forb content in the forage, suggesting that digestibility of the forage was the limiting factor for offspring growth.

Reproductive probability

In our models the reproductive function is used to estimate the chance that a female will produce at least one offspring (either male or female) that will emerge from the natal burrow. Before substitution population B had the highest estimated reproductive rate, followed by population C with population A having the lowest. For population A substitution with the other two populations' reproductive function caused an increase in the reproductive rate as expected and an increase in λ and R_0. Both substitutions also saw a drop in the offspring weight and recruitment rate estimates, suggesting that the populations were potentially more r selected under the r-K theory with the substitutions in effect. Interestingly substitution of the reproductive function from population C into population B caused an increase in the reproductive rate, λ and R_0. Again this can be attributed to the lack of a quadratic term for the reproductive function of population B. Substitution of population C's reproductive function saw the opposite effect to population A's substitutions. Again these changes could be partially explained by r-K theory with the population becoming more K selected.

Differences in reproductive success between the three populations could be possibly explained by a number of factors, but care has to be taken when comparing the estimates from our IPMs to the results from previous studies. In many studies the reproductive success is a measure of the chance the female will raise young to the yearling age, combining both the reproductive chance and offspring recruitment estimates from our IPMs into one. Female Columbian ground squirrels have been found to optimise their reproductive success based on available resources, both during pregnancy and weaning (Neuhaus, 2000). They are considered to be income breeders, relying on daily resource acquisition to support offspring (Broussard et al., 2005), particular during the period of lactation (Clutton-Brock et al., 1989).

Litter size

The litter size function in the models represents the number of female offspring emerging from the natal burrow. Before substitution population C had the highest estimated litter size, followed by population B, with population A having the smallest. An increase in the litter size also saw an increase in λ and R_0, whilst there was small decreases in mean weight, survival rate, reproductive rate and reproductive weight estimates, a decrease in the litter size resulted in the opposite. The changes in the estimates mostly supports r-K theory, although there is no change, or only very small change, in the generation length estimate.

As to why we see differences between the three populations, the same factors that potentially effect the reproductive probability function can also impact the litter size function. Previous studies have suggested that mothers are able to optimise litter size depending on available resources (Neuhaus, 2000) taking into account both the quality of offspring and future reproduction.

Inheritance

The inheritance function estimates the weight of female offspring that emerge from the natal burrow, based on the weight of the mother at emergence from hibernation in spring. Population A had the heaviest mean offspring weight and highest standard deviation before substitution, followed by population C, with population B having the lightest mean weight and smallest standard deviation. An increase in mean weight, due to substitution of the inheritance function, was associated with an increase in the recruitment rate and R_0. Accept for when the population B's inheritance function was substituted or was used as a substitute, in which case R_0 decreased. The difference with population B was again due to population B's inheritance function not having the quadratic term. A decrease in mean offspring weight, with the substitution of the inheritance function, resulted in the opposite effect. The inheritance function was also the main determiner of changes in the variation in offspring weight.

There are clear differences between the three populations due to the inheritance function, a number of factors could be driving these differences. As mentioned above, Columbian ground squirrels are income breeders, relying on resources gathered on a daily basis rather to provide sustenance for their offspring (Broussard et al., 2005). Therefore climate and the environmental differences could possibly both have an impact on the weight of offspring emerging from the natal burrow. Although studies have found a correlation between the spring weight of mothers, at emergence from hibernation, with the weight of their offspring (Dobson and Kjelgaard, 1985a,b; Murie and Dobson, 1987). Additionally the total litter size was found to impact the weight of the weaned individuals, with larger litters having smaller individuals (Skibiel et al., 2009).

Conclusion

In conclusion the differences in the estimates between the three population are in some cases large, for example between population B and C, the effect of substitution on the survival function on the generation length and R_0. From what we know about the life histories of this species they show considerable plasticity, adapting to differences in habitat and climate (Dobson and Kjelgaard, 1985a). From the perturbation analysis, a change in just one of the demographic or trait transition functions not only impacts directly related estimates but also some or all of the other estimates. For example an increase in the survival function not only increases the survival rate estimate, but also impacts the mean weight, the reproductive weight, reproductive rate, generation length and R_0. Potentially all the demographic and trait transition functions could be driven by changes in the environment and climate, either directly or indirectly through the availability and quality of resources, to a great or lesser extent (Bennett, 1999; Broussard et al., 2005; Dobson and Kjelgaard, 1985a; Neuhaus and Pelletier, 2001; Neuhaus, 2000). Therefore a change in the environment or climate, for example a change in the grazing regime of the cattle, is going to have the chance to impact all the functions. It is clear from the perturbation analysis that r-K theory can explain some of the changes in the estimates, but it does not provide a complete explanation for the differences in the life histories of the three populations of the Columbian ground squirrel.

The take away from this study is that there is possibly a great deal of variation between populations of the same species even when the environment and climate is believed to be similar. For example changes that impact survival are going to potentially impact all population level estimates. Extreme care therefore needs to

be taken when making predictions on differences between species, that are based on data from only single populations.

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Supporting Information

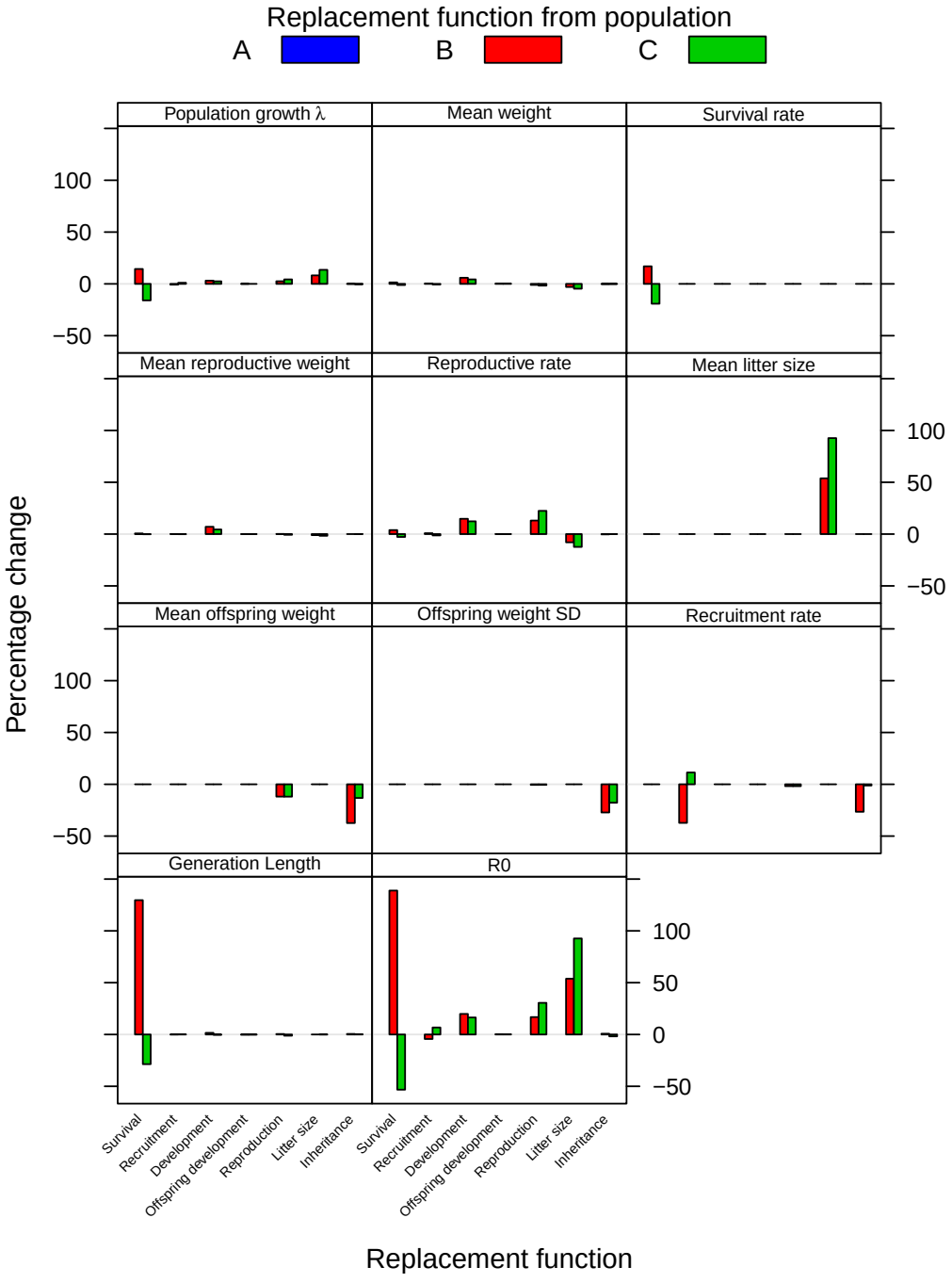


Figure S3.1. Percentage change to the IPM estimates for population A when subsituting the demographic and trait transition rate functions from the other two populations

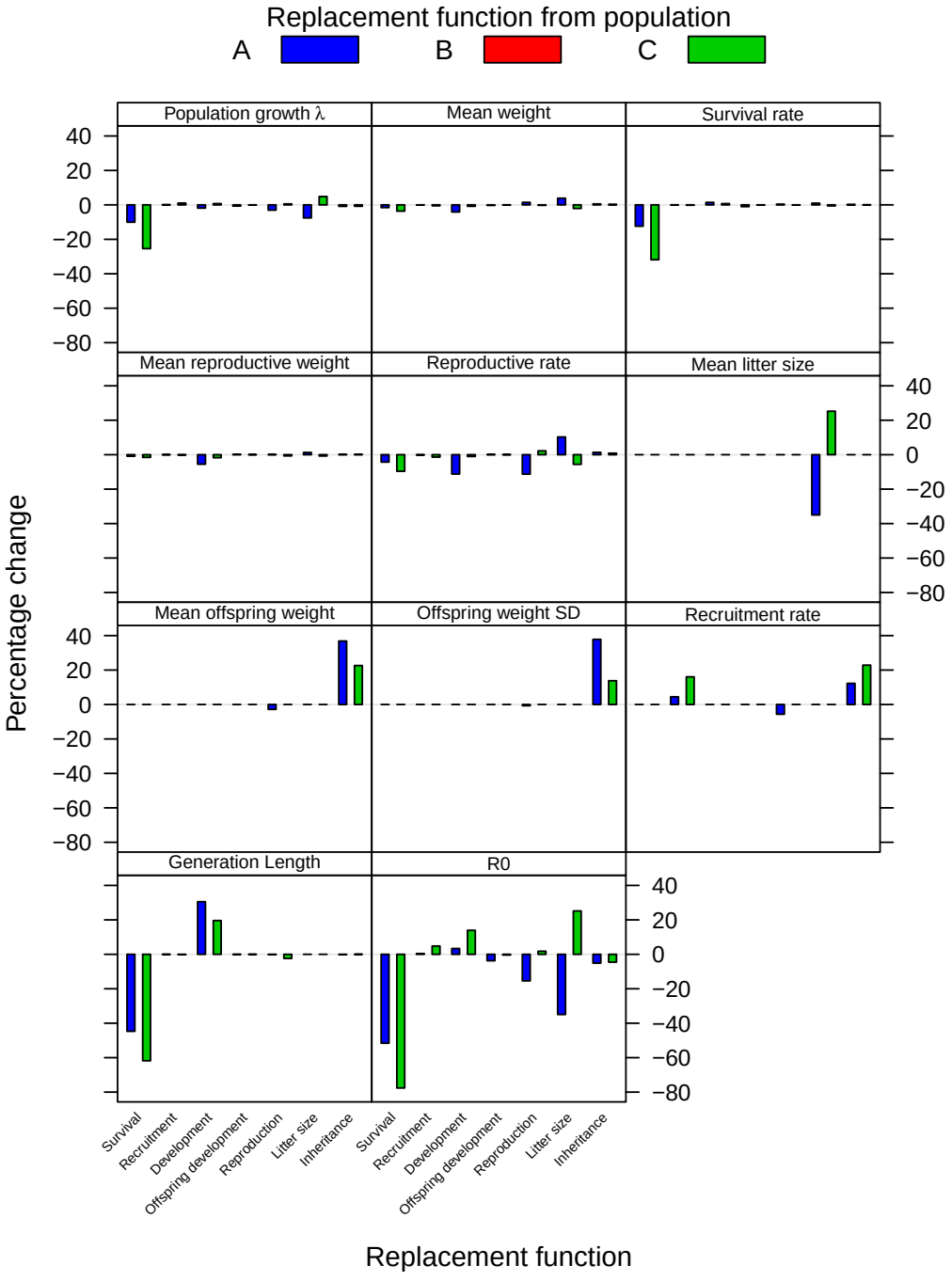


Figure S3.2. Percentage change to the IPM estimates for population B when subsituting the demographic and trait transition rate functions from the other two populations

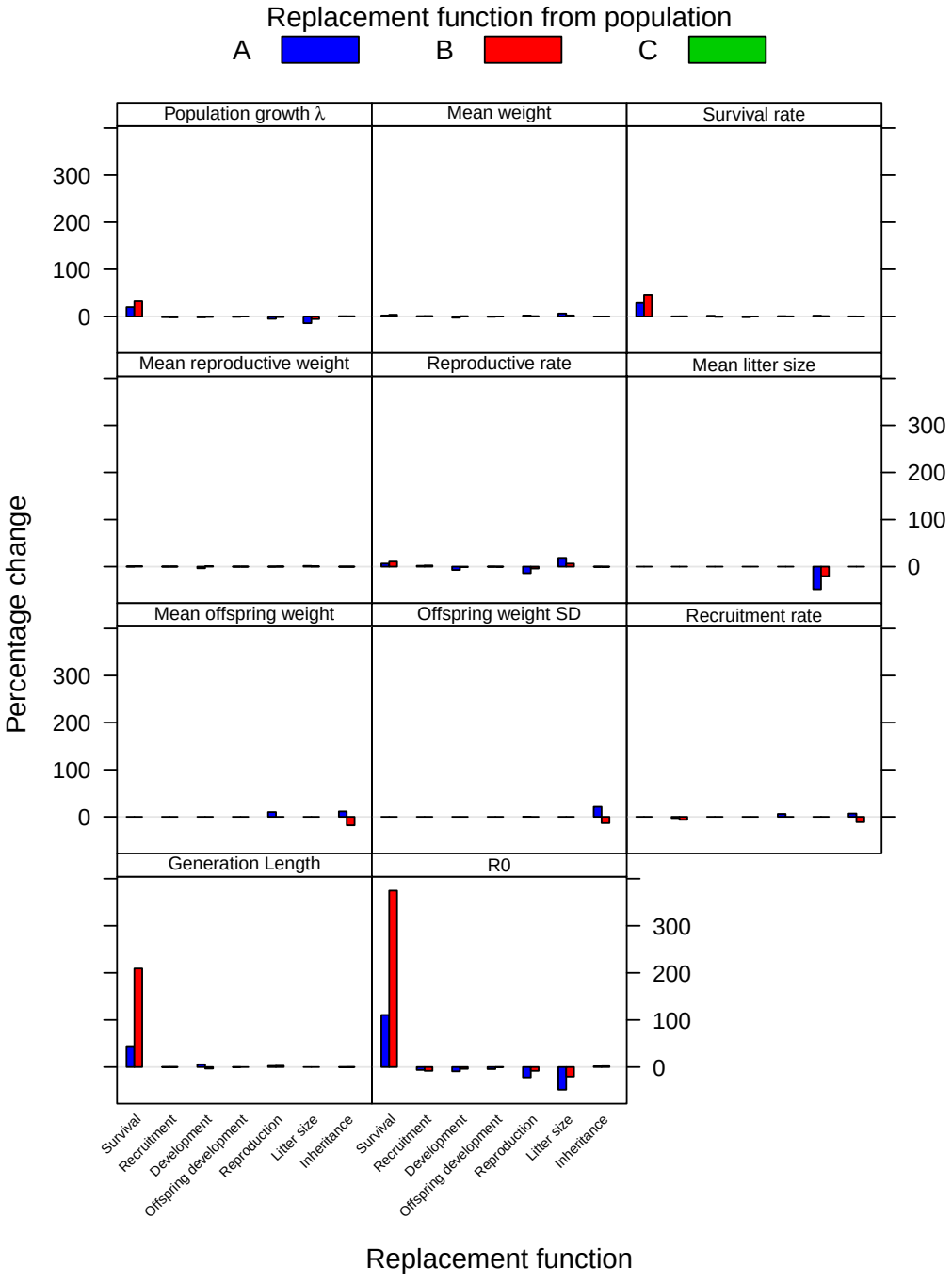


Figure S3.3. Percentage change to the IPM estimates for population C when subsituting the demographic and trait transition rate functions from the other two populations

4

Analysis on population level reveals trappability of wild rodents is determined by previous trap occupant

Running head

Previous trap occupant effects subsequent trappability

Title

Analysis on population level reveals trappability of wild rodents is determined by previous trap occupant

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Abstract

Live trapping is central to the study of small mammals. Thus, any bias needs to be understood and accounted for in subsequent analyses to ensure accurate population estimates. One rarely considered bias is the behavioural response of individuals to the trap, in particular the olfactory cues left behind by previous occupants (PO). We used a data set of 8,115 trap nights spanning 17 separate trapping sessions between August 2002 and November 2013 in Wytham Woods, Oxfordshire, UK to examine if the decision to enter a trap was affected by the PO, if this was detectable in traditional Capture-Mark-Recapture trapping data (i.e., individuals not uniquely marked), and if it was possible for this effect to bias the population estimates obtained. Data were collected on *Apodemus sylvaticus*, *Myodes glareolus*, and *Microtus agrestis*. Three Generalised Linear Models revealed a significant tendency for the three species to enter traps with same-species PO. With, for example, *A. sylvaticus* 9.1 times more likely to enter a same species PO trap compared to one that contained a *M. agrestis* in the grassland during the nocturnal period. Simulation highlighted that, when all other factors are equal, the species with the highest PO effect will have the highest capture rate and therefore return more accurate population estimates. Despite the large dataset, certain species-, sex-, and/ or age-combinations were under-represented, and thus no effects of any additional individual-specific characteristics could be evaluated. Uniquely marking individuals would allow for the PO effect to be disentangled from other biases such as trap-shyness and spatial heterogeneity, but may not be possible in all cases and will depend on the aims of the study and the resources available.

Introduction

Small mammal community dynamics are typically studied using single capture live traps (Gurnell and Flowerdew, 2006). Many small mammals live in the leaf-litter or below ground and are nocturnal. Consequently live-trapping is the most effective way to generate population estimates. Live trapping is, however, not a random sampling technique (Smith, 1968). Yet many traditional methods of estimating population densities (Minimum Number Alive (Krebs, 1966), Lincoln-Petersen Index (Lincoln, 1930; Petersen, 1896)) rely on an equal chance of capturing each species (or sex) present inside the trapping grid (Bailey, 1951, 1952; Jolly, 1965; Petersen, 1896). Methods have been developed to account for some of these issues (Cubaynes et al., 2010; Huggins, 1989, 1991), but they require for each animal to be marked uniquely. Nevertheless as marking each animal uniquely can be logistically difficult and costly in terms of resources, it is not always implemented; instead animals are marked to identify recapture only. One potential bias that is rarely considered when looking at rodent communities, is the behavioural responses to the trap, and in particular how the previous trap history affects trappability of particular species or sub-groups (e.g. different sex/age classes of individuals)(Stoddart and Sales, 1985; Summerlin and Wolfe, 1973). Can this process generate sufficient bias to invalidate assumptions about small mammal community dynamics based on standard trapping protocols when individuals are not uniquely marked?

Traps are usually set for a number of consecutive nights (Strachan, 1995), and checked once or multiple times each day depending on the trap type, grid configuration, habitat, environmental conditions and species (Krebs, 2006). The chance of capturing a particular individual or species, during any given trapping period, is comprised of three components (Stoddart, 1982a) (i) the mechanical effective-

ness of the trap being used, (ii) the chance that the trap will be encountered, and (iii) the behavioural response to the trap (trap-shyness/boldness of the individual or species). All three components can generate biases that influence the results obtained from small mammal trapping. The mechanical effectiveness, varying with trap type, can result in variation in trap rates of different species/sub-groups (for review see (Gipps, 1985)). The encounter chance can change due to the number of traps placed during the trapping and their spacial positioning in the macro- as well as micro-habitat (Gurnell and Langbein, 1983); as the number of traps encountered by all individuals will not be the same (Montgomery, 1979; Myllymäki, 1977). The heterogeneity of individual-, sex- and species-specific behavioural responses to a trap is governed by a number of factors; some species are neophobic and thus exhibit an aversion to new objects within their range, the temporal length of which can vary among species. To counteract this effect, trap prebaiting, where the trap is locked open for a period of time before trapping, with bait available inside the trap, is often used (Edalgo and Anderson, 2007) to allow all individuals in the population to become familiar with the trap (Gurnell and Flowerdew, 2006). Mounting evidence, however, suggests that familiarity with the trap is not the most important factor determining whether an individual will enter. The olfactory cues in and around a trap can also greatly influence trap entry (Stoddart and Smith, 1986).

It is common for the traps to not be cleaned at each trap check and bedding to be re-used, potentially leaving olfactory cues (faeces, urine-soiled bedding etc) in the traps. Small mammals rely heavily on olfactory cues when foraging, to gain information about their environment (Shillito, 1963), conspecifics (including sex) and other species. The utilisation of areas that smell of predators and other competitive species is often reduced (Herman and Valone, 2000). This scent-

contamination results in the possibility that recent trapping history can alter the probability of future captures, such as capturing rodents of the same/different sex or species to the previous trap occupant on any given night (Rowe, 1970; Stoddart, 1976, 1980, 1982a,b, 1983; Stoddart and Sales, 1985). Olfactory cues provide mammals with numerous details about the scent-donor (i.e. the individual from which the odour originated). The response to olfactory cues left in traps can vary depending on the species (Stoddart, 1983), sex (Drickamer, 1995; Gurnell and Little, 1992; Simeonovska-Nikolova, 2007), breeding condition (Daly et al., 1980), age (Stoddart and Smith, 1986), social ranking (Daly et al., 1978; Stoddart, 1982a; Summerlin and Wolfe, 1973), and deme membership (Rowe, 1970) of the previous as well as future occupant(s) of the trap. Conspecific odours can have an effect on the response of which animals enter traps (Boonstra and Krebs, 1976; Daly et al., 1980, 1978; Mazdzer et al., 1976; Stoddart, 1982b; Stoddart and Smith, 1986; Summerlin and Wolfe, 1973; Wuensch, 1982). Most studies indicate that conspecific odours are attractive, but it is also possible for conspecific odours to be repellent, where the repellent affect results from the relative social standing of the respective individuals (i.e, subordinate individuals avoid traps scented by dominant animals: (Daly et al., 1978; Stoddart, 1982b; Summerlin and Wolfe, 1973)). Conversely, the response to inter-species heterospecific odours, varies not only with the species involved (Stoddart, 1983) but interestingly also with season (Hayes et al., 2006; Simeonovska-Nikolova, 2007). Among rodents, the detection of heterospecific odours is involved in socio-spatial geometrics, and can aid in avoiding aggressive encounters between species that compete for habitat resources (Heth et al., 1996; Simeonovska-Nikolova, 2007).

Although the effects of odour and their potential impacts on capture success have been studied extensively (Tew et al., 1994), few studies have investigated large-scale

trapping data to uncover the implications of these effects on species community composition and relative abundance. Here we use long-term, low-intensity trapping data collected over 10 years to determine the effects of the species (and sex) of the previous animal occupying a trap on subsequent occupancy, and thus on the derived population estimates, while taking into account other factors (such as habitat, trap time and season) that can impact trappability. We then apply the effects of these biases to mathematical simulations to model how significant/extensive the implications of trap occupancy could be on population estimates.

Methods

Ethical Statement

All small mammal trapping and handling undertaken in this study was approved by institutional ethical review (Animal Welfare and Ethical Review Board U1; Department of Zoology; University of Oxford). The Longworth traps used included shrew escape holes, although a Shrew Trapping Licence (under the UK Wildlife & Countryside Act, 1981) was in place for incidental captures. Traps were provisioned with bait, including a source of moisture, placed in shaded areas and checked early morning and evening. Fur clips were used as a sufficient, non-invasive identification method, and thus this work fell below the threshold of the UK Animals (Scientific Procedures) Act, 1986. Work was conducted on an Estate (Wytham) owned by the University of Oxford, and all permissions were in place via the Wytham Research Committee.

Data collection

Trapping data were collected in Wytham Woods, Oxfordshire, UK (SP462080) during 17 trapping sessions between August 2002 and November 2013, comprising 2 different habitat types (mixed woodland and calcareous grassland), for a total

trapping effort of 8,115 trap nights (for details see S2.3 Table). For a detailed description of the site see Savill et al. (2010).

Following the methodology described in Buesching et al. (2008), trapping was conducted with Longworth traps, equipped with shrew escape holes. Traps were provisioned with hay for bedding and baited with a mixture of grain and hamster food, with carrot or apple as a source of moisture, and traps placed in the open were shaded with vegetation across the nest box. The traps were initially set in the evening and then checked the following morning. They were left set for the period of trapping (either 3 or 4 nights) and checked twice daily, morning and evening (intervals not exceeding 14 hours), giving data for both nocturnal and diurnal activity. Bedding was replaced only if it was damp or in the rare event that the trap had caught a weasel, in which case both bedding and trap were replaced (only 7 weasels were caught over the study period). Individuals were marked with fur clips (Gurnell and Flowerdew, 2006) as a means of identifying either individuals or batches of captures, depending on specific study foci. The same traps were used for all the trapping sessions, traps were only replaced when damaged or worn (<50 over the years). The traps were not left out between trapping sessions; they were cleaned from all bedding, food remains, faeces and urine, and stored in metal boxes with lids but not washed between trapping sessions. The traps were only ever used in the Wytham Woods study area.

Comparisons between species capture probabilities were made using Welch's unequal variances t-test, with the reported degrees of freedom approximated using the Welch-Satterthwaite equation for the variance estimate.

Species Models

To understand how the previous occupant (PO) affected subsequent occupants (SO), Generalised Linear Models (GLMs) were fitted to the data; one model for

each of the three main species caught, wood mice (*Apodemus sylvaticus*), field voles (*Microtus agrestis*) and bank voles (*Myodes glareolus*). The response variable recorded whether an individual of the focal species had been caught (1) or not (0) in each trap on each trap night. As these data were distributed binomially, a logit link function was employed. Although there is the possibility of three species of PO, field voles were almost exclusively found in the grassland and bank voles in the woodland, thus PO was included in the models as a two level explanatory factor, with the values mouse or vole. The models only included traps that had previously caught a rodent during the current trapping session, and it was assumed that the last occupant in the trap was the one that had the greatest impact on subsequent captures. Additionally the data were subsetted to remove the very rare cases were a bank vole was caught in the grassland or a field vole in the woodland. Month was included in the models to account for any seasonal factors affecting intra-annual variation in trappability such as breeding condition, weather etc. Cumulative number of trap checks was included to account for temporal variation in capture probability (e.g. due to decrease in human scent, habitation / possible reduction neophobic response to traps). To determine if there was any deterioration of the PO effect during the trap session, the number of trap checks since the last capture was also included. Habitat was included as a two level factor for wood mice. All statistical analyses were conducted with R version 3.1.0 (R Core Team, 2014). The models with all the explanatory variables and their two-level interactions were fitted to the data and then simplified, by model reduction, until the minimal model was determined (Crawley, 2013). The R predict function was used to derive probabilities for the previous occupant effect, from the three models for both the diurnal and nocturnal periods.

Sex Models

To assess the impact of PO sex on subsequent trap success, a proportion test (prop.test (R Core Team, 2014)) was run for the three species. For this analysis, a subset of the data was used to include only trappings where PO and SO involved the same species. It was not possible to include sex in the Species Models because, despite of the large dataset, not enough individuals of each species/sex combination were caught causing certain classes of event to be very rare (for further description of problem see Gurnell and Little (1992)).

Simulation

To understand under what circumstances the PO effect can bias population estimates, a simulation was coded in Java (version 1.8.0). The parameters for the simulation are listed in S2.1 Table. Each simulation was run for the woodland habitat and the grassland habitat separately. As above, the simulation only considered wood mice and the one vole species in each habitat type. The parameter values for the simulation were calculated from the data (see Simulation section in Results) and the species models (see Species models section in Results).

The simulation determined the chance of capturing any uncaught individuals in a given trap based on the parameter values. Therefore capture chance for an uncaught individual was based on its species (M_c or V_c), and if there was a PO in the trap. In this case a multiplier was applied to the value depending on if the PO was of the same or different species (M_s, M_d, V_s or V_d). Finally this value was divided by the total number of individuals in the population of the same species as the uncaught individual ($N(mice)$ or $N(voles)$). This then gave the final capture chance for the individual. To determine which, if any, individual was caught in a trap, Java's TreeMap class was used (Oracle, 2015). The process can be visualised as a bar that runs from 0 to 100, where the available individuals are

placed along the bar, with the amount of bar they occupy determined by their capture chance. The system then randomly chooses a location along the bar, if an individual occupies that location, then it is caught, otherwise no capture is made. For a formalisation of the simulation, see S2.1 Text.

To understand how the PO effect influences capture rate, with differing numbers of each species in the population, the simulation runs were repeated twice. First with an equal number of each species (20 mice and 20 voles), and second with unequal numbers, 20 mice to 5 voles for the woodland habitat and 20 mice to 80 voles in the grassland habitat. In both cases the number of traps was set to 50. As population estimates derived from our data set could be biased by the PO effect, the species population numbers used above were estimated from the literature (Harris and Yalden, 2008), with 50 traps representing a trapping area of approximately half a hectare. The capture proportions were then compared, with capture proportion being defined as the number of individuals of a particular species caught divided by the total number of individuals of both species caught during the trapping session. The expected capture proportion for voles $E_v = \frac{N(voles)}{N(voles)+N(mice)}$ was compared to the vole capture proportion from the simulation $S_v = \frac{n(volescaught)}{n(volescaught)+n(micecaught)}$ using a one-sample t-test. The simulated capture proportion for voles S_v was also compared against the expected capture proportion based on the capture chance without any previous occupant effect $C_v = \frac{V_c}{V_c+M_c}$ using a one-sample t-test.

Finally, to determine how differing levels of the PO effect can bias the estimates from small mammal studies, the simulation was run multiple times with both species being set to the same constant parameters values except for the mouse same species multiplier which was varied from 0.1 to 4 by increments of 0.01. The capture chance for both species was set to 20% and the other PO multipliers set to 1, with 50 traps over 5 trap checks and 50 individuals of both species.

Results

During the study period, a total of 1,343 traps were set, comprising 8,115 trap checks, which resulted in 359 captures (251 individuals) of wood mice (*Apodemus sylvaticus*), 325 captures (149 individuals) of field voles (*Microtus agrestis*), and 257 captures (171 individuals) of bank voles (*Myodes glareolus*), totalling 941 captures (571 individuals) across the three species. Yellow-necked mice (*Apodemus flavicollis*) were excluded from all analyses as only one individual was caught. Due to the shrew escape holes, data on shrews were not recorded. In the woodland, traps that had not caught an individual previously (no previous occupant (PO) effect), caught wood mice (8.26%) more often than bank voles (3.95%) during the nocturnal period ($\mathbf{t}(3919)=5.97$, $\mathbf{p}<0.001$) but, as expected from their biology, during the day bank voles (2.02%) were more likely to be caught than were wood mice (0.63%) ($\mathbf{t}(2261)=-3.27$, $\mathbf{p}=0.001$). In the grassland, field voles were more likely to be caught both during the nocturnal (4.51%) ($\mathbf{t}(2601)=-6.53$, $\mathbf{p}<0.001$) and the diurnal (3.48%) ($\mathbf{t}(1467)=-6.90$, $\mathbf{p}<0.001$) periods than were wood mice (0.99%/0.07%, respectively). If the trap had a PO, there was a strong bias towards trapping same-species occupants subsequently (Fig 4.1). The proportion of traps capturing an animal initially (no PO) were higher during the nocturnal trapping period (woodland 12.21 %/ grassland 5.50%) compared to the diurnal period (woodland 2.64% / grassland 3.55%) for both habitats (Woodland $\mathbf{t}(3371)=11.68$, $\mathbf{p}<0.001$, Grassland $\mathbf{t}(3217)=2.69$, $\mathbf{p}<0.01$). This held for wood mice (nocturnal 4.96% / diurnal 0.35%) ($\mathbf{t}(4796)=12.76$, $\mathbf{p}<0.001$) and bank voles (nocturnal 2.30% / diurnal 1.09%) ($\mathbf{t}(6835)=3.96$, $\mathbf{p}<0.001$) but not field voles (nocturnal 2.08% / diurnal 1.72%) ($\mathbf{t}(6445)=1.08$, $\mathbf{p}=0.2824$).

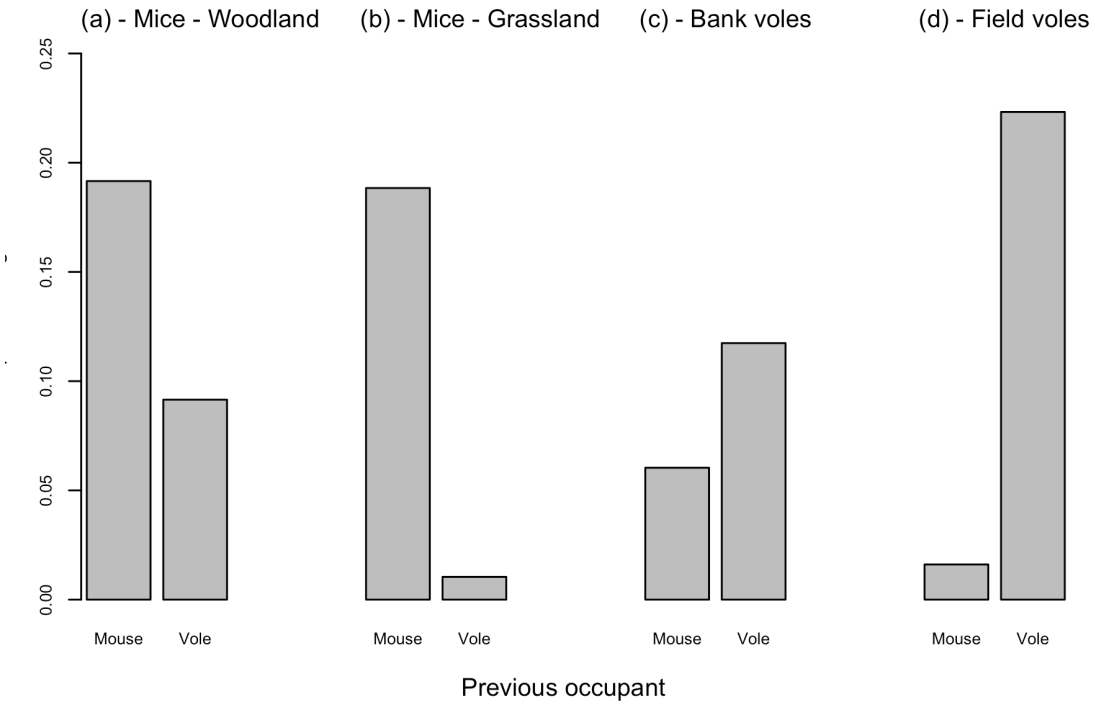


Figure 4.1. The proportion of each species caught. Depending on the previous occupant in the trap. The values were calculated from the raw data.

Species models

A preference for conspecific POs was evident in all three models; with wood mice not being caught as frequently in vole (either bank or field vole) scented traps compared to mouse-scented traps (-3.36 ±0.61, **z**=-5.55, P<0.001) and both bank voles (1.58 ±0.24, **z**=6.49, P<0.001) and field voles (1.36 ±0.46, **z**=2.96, P<0.01) preferring vole-scented traps compared to mouse-scented traps. For wood mice, PO was the second most influential explanatory variable, after trapping time (diurnal or nocturnal) in explaining variance of trap success in the model; for bank voles and field voles, PO explained the most variance (Table 4.1). Capture rates were lower during the diurnal period compared to the nocturnal period for all three species models (wood mice: -3.43 ±0.41 **z**=-8.33, P<0.001; bank voles: -0.81 ±0.23, **z**=-3.46, P<0.001; field voles: -0.65 ±0.21, **z**=-3.10, P<0.01), as would be expected

from the biology of these species. For wood mice there was an interaction between habitat and PO (Fig 4.2), with higher capture success when bank voles were the PO in the woodland habitat (2.41 ±0.66, **z**=3.64, P<0.001). Estimates from the predict function inferred that same-species predominated in PO traps, with higher values during the nocturnal period compared to the diurnal period (Table 4.2).

Table 4.1. The explained deviance percentage for each of the covariants in the three species GLMs

	Explained deviance %		
	Wood mice	**Bank voles**	**Field voles**
Previous Occupant	26.6	69.8	30.3
Trapping Time	54.0	15.4	9.4
Trapping Month	9.0	14.8	26.2
Habitat	5.2		
Previous Occupant / Habitat	5.2		
Trap Checks			7.6
Trap Checks since last capture			26.5

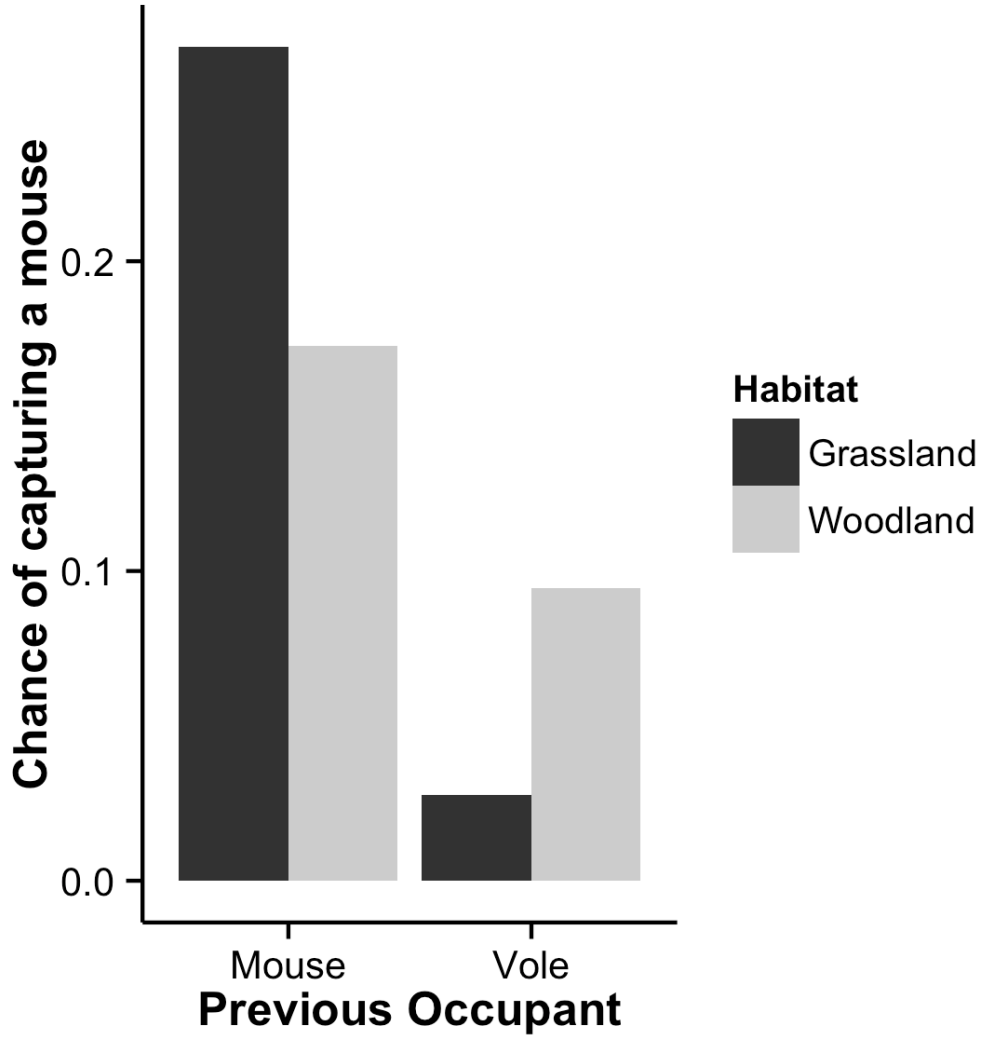


Figure 4.2. Previous Occupant, habitat interaction plot for wood mice. The interaction would suggest that the effect the PO is less pronounced in the woodland compared to the grassland Habitat. Wood mice are less likely to enter traps that previously contained field voles compared to those that contained bank voles.

Table 4.2. Predicted Captures Probabilities from the three species GLMs

			Capture probabilities	
Species caught	**Habitat**	**Trapping Time**	**Previous mouse**	**Previous vole**
Wood mouse	Woodland	Nocturnal	0.3229	0.1801
Bank vole	Woodland	Nocturnal	0.0750	0.2611
Wood mouse	Woodland	Diurnal	0.0226	0.0090
Bank vole	Woodland	Diurnal	0.0354	0.1445
Wood mouse	Grassland	Nocturnal	0.4882	0.0537
Field vole	Grassland	Nocturnal	0.1413	0.3166
Wood mouse	Grassland	Diurnal	0.0504	0.0020
Field vole	Grassland	Diurnal	0.0878	0.2216

Sex models

There was a higher probability for female field voles to enter traps that contained females previously, compared to any other sex pairings ($x^2(3)$=99.46, $\mathbf{p}$<0.001). A similar trend was apparent in bank voles although the effect was slightly below significance ($x^2(3)$=7.73, $\mathbf{p}$=0.052). Wood mice, however showed no evidence of this effect ($x^2(3)$=3.62, $\mathbf{p}$=0.31) (S2.2 Table).

Simulation

The parameters used in the simulation for the initial species capture probability were calculated from the data directly (Table 4.3) and from the Species models, for the PO multipliers, using the R predict function (Table 4.2). The values of the parameters highlighted that all traps that had a previous occupant also had a higher projected chance of capturing a SO, compared to traps that had not yet caught an animal. In the grassland there was a higher probability of projected

capture for wood mice when the PO was the same species compared to no PO (49.31 times greater for diurnal period and 72 times greater for the nocturnal period (S2.4 Table)), if the initial capture chances for mice and voles were equal, but the sum of the species multipliers were not, then there would be a bias due to the PO effect (S2.1 Text).

Table 4.3. Capture probabilities for wood mice, bank voles and field voles in the two habitats, for both time periods. The values were averaged from the raw data.

Species caught	Habitat	Trapping Time	Capture probabilities
Wood Mouse	Woodland	Nocturnal	0.0826
Bank vole	Woodland	Nocturnal	0.0395
Wood mouse	Woodland	Diurnal	0.0063
Bank vole	Woodland	Diurnal	0.0202
Wood mouse	Grassland	Nocturnal	0.0099
Field vole	Grassland	Nocturnal	0.0451
Wood mouse	Grassland	Diurnal	0.0007
Field vole	Grassland	Diurnal	0.0348

The results from the simulation are summarised in Figs 4.3 and 4.4, S5 and S6 Tables. When simulating with equal species population densities, in the woodland nocturnal simulation fewer voles were caught than expected from the population density but more than would be expected due to capture chance alone, indicating a PO effect in favour of voles. The PO effect in favour of voles was also evident in the diurnal woodland simulation. In the grassland simulation, voles dominated both the nocturnal and diurnal periods, but field vole captures during the nocturnal period were lower than would be expected from the capture chance alone, indicating a PO effect in favour of the mice. When the simulation was set for

unequal population densities (4 mice to 1 bank vole in the woodland and 1 mouse to 4 field voles in the grassland) in the woodland, during both periods there was a PO effect in favour of the mice, which was also the case during the nocturnal period in the grassland. But during the diurnal period, in the grassland, the PO effect favoured the field voles.

Repeating the simulation with an increasing mouse same species multiplier (M_s), the number of mice caught compared to voles increased with increased values of M_s. When all other values were equal for both species (Fig 4.4) it is evident that PO effect can bias population estimates. An increasing M_s only slightly decreased the number of voles caught but the increase in mice caught was clearly visible in the results (S2.1 Figure).

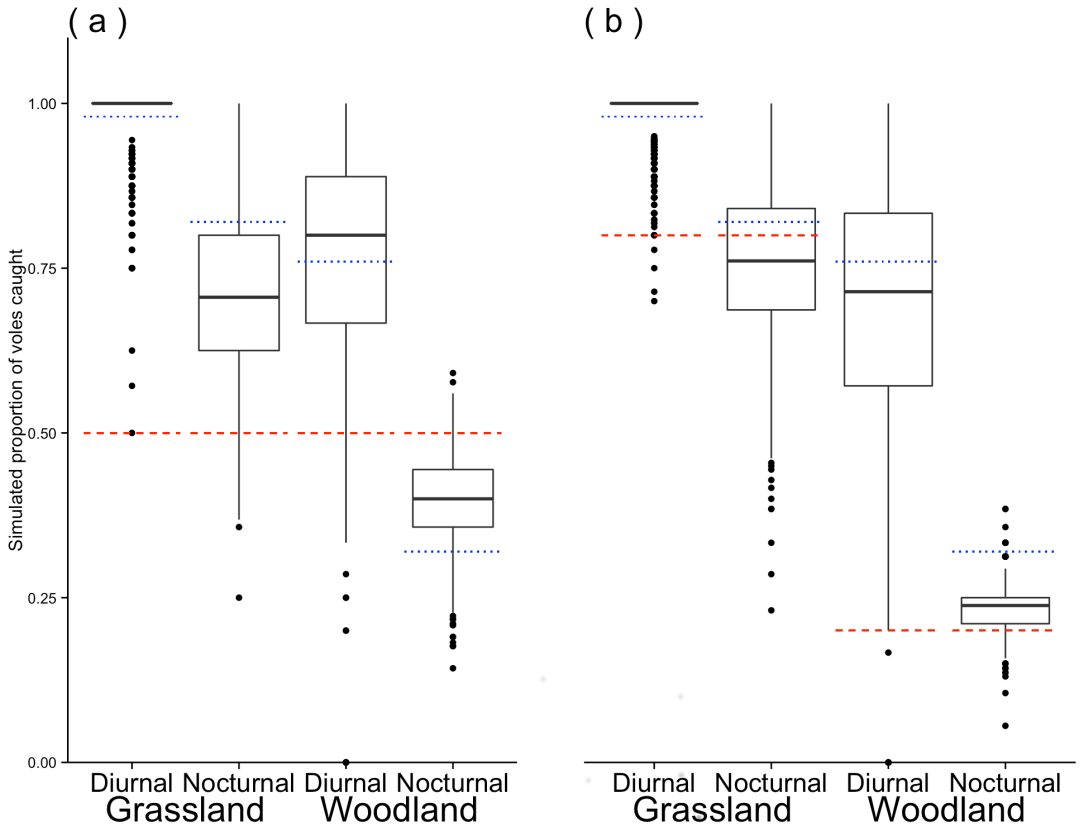


Figure 4.3. Simulated captures showing the proportion of voles caught. (a) with a 1:1 species ratio of mice to voles, (b) with a 1:4 species ratio of mice to voles in the grassland and a 4:1 ratio of mice to voles in the woodland. The red dashed line indicates the expected proportion of voles caught during the trapping simulations based just on the species ratio E_v. The blue dotted line represents the expected proportion of voles caught during the trapping simulations based on the capture chance without any previous occupant effect C_v. Capture proportion being defined as the number of individuals of a particular species caught divided by the total number of individuals of both species caught during the trapping session.

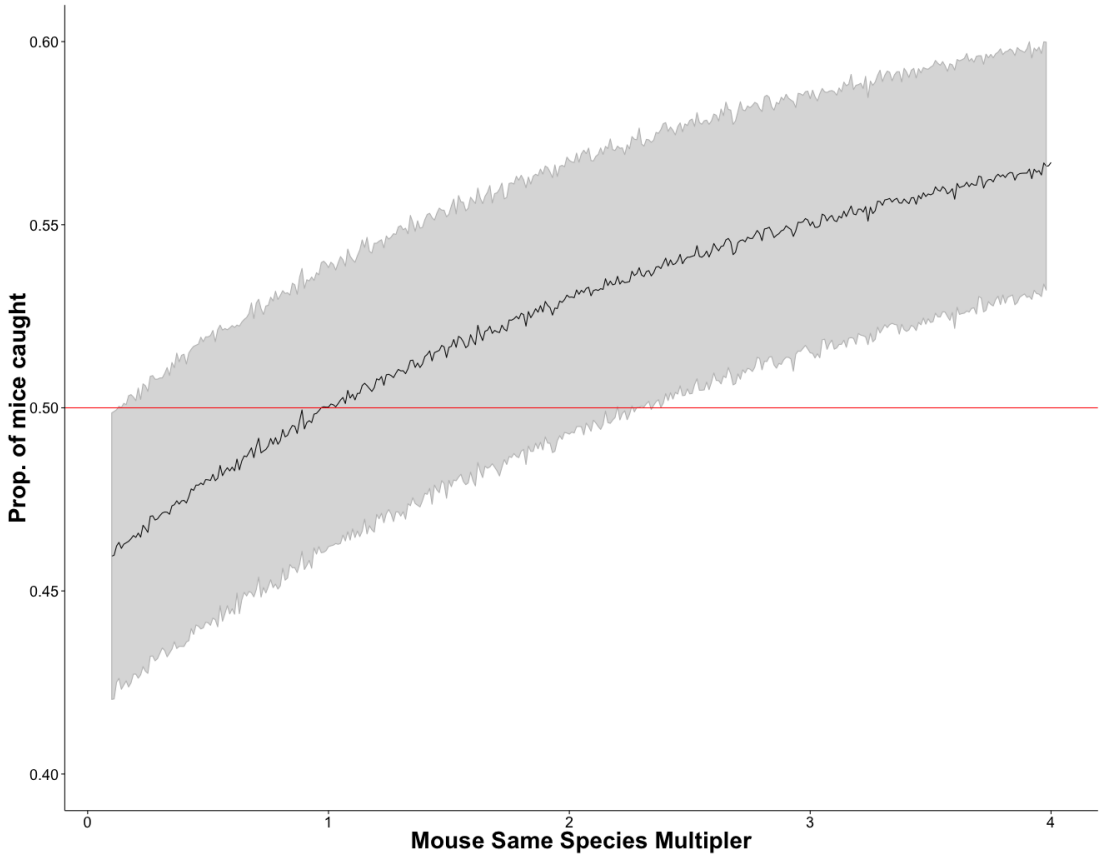


Figure 4.4. Repeat runs of simulated captures varying mouse same species multiplier. The proportion of mice caught compared to voles, for increasing values of mouse same species PO multiplier (C_s). The initial capture chance was 20% and the other PO multipliers were set to 1.0 for both species and kept constant for all runs of the simulation.

Discussion

Live trapping is central to the study of small mammal population dynamics. Consequently it is important to understand any potential biases that may arise from the methods employed. The biases that result from the mechanical effectiveness of traps and their placement within the habitat have been accounted for historically by randomising the placement of the individual traps and making sure that enough traps are deployed, so that a significant proportion are left empty during the trapping (Gurnell and Little, 1992). Nevertheless the behavioural re-

sponse to traps is rarely considered. Therefore this study focused on distinguishing the effects of species and sex on recapture rates recorded during traditional trapping studies. Previous studies have demonstrated the importance of olfactory cues in determining subsequent captures (Stoddart and Sales, 1985; Summerlin and Wolfe, 1973). The previous occupant (PO) effect, in traditional trapping data, encapsulates an individual's prior knowledge of the trap as well as the non-random distribution of rodent species (Kikkawa, 1964; Smith, 1968; Wolton and Flowerdew, 1985) in addition to trap-specific olfactory cues from potential other same- or different species- POs.

This study clearly shows that the PO can lead to a strong bias in subsequent captures. The significant tendency for all three species to enter traps with a same-species PO, observed in this study is in accord to what has been found previously (Stoddart and Smith, 1986). The PO effect can be seen clearly in the simulation results, for example in the grassland habitat during the nocturnal period, vole numbers were lower than would be expected from capture chance alone. Traps with no PO had a lower capture rate in all cases. Although this may suggest strong benefits of pre-baiting to increase the capture rate, caution is required. The benefits of increased captures, at the start of trapping, have to be balanced against the potential bias that can result due to the unknown (potentially multiple) POs. Previous studies have shown a higher trappability for all three species reported in this study (Jensen, 1975; Krebs and Boonstra, 1984), although our low capture probability may be due in part to the neophobic response to traps (in particular field voles). The high multiplier value for mouse PO effect, during the diurnal period, in the grassland also deserves consideration. Although the high value would suggest increased captures, it is still reliant on having a PO in the trap, the chance of which is low due to the low initial capture chance. The results from the sim-

ulation reflect this with nearly all captures during the diurnal period being voles. This is also correct from what we know about wood mice, which are nocturnal and rarely active during the day.

The species models and the simulation concentrate on the species level effects and did not consider additional characteristics of the individuals. Even though we had a large dataset, certain combination of characteristics were under-represented in the data and could not be analysed; we were reliant on PO providing the 'test' traps for subsequent captures (Gurnell and Little, 1992). The sex models only showed a significantly higher probability for female field voles to follow female field voles, but it is conceivable that additional factors are in effect, but could not be detected, as we could not include other characteristics. Breeding condition (Daly et al., 1980) and age (Stoddart and Smith, 1986) of both, the PO and SO have been shown to influence trap entry decisions. In addition it has been suggested that social rank (Daly et al., 1978; Stoddart, 1982a; Summerlin and Wolfe, 1973) and deme membership (Rowe, 1970) can influence the decision to enter the trap, although it is not possible to detect these influences from standard trapping data.

The trapping rates during the nocturnal and diurnal periods conformed with what is known about the activity patterns of the three species; wood mice are substantially nocturnal and voles are cathemeral, with bank voles having peaks of activity at dawn and dusk (Harris and Yalden, 2008). Consequently, mice were rarely caught during the day, while vole captures were almost evenly distributed between morning and evening captures. Because mice and voles both preferentially choose traps that had caught a PO of the same species, this could have a strong bearing on when researchers should put out the traps to estimate population densities; for example if traps are first deployed in the evening after sunset, population estimates will be more accurate for wood mice. As olfactory cues can

remain in the traps (Drickamer, 1995) for at least as long as most trapping surveys are conducted, the effect of first trap placement time can persist throughout the whole survey.

Small mammal trapping can be employed to answer a variety of different research questions, and, the importance of the issues highlighted above will vary between them. If the study is only interested in confirming presence / absence of species in a particular area, then the PO effect may be of little importance. But if accurate population estimates are required, then it is possible that the conclusions drawn from traditional data may be inaccurate. For example it has been suggested that small mammals can be used as environmental indicators (Macdonald et al., 1998) of climate change or for habitat degradation and the impacts of habitat interventions, such as forestry operations. The PO effect will be particularly problematic if the aim of the study is to census multiple small mammal species in the same habitat and their interactions.

Traditional methods of estimating population densities rely on equal chances of capture. The issues highlighted above can all lead to bias in the estimates from these methods. If individuals are marked uniquely, then more advanced statistical methods such as MARK (White and Burnham, 1999) or E-SURGE (Choquet et al., 2009) can be used to disentangle the PO effect due to behavioural choices (for example due to the olfactory cues) from repeat captures of the same individual. Unfortunately, marking of individuals can be difficult as the standard fur clipping patterns only allow a finite number of unique marks (Gurnell and Flowerdew, 2006) and PIT tagging individuals requires a higher level of competence. Replacing the traps that have caught an animal with a clean trap may be possible in some situations, which would remove the bias due to olfactory cues left in the traps. Nevertheless, this could potentially reduce total capture rates. Interestingly, in a

previous study, no significant effects on trappability have been found due to odours left from washing the traps in a bleach solution (Yunger and Randa, 1999). The formalisation of the simulation suggests that, when all other factors are equal, the species with the highest PO effect will have a higher capture rate. This is in accordance with what has been suggested for the olfactory cues left in the traps (Gurnell and Little, 1992). The simulation also suggests that the PO effect can interact with other bias to either magnify or reduce them to a greater or lesser extent.

In summary the PO effect can bias the estimates obtained from repeat trapping and traditional population estimation methods. It is possible to detect some of the biases due to the PO effect in traditional trapping data. Using clean traps to replace traps that have caught animals can reduce the bias due to the olfactory clues, but may also reduce total capture rates. If individual marking is not practical, then designing the experiment so that enough traps are left empty during the trapping to always give individuals a choice of traps (Gurnell and Little, 1992), may reduce (albeit not eliminate) these biases. Including additional analyses, as we have done here, may provide an idea of the strength of the PO effect, which should be taken into account in any conclusions drawn from the study. In contrast, in mark-recapture studies of uniquely marked individuals it is possible to correct for trap-happiness, trap-shyness, spatial heterogeneity in capture and survival probability, as well as covariates that can impact each of these processes. Unfortunately it is much harder to correct for these processes in systems where individuals are not identified uniquely. However, even here, these processes will still have the potential to bias results. If an in-depth knowledge of the population dynamics is required then collecting life history data for individuals at regular intervals instead of repeat trapping may be most appropriate. Collecting data in this way, allows the use of

more advanced models such as Integral Projection Models (IPMs) (Coulson, 2012). Additionally recent advances in technology are offering promising alternative ways to estimate population densities of small mammals (Villette et al., 2015). In the end the best methods to use will depend on the aims of the study and the resources available.

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Supporting Information

S2.1 Table

Simulation Parameters. The values for these parameters were calculated from the raw data and from the species models using the R predict function.

S2.2 Table

Test of the equality of proportions for each sex caught, depending on the previous occupant's sex, for each of the three species. Wood mice (*Apodemus sylvaticus*), bank vole (*Myodes glareolus*) and field voles (*Microtus agrestis*). Column headers indicate the sex of the two individuals, e.g. FM = Female previous occupant, followed by a male subsequent occupant.

S2.3 Table

Trap session details. Includes the habitat type the trapping was conducted in, the start date of the trapping and when the trapping concluded.

S2.4 Table

Simulated scenarios. All the simulations were run 1,000 times with 50 traps over 5 trap checks. The M_c and V_c values are taken from the capture proportions and the M_s, M_d, V_s and V_d, values are calculated from the predicted capture proportions.

S2.5 Table

Expected vs simulated vole proportions. Results of the t-tests comparing the expected vole proportion E_v against the results from the simulations S_v.

S2.6 Table

Capture Chance vs Simulated. Results of the t-tests comparing the expected vole proportion based on the capture chance without any previous occupant effect C_v against the results from the simulation S_v.

S2.1 Text

Formalisation of Simulation.

S2.1 Code

Simulation source code. The Java source code for the simulation. Java 1.8 is required to compile and run the simulation. Please see README.TXT in root of archive for more information. Code is available from `https://github.com/marcbrouard/SmellyMice`

S2.1 Figure

The number of each species caught, for increasing values of mouse same species PO multiplier (C_s).

S2.1 Data

Data used in the three species GLMs Includes SessionID, TrapID, Seq (trap check number), Month (1 to 12), Year, Habitat (Woodland or Grassland), Time (Nocturnal or Diurnal), Step (when was the last capture in this trap, 0 for no previous capture. Measured in trap checks), AsCaught (if a wood mouse was caught), MaCaught (if a field vole was caught), MgCaught (if a bank vole was caught), Prev (what was the last capture in the trap during the current trapping session. Vole, Mouse or NA). `doi:10.1371/journal.pone.0145006.s010`

Table S4.1. Simulation Parameters The values for these parameters were calculated from the raw data and from the species models using the R predict function.

Parameter	Description
M_c	The chance of capturing a mouse in a trap with no previous occupant.
M_s	Multiplier for the mouse capture chance that determines how a previous occupant of the same species changes subsequent capture chances.
M_d	Multiplier for the mouse capture chance that determines how a previous occupant of a different species changes subsequent capture chances.
V_c	The chance of capturing a vole in a trap with no previous occupant.
V_s	Multiplier for the vole capture chance that determines how a previous occupant of the same species changes subsequent capture chances.
V_d	Multiplier for the vole capture chance that determines how a previous occupant for a different species changes subsequent capture chances.
$N(mice)$	The number of mice in the population.
$N(voles)$	The number of voles in the population.
T	The number of traps set.
T_c	The number of times that the traps were checked during the trapping.

Table S4.2. Test of the equality of proportions for each sex caught, depending on the previous occupant's sex, for each of the three species. Wood mice (*Apodemus sylvaticus*), bank vole (*Myodes glareolus*) and field voles (*Microtus agrestis*). Column headers indicate the sex of the two individuals, e.g. FM = Female previous occupant, followed by a male subsequent occupant.

Species	FF	FM	MF	MM	X-squared	df	p-value
Wood mice	0.289	0.178	0.278	0.256	3.6148	3	0.3062
Field voles	0.543	0.154	0.167	0.136	99.4568	3	< 0.001
Bank voles	0.346	0.192	0.282	0.179	7.7265	3	0.0520

Table S4.3. Trap session details. Includes the habitat type the trapping was conducted in, the start date of the trapping and when the trapping concluded.

Habitat	**Start Date**	**End Date**
Woodland	2013-11-10	2013-11-12
Woodland	2013-11-13	2013-11-15
Woodland	2013-11-10	2013-11-12
Woodland	2013-11-13	2013-11-15
Woodland	2013-07-16	2013-07-18
Grassland	2002-08-04	2002-08-06
Grassland	2002-09-29	2002-10-02
Grassland	2004-07-09	2004-07-14
Grassland	2004-08-08	2004-08-11
Woodland	2003-07-14	2003-07-16
Woodland	2003-08-10	2003-08-12
Woodland	2003-07-24	2003-07-26
Woodland	2003-08-24	2003-08-27
Woodland	2003-09-28	2003-10-01
Woodland	2003-07-31	2003-08-02
Woodland	2003-09-27	2003-09-29
Woodland	2007-06-21	2007-06-23

Table S4.5. Expected vs simulated vole proportions. Test of the equality of proportions for each sex caught, depending on the previous occupant's sex, for each of the three species, wood mice (*Apodemus sylvaticus*), bank vole (*Myodes glareolus*) and field voles (*Microtus agrestis*). Column headers indicate the sex of the two individuals, e.g. FM = Female previous occupant, followed by a male subsequent occupant.

Species	FF	FM	MF	MM	X-squared	df	p-value
Wood mice	0.289	0.178	0.278	0.256	3.6148	3	0.3062
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Bank voles	0.346	0.192	0.282	0.179	7.7265	3	0.0520

Table S4.4. Simulated scenarios. All the simulations were run 1,000 times with 50 traps over 5 trap checks. The M_c and V_c values are taken from the capture proportions and the M_s, M_d, V_s and V_d, values are calculated from the predicted capture proportions.

	Parameters							
Scenario	M_c	M_s	M_d	V_c	V_s	V_d	M	V
Woodland Nocturnal, wood mice 1:1 bank voles	0.0826	3.91	2.18	0.0395	6.61	1.90	20	20
Woodland Diurnal, wood mice 1:1 bank voles	0.0063	3.59	1.43	0.0202	7.15	1.75	20	20
Grassland Nocturnal, wood mice 1:1 field voles	0.0099	49.31	5.42	0.0451	7.02	3.13	20	20
Grassland Diurnal, wood mice 1:1 field voles	0.0007	72.00	2.86	0.0348	6.37	2.52	20	20
Woodland Nocturnal, wood mice 4:1 bank voles	0.0826	3.91	2.18	0.0395	6.61	1.90	20	5
Woodland Diurnal, wood mice 4:1 bank voles	0.0063	3.59	1.43	0.0202	7.15	1.75	20	5
Grassland Nocturnal, wood mice 1:4 field voles	0.0099	49.31	5.42	0.0451	7.02	3.13	20	80
Grassland Diurnal, wood mice 1:4 field voles	0.0007	72.00	2.86	0.0348	6.37	2.52	20	80

Table S4.6. Results of the t-tests comparing the expected vole proportion based on the capture chance without any previous occupant effect C_v against the results from the simulation S_v.

Scenario	C_v	$\overline{S_V}$	$\overline{S_v}$ SE	t-test results		
Woodland Nocturnal, wood mice 1:1 bank voles	0.32	0.40	0.002	$t(999) =$	35.91	$\mathbf{p} =$	< 0.001
Woodland Diurnal, wood mice 1:1 bank voles	0.76	0.78	0.006	$t(999) =$	3.82	$\mathbf{p} =$	0.001
Grassland Nocturnal, wood mice 1:1 field voles	0.82	0.71	0.004	$t(999) =$	−27.33	$\mathbf{p} =$	< 0.001
Grassland Diurnal, wood mice 1:1 field voles	0.98	0.98	0.002	$t(999) =$	−1.85	$\mathbf{p} =$	0.06
Woodland Nocturnal, wood mice 4:1 bank voles	0.32	0.23	0.001	$t(999) =$	−80.36	$\mathbf{p} =$	< 0.001
Woodland Diurnal, wood mice 4:1 bank voles	0.76	0.72	0.006	$t(999) =$	−7.04	$\mathbf{p} =$	3.53
Grassland Nocturnal, wood mice 1:4 field voles	0.82	0.76	0.004	$t(999) =$	−15.99	$\mathbf{p} =$	< 0.001
Grassland Diurnal, wood mice 1:4 field voles	0.98	0.98	0.001	$t(999) =$	0.79	$\mathbf{p} =$	0.43

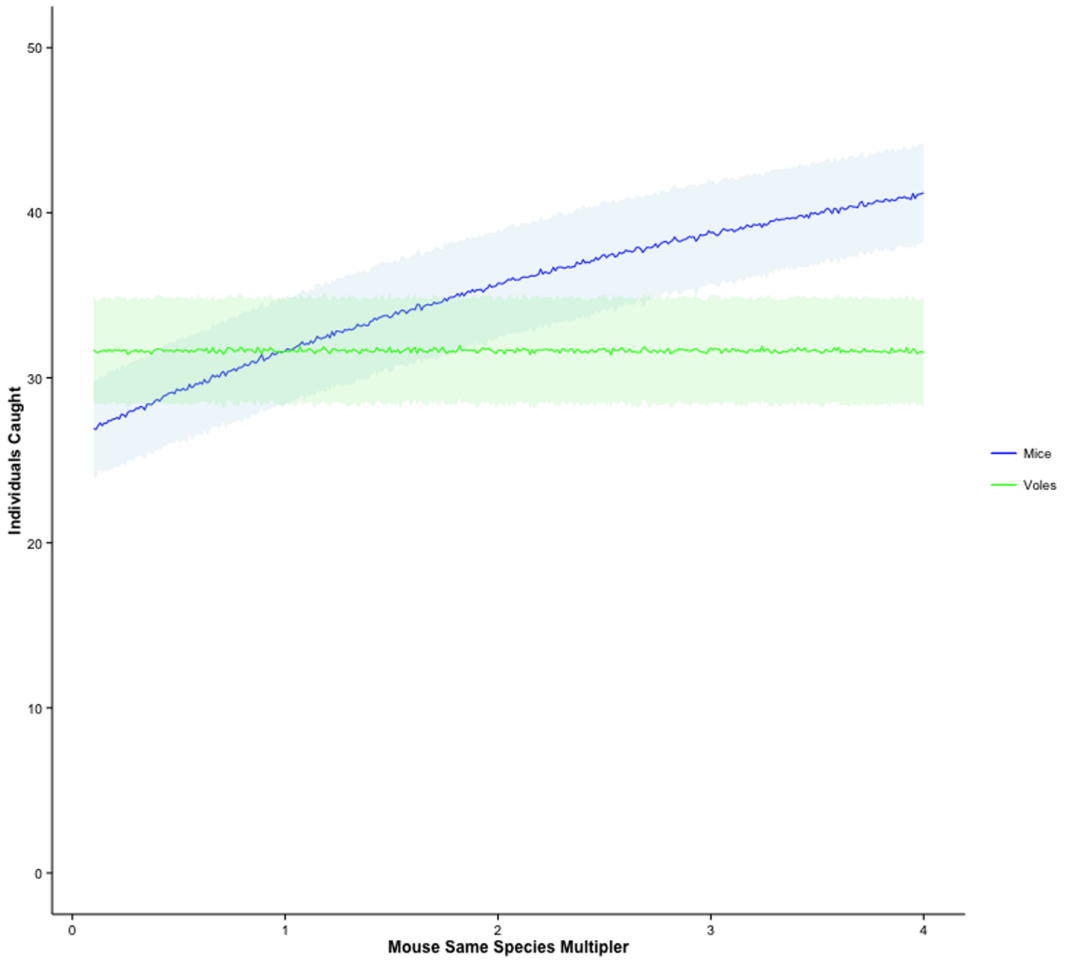


Figure S4.1. The number of each species caught, for increasing values of mouse same species PO multiplier (C_s).

Text S2.1. Formalisation of Simulation.

The simulation can formalised as follows. To avoid invalid capture chances the following restrictions were placed on the parameters:

$M_c + V_c$ must be between 0 and 1.

$(M_c \cdot M_s) + (V_c \cdot V_d)$ must be between 0 and 1.

$(M_c \cdot M_d) + (V_c \cdot V_s)$ must be between 0 and 1.

The following variables are used within the simulation.

Parameter	Description
$n(mice)$	The number of available mice, not currently caught in a trap.
$n(voles)$	The number of available voles, not currently caught in a trap.
$n(micecaught)$	The number of individual mice caught during the trapping.
$n(volescaught)$	The number of individual voles caught during the trapping.

We introduce random variables

$$c = \begin{cases} m & \text{mice caught} \\ v & \text{vole caught} \\ 0 & \text{nothing caught} \end{cases}$$

and

$$p = \begin{cases} m & \text{mice caught previously} \\ v & \text{vole caught previously} \\ 0 & \text{nothing caught previously} \end{cases}$$

We calculate that

$$P(c = m|p = 0) = \frac{M_c \cdot n(mice)}{N(mice)}$$

$$P(c = v|p = 0) = \frac{V_c \cdot n(voles)}{N(voles)}$$

$$P(c = 0|p = 0) = 1 - \left(\frac{M_c \cdot n(mice)}{N(mice)} + \frac{V_c \cdot n(voles)}{N(voles)} \right)$$

$$P(c = m|p = m) = \frac{M_c \cdot M_s \cdot n(mice)}{N(mice)}$$

$$P(c = v|p = m) = \frac{V_c \cdot V_d \cdot n(voles)}{N(voles)}$$

$$P(c = 0|p = m) = 1 - \left(\frac{M_c \cdot M_s \cdot n(mice)}{N(mice)} + \frac{V_c \cdot V_d \cdot n(voles)}{N(voles)} \right)$$

$$P(c = m|p = v) = \frac{M_c \cdot M_d \cdot n(mice)}{N(mice)}$$

$$P(c = v|p = v) = \frac{V_c \cdot V_s \cdot n(voles)}{N(voles)}$$

$$P(c = 0|p = v) = 1 - \left(\frac{M_c \cdot M_d \cdot n(mice)}{N(mice)} + \frac{V_d \cdot V_s \cdot n(voles)}{N(voles)} \right)$$

We can conclude that, if there is no difference between the capture chance for mice M_c and voles V_c, then if

$$(M_d + M_s) \neq (V_d + V_s)$$

there will be a bias in the capture rates due to the previous occupant effect.

5

Factors affecting woodland rodent growth

Running head

Factors affecting woodland rodent growth

Title

Factors affecting woodland rodent growth

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Abstract

Very little information exists on the growth rates of woodland rodents and the drivers of body size dynamics that are observed in British populations. In this study we use mark recapture data collected on two species living in sympatry, wood mice (*Apodemus sylvaticus*) and bank voles (*Myodes glareolus*). A third species of rodent, the yellow necked mouse (*Apodemus flavicollis*) was also caught occasionally. We found the density of this third species negatively impacted the growth rate of both wood mice and bank voles. Environmental factors only impacted growth for some groups of rodents and we suggest that the woodlands may partially or fully mitigate some environmental effects. No impact of conspecific population density on growth for either species was found. Previous studies have suggested high conspecific population density can impact growth for some individuals of the population, but our populations may have not reached the densities required to elucidate these effects during the study.

Introduction

Body size is an important phenotypic trait in ecology. There are a number of general rules of ecology, including Cope's rule, which states that individuals of a species will increase in size with evolutionary time (Stanley, 1973). Although there are a number of exceptions to this rule, including the weasel *Mustela nivalis* (King, 1989) which has evolved a smaller size over time, most species adhere to these general patterns. However, why we see these general rules is a bit of an enigma, particular because within populations larger individuals are frequently fitter than their smaller conspecifics yet body size does not tend to evolve as predicted by theory (Merilä et al., 2001). However, for many free-living species, including rodents, little is known about the dynamics of body size. Hone and Benton (2005)

lists the advantages and disadvantages of a large body size, but for rodents there is additional advantages to have a smaller size. They are able to increase their reproductive effort quickly when there is increases in food supply (Watts, 1970), by having more litters with more offspring in each litter. In the case of wood mice (*Apodemus sylvaticus*) their small size allows them to utilise the trees in the woodland to avoid predation and conflict with other species (Buesching et al., 2008).

Understanding the development of individuals, and in particularly how they grow and the factors that influence their growth rates, is a core component of mammal ecology. Larger individuals are often fitter than smaller individuals in the same population. Their increased fitness comes from an increased ability to avoid predators, to compete more strongly for mates or resources, or lower thermal regulation costs due to a lower surface to volume ratio compared to their smaller conspecifics. However, larger individuals do require more resources (Hone and Benton, 2005).

Very little information exists for growth patterns of wild, free-ranging rodents; population studies of rodents have tended to concentrate on density rather than phenotypic characteristics of individuals. However, body size has been proposed to covary with density in many populations, so an understanding of what drives changes in population size could help increase our understanding of the body size dynamics of rodents. In this study we look at what drives the growth of rodents in native British woodlands. Rodents provide a good study system for this kind of work. They have short generation times, so in any given year the majority of individuals will have been reared under the same ecology. This means that we can be more confident in how ecology is driving the body-size dynamics, with the potential knock-on effects on populations. But before we consider rodent growth

we start by considering factors that influence population dynamics at a general level.

The dynamics of population density have been studied intensively. Food availability is a major factor influencing population density (Montgomery and Montgomery, 1990), but it is by no means the only factor, with some species having found ways to mitigate or offset periods of limited food availability. For example *Apodemus spp.* will cache seeds throughout their range for later consumption (scatter hoarding) (Vander Wall, 1990). For some species, cover has also been found to be important, *Myodes glareolus* have been found to preferentially choose areas of dense cover over those with high food availability (Mazurkiewicz, 1994), but cover is less important for *Apodemus sylvaticus* (Fernandez et al., 1994; Kotzageorgis and Mason, 1997; Mazurkiewicz, 1994). Abiotic environmental factors can also have an impact, with cold, wet periods reducing foraging activity (Brown, 1956) and periods of high moon illumination having also been reported to reduce foraging activity too (Orrock et al., 2004). Biotic environmental drivers can also have an effect on population dynamics: aggressive behaviour by adults at the beginning of the breeding season can increase juvenile mortality (Flowerdew, 1974; Montgomery et al., 1997). Finally some studies have suggested density-dependence (Watts, 1969), whilst others have found that heavy mast crops can mask density dependent patterns (Flowerdew, 1985).

Wild populations do not increase without limit: all populations must be regulated in some way (Krebs, 1978). A number of mechanisms have been proposed to explain this regulation along with factors that generate the variation in population size observed over time, including the Chitty hypothesis of population regulation.

This hypothesis states that all species are capable of self regulation, but Chitty (1967) noted that not all populations are self regulated (e.g. invasive species). Chitty's study of voles (1952; 1957; 1960) revealed a multi-year cycle in population numbers, with declines even in apparently favourable years. This gave him the idea that large population effects can be caused by the behaviour of a few individuals. At high densities individual voles existed that were larger and very aggressive; these individuals reduced the space available to, growth and reproduction of the rest of the population. He further suggested that these effects were partly phenotypic and partly genetic (Chitty, 1967).

Although Chitty's hypothesis has generated considerable interest, the growth patterns of individuals has received less interest. It is known that woodland rodents show different growth trajectories depending on whether they are born at the beginning of the breeding season or towards the end (Schwarz et al., 1964). Individuals born at the beginning of the breeding season grow and mature quickly and are able to breed in the same year, while late born individuals do not become sexually mature until the following spring (Green, 1979). When food is plentiful, it is possible for the breeding season to be extended and in some cases for the non-breeding season to be skipped altogether (Montgomery et al., 1991), but high population densities can inhibit breeding. High population densities can also retard growth in *M. glareolus* (Kviljo et al., 1992) and maturation of female *M. glareolus* can be suppressed by high densities of adult females (Myllymäki, 1977) and high densities of other competitors (Eccard et al., 2002). However Amori and Luiselli (2011a) found no evidence for density dependence in their study of *M. glareolus*. Whilst their study of *A. flavicollis* (Amori and Luiselli, 2011b) did find density dependence, with growth being retarded at high population levels. The same two

studies found differences in growth rate as a function of sex for *A. flavicollis* but not for *M. glareolus* and both studies suggested considerable variation in growth rates between years. Case (1978) suggests that inter-specific variation in average growth rates can be accounted for by the feeding requirements of the animal, the availability of food to the parents and infant mortality rates.

Woodland rodents are normally studied by live trapping using mark-recapture methods. The age at which an individual first enters a trap can vary as not all individuals are equally trappable (Brouard et al., 2015). As individuals will not enter the trappable population until after weaning, the growth of suckling rodents is not included in mark-recapture studies. Even in captive animals, measuring this life stage is problematic, as the mother is likely to commit infanticide, if offspring are disturbed (Gurnell and Rennolls, 1983). This makes calculating growth problematic, although a number of methods have been suggested for ageing rodents, most require the individual to be dead (Frynta and Zizkova, 1992). Even with these limitations live trapping still remains the best method we have to study woodland rodent populations.

Another issue comes from which measurements to use, a number of measurement have been used in previous studies, but all have their limitations. Adamczewska-Andrzejewska (1973) and Hacker and Pearson (1944) have reviewed the merits and limitations of different rodent measurements, but they will be summarised here for ease of reference. Tail length can be measured with a high level of accuracy, but the skin of the tail is delicate, particularly in *Apodemus spp.*. Reduction in tail length due to damage is not uncommon for *Apodemus spp.* and the damage is not always evident. Body length can provide an accurate indication of growth, but the

animal needs to be anaesthetised to get an accurate measurement. Anaesthetising rodents can be problematic, as intensive procedures can cause a loss in weight due to stress (McLaren et al., 2004). Foot length can be easily measured, even if the animal is not anaesthetised, but foot length will reach it's maximum size long before the individual stops increasing in weight. The last measurement is body mass or weight, which is easy to measure but encapsulates more than just the size of the individual. In addition to size, weight comprises the fat stores, the reproductive organs (testes in the male and the uterine casing and embryos for the females) and the stomach contents (Hacker and Pearson, 1944). Gurnell and Rennolls (1983) suggests that if *ad libitum* food is provided in the trap then all individuals will have full stomachs when weighed, and any error will be minimised. This study uses body weight, with *ad libitum* food to avoid the problems associated with the other measurements and to minimise the amount of stress to each individual. We therefore believe that weight is the most appropriate measurement to use, as individuals in this study were caught at short regular intervals.

In this study we look at the dynamics of rodent growth throughout the year, including both the breeding and non-breeding seasons. Most studies looking at rodent growth have not trapped over an extended period as we have done in this study, although the Amori and Luiselli (2011a,b) study ran for 12 years (non-continuous), they trapped only during the breeding season (April to October), so did not consider the non-breeding season.

As food availability is a major factor in determining population density (Montgomery et al., 1991); we would expect it to also have an impact on rodent growth. Likewise we would expect areas of increased cover and nights with low moon il-

lumination to have higher growth rates. The effects of population densities differ between studies and species, but we would expect to see some impact on rodent weight from both conspecifics and hetrospecifics. Particularly for females, as previously mentioned high densities can reduce the number of breeding individuals.

Methods

In this paper we use weight to assess changes in growth of individuals through time. Weight is quick to measure and does not require the rodents to be anaesthetised, therefore the impact on individuals is low. This is important when individuals are trapped at short regular intervals, as in this study (McLaren et al., 2004).

Ethical statements

The small mammal trapping and handling undertaken at Silwood Park were approved by Imperial College London's internal review committee. All Sherman traps were provisioned with bedding and food, including a source of moisture. PIT tagging and fur clipping were used as a form of identifying individuals. Although all work fell below the threshold of the UK Animals (Scientific Procedures) Act, 1986, a Home Office project licence was obtained. Work was conducted on the Silwood Park estate owned by Imperial College London.

Study site

The study site was located at the Silwood Park campus of Imperial College London, just outside Ascot in Berkshire, United Kingdom (OS grid ref.: SU 943 692). The tree canopy of this site was dominated by birch (*Betula pubescens*) and the site is classified as W11 (*Quercus petraea* - *Betula pubescens* - *Oxalis acetosella* woodland) using the National Vegetation Classification System (Rodwell, 1991). The understorey is composed of hazel (*Corylus avellana*) and rhododendron (*Rhododen-*

dron ponticum). Ground cover is mostly bracken (*Pteridium aquilinum*) during the summer and autumn periods, and common bluebell (*Hyacinthoides non-scripta*) during the spring.

The site comprised a 2.43 hectare trapping grid divided into 243 10m x 10m squares. Data were collected between 9th October 2008 and 1st December 2015. Trapping sessions were conducted weekly between 9th October 2008 and 10th November 2010, then fortnightly until 26th November 2014 and finally every 3 weeks until 1st December 2015. Only half the squares would be trapped during each trapping session with the untrapped squares being trapped the following trapping session, with the initial square selection being determined randomly.

Trapping protocols

Traps were placed at sunset and then collected before sunrise the following day. One Sherman trap was placed in each of the selected trapping squares. The traps were baited with peanuts, apple for a source of moisture and waterproof cotton wool for bedding. The amount of bait used was kept constant and provided *ad libitum* food; to reduce the biased effects on weight caused by the stomach content variation. All traps were cleaned between trapping sessions if they had come into contact with a rodent during the previous trapping session and new bedding was used. This avoided the potential trapping bias due to a previous occupant in the trap. Caught rodents were weighed, sexed and had their breeding condition and a measure of their body fat (body condition) recorded. Age was estimated from weight and size of the individual by the researchers, with three categories, Juvenile, Sub-Adult and Adult. *Apodemus sylvaticus* and *Apodemus flavicollis* additionally had their rear foot length and anal genital distance (AGD) measured. We found this not practical with *Myodes glareolus*, as the additional handling required caused

undue stress. For a description of the methods used to measure body condition and AGD see Godsall et al. (2014). Rodents >14g were tagged using a 12mm x 2mm RFID tag, smaller individuals were marked using fur clipping. All individuals were released at the point of capture.

Data preparation

The data were prepared for analysis using Microsoft Access and all statistical analysis was conducted using R version 3.2.2 (R Core Team, 2015). The use of a relational database allowed for the data to be checked for consistency and validity. This included making sure that an individual was not marked as a younger age category in subsequent captures. As the ageing of individuals depended on the experience of the researcher, it was a potential source of measurement error. The onset of the breeding season, for each species, was determined when more than half the males were in breeding condition. When no caught individuals of a species showed signs of being in breeding condition, this marked the end of the breeding season. Additionally for *A. sylvaticus*, the breeding season was divided into early and late, with the start of the late breeding season being determined by the onset of the tree seed fall. The start of the seed fall marks a change of diet for *A. sylvaticus* (Gurnell, 1993; Hansson, 1985; Watts, 1969). Moon illumination proportion was calculated using the method described by Meeus (1991). Precipitation and temperature data was taken from the MIDAS Land and Marine Surface Station Data produced by the Met Office (Met Office, 2012), provided at an hourly resolution.

As the statistical models required for the period between each trapping session to be the same, the data were summarised to three week periods. This meant that some individuals were caught more than once during the three week period. To

accommodate this, the following transformations were applied to the variables.

Weight Mean of the measurements.

Age The oldest age category recorded during the period.

Breeding Season As the captures for an individual during a three week period can cross more than one breeding season; the breeding season with the highest reproductive rate was chosen. For *A. sylvaticus* the late breeding season has the highest reproductive rate, followed by early breeding season and finally the non breeding season. For *M. glareolus* because the breeding is not split into early and late, it is just breeding season or non breeding season, with the breeding season having the highest reproductive rate.

Moon illumination Mean of the nights illumination.

Temperature Mean of each night's temperature, with the temperature for each night being the mean of the maximum and minimum temperature from 6:00pm to 6:00am.

Rhododendron cover If the individual was caught during the period at least once under the cover of rhododendron, then this was set to TRUE else FALSE.

Pregnant If an individual female was identified as pregnant at any capture during the period then TRUE else FALSE. Set to NA for males.

Breeding condition If an individual male's testicles were visible at any capture during the period. Set to NA for females.

Population density Calculated using a Jolly-Seber open population model (R package FSA (Ogle, 2016)) for *A. sylvaticus*, *M. glareolus* and *A. flavicollis*.

Rodent ID An unique identifier for each individual rodent.

Period ID An unique identifier for each three week period.

Tables were produced using the xtable (Dahl, 2016) and texreg (Leifeld, 2013) packages and graphs with the ggplot2 package (Wickham, 2009).

Statistical Models

To understand changes in weight (t to $t+1$), linear mixed effects (LME) models were fitted to the data using the lme4 package (Bates et al., 2014). A separate model for each species and sex was run. Running multiple models avoided the complexity of multiple species, sexes and the requirement for multi-level interactions. The response variable was set to weight at next capture (in grams), with a Gaussian distribution and an identity link. The explanatory variables were weight this capture (in grams), breeding season, pregnancy or breeding condition, moon illumination proportion, precipitation (in mm), temperature (in °C), rhododendron cover and population estimates for *A. sylvaticus*, *A. falvicollis* and *M. glareolus*. A random effect for trapping session was also included. Model reduction was conducted using comparison of AIC values, to find the best fitting model. Because using AIC with models fit with REML will inform only about the fit of the random effects, REML was set to false for model comparisons. Model fit was assessed using the *sem.model.fits* function from the R package piecewiseSEM (Nakagawa and Schielzeth, 2013), which includes a marginal R^2 value for just the fixed effects and a conditional R^2 value for the combined fixed and random effects.

Results

There was a total of 6,113 captures (4,291 *A. sylvaticus*, 415 *A. falvicollis* and 1,407 *M. glareolus*), with 1,476 unique individuals (892 *A. sylvaticus*, 149 *A. falvicollis* and 435 *M. glareolus*). On average each individual was caught 4.24 times (*A. sylvaticus* 4.92 times, *A. falvicollis* 2.91 times and *M. glareolus* 3.29 times). On trapping nights the mean(±standard error) moon illumination was 0.4868±0.02, the mean rainfall was 0.4352±0.09 mm, the mean minimum temperature was 8.2736±0.34 °C and the mean maximum temperature was 13.2648±0.41 °C. The

proportion of captures made under the cover of rhododendron was 0.54 (0.53 for *A. sylvaticus* and 0.58 for *M. glareolus*). 8.53% of females caught were pregnant (7.73% for *A. sylvaticus* and 10.50% for *M. glareolus*) and 53.83% of males were in breeding condition (53.75% of *A. sylvaticus* and 54.11% of *M. glareolus*). These values exclude the *A. flavicollis* species.

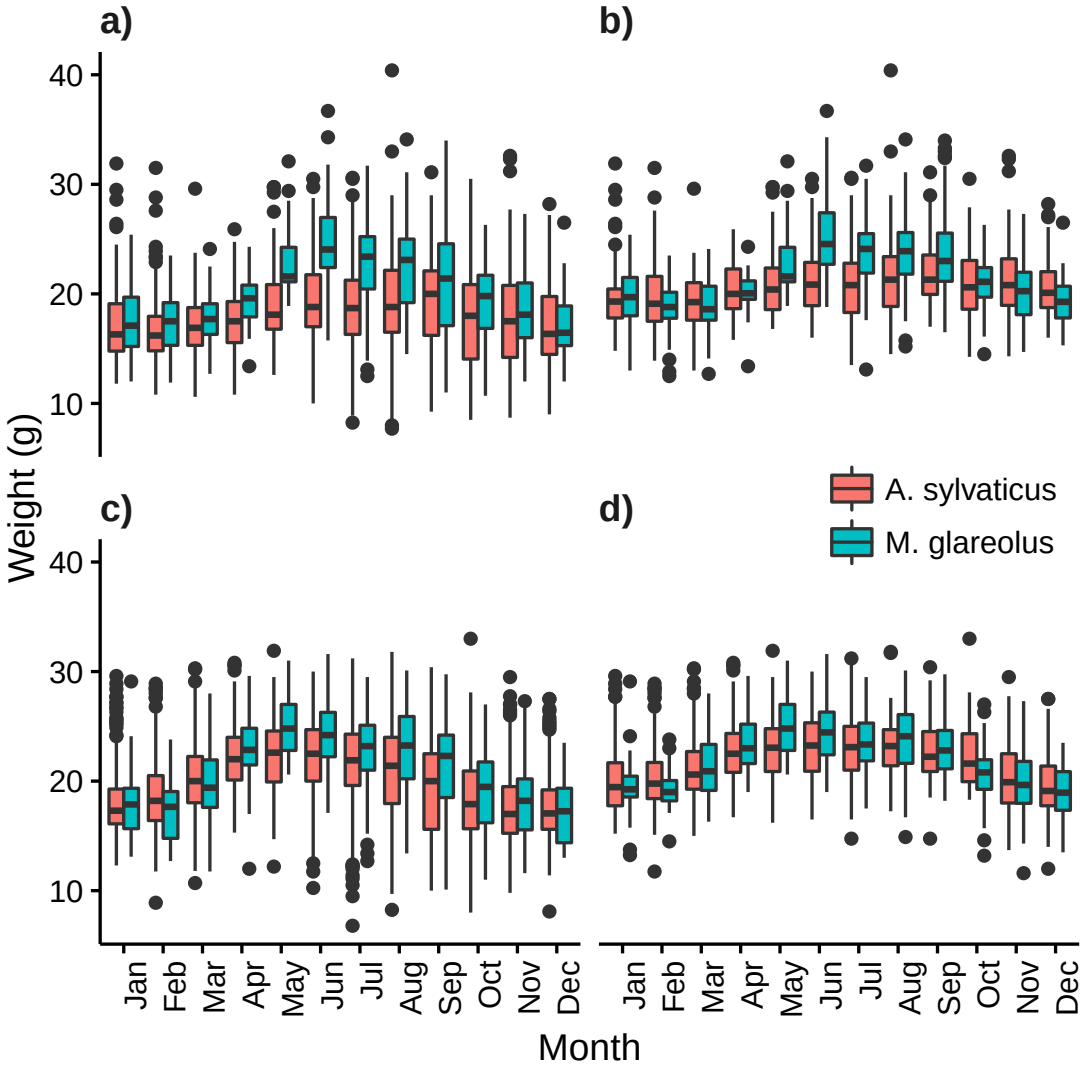


Figure 5.1. Rodent weight summarised by month. a) Females, all age classes, b) Females, adults only, c) Males all age classes, d) Males, adults only

When summarising the mean weight of individuals by month, for males both species showed a similar trend with weight increasing from March, reaching a peak in May and June and then starting to decline in August/September (figure 5.1c). This trend for males is not changed if only adults are considered (figure 5.1d). For female *A. sylvaticus* there is little change in mean weight, although there is

considerable variation if all age classes are included (figure 5.1a). In comparison female *M. glareolus* mean weight shows an increase in May/June before decreasing again in September, even when only adults are considered (figure 5.1a & 5.1b). During this period of increase the mean female *M. glareolus* weight is higher than mean female *A. sylvaticus* weight. If mean weight is summarised by trapping session the increase in weight during the breeding season is evident, although there is variation between years (figure S5.2). In comparison, the estimated population density at three week intervals showed a 2 year cycle in density, although this is not evident in all species for all years, it is particularly evident for *A. sylvaticus* (figure S5.1).

Growth models

After model reduction the linear mixed effects (LME) growth models (table 5.1 and figures 5.2 and 5.3) predict an increase in weight during breeding season for *A. sylvaticus* males and *M. glareolus* males and females, but not *A. sylvaticus* females. *A. sylvaticus* females showed a decrease in weight at time $t+1$ if pregnant at time t but this was not found significant for *M. glareolus* females. Conversely *A. sylvaticus* males showed an increase in weight from t to $t+1$ if they were in breeding condition, but *M. glareolus* did not. With increasing temperature there was an increase in weight for *A. sylvaticus* females, with increasing precipitation there was a decrease in weight for *A. sylvaticus* males and with increasing moonlight there was a decrease in weight for *M. glareolus* females. Both *M. glareolus* male and females showed an increase in weight with increasing density of *A. sylvaticus*. With increasing density of *A. flavicollis* both species and sexes showed a decrease in weight. Finally both species and sexes are heavier at time $t+1$ with increased weight a time t. Model reduction is detailed in tables S5.2, S5.3, S5.4 and S5.5 (for variable abbreviation

please see table S5.1).

Table 5.1. Comparsion of the Silwood rodent growth linear mixed effect models. Late and Early breeding season apply only to *A. sylvaticus* and Breeding season applies only to *M. glareolus*. Table produced with the texreg package in R (Mazurkiewicz, 1994)

	A. sylvaticus ♀	*A. sylvaticus* ♂	*M. glareolus* ♀	*M. glareolus* ♂
(intercept)	3.22 (0.53)	4.18 (0.30)	5.29 (1.19)	3.33 (0.83)
Weight	0.78 (0.02)	0.80 (0.01)	0.79 (0.04)	0.79 (0.04)
♀ pregnant	−0.98 (0.28)			
Temperature	0.18 (0.03)			
A. flavicollis density	−0.08 (0.02)	−0.03 (0.01)	−0.06 (0.04)	−0.07 (0.03)
Early breeding season		0.90 (0.22)		
Late breeding season		0.25 (0.21)		
♂ in breeding condition		0.39 (0.14)		
Rain		−0.01 (0.01)		
Breeding season			1.28 (0.47)	1.04 (0.52)
Moonlight illumination			−4.33 (1.93)	
A. sylvaticus density			0.02 (0.01)	0.02 (0.01)
AIC	3308.16	3762.29	1051.69	886.96
BIC	3340.76	3806.85	1079.40	910.42
Log Likelihood	-1647.08	-1872.14	-517.84	-436.48
Num. obs.	778	1045	236	211
Num. groups: Session	109	105	71	64
Var: Session (Intercept)	1.79	0.36	1.35	1.03
Var: Residual	3.27	1.87	3.65	2.76

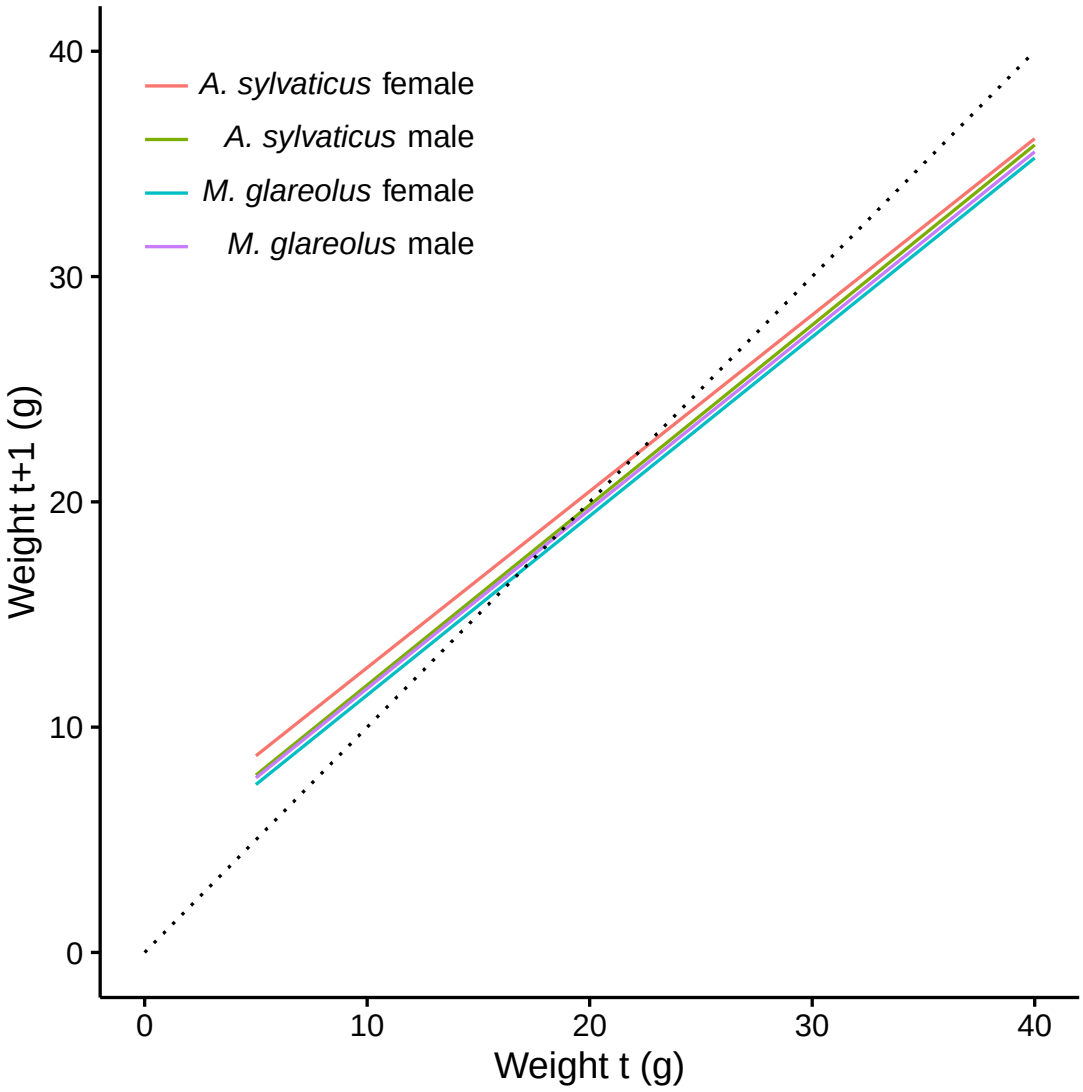


Figure 5.2. Predicted rodent weight next session $(t+1)$ based on weight this session (t) in the non-breeding season for non-pregnant females and non-breeding condition males with a mean population density of *A. flavicollis* (4.46) and *A. sylvaticus* (35.30), mean temperature (10.86°C), precipitation (12.13mm) and moonlight (0.49)

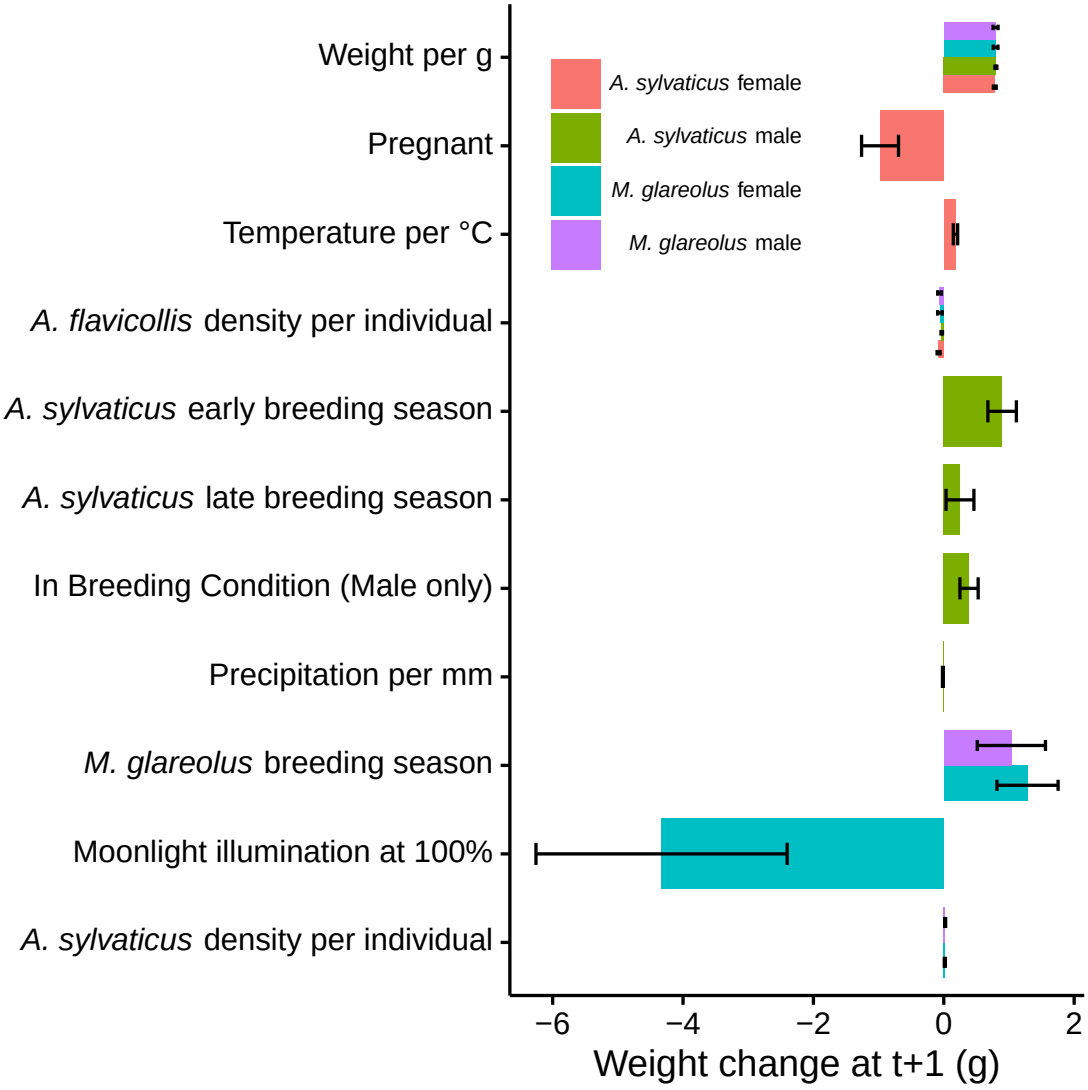


Figure 5.3. The estimated effect size changes in weight from t to $t+1$ for the covariates of the models. The error bars denote the standard error of the estimates.

Discussion

Woodland rodents are vital to the healthy functioning of native British woodlands. Being an important food source for many mammals, birds and reptiles and although some rodent species are seed consumers they are also an essential seed

dispersal vector for many native British tree species (Muñoz and Bonal, 2011). For woodland rodents, an individual's size has a major impact on nearly all of its life history (Kingsolver and Pfennig, 2004), it is therefore important to understand the drivers of growth within these populations of rodents. Information on the growth of wild free living woodland rodents is scarce in the literature (Amori and Luiselli, 2011a,b), with most studies concentrating on population density.

This study looks at the growth of two species of woodland rodents living in sympatry, *Apodemus sylvaticus* and *Myodes glareolus*. A third species, *Apodemus flavicollis* was occasionally caught but with not enough frequency to be included in the analysis. An estimate of *A. flavicollis* population density was included as covariates in the models for the other two species, as it is known to impact the other two species, reducing fecundity in some cases (Montgomery, 1981).

von Bertalanffy (1938) defines growth as "the measurable increase of an organic system in weight or length...". Measuring growth normally requires the accurate ageing of individuals, this presents a specific problem when looking at growth of free living wild woodland rodents, which are very difficult to age without killing them (Frynta and Zizkova, 1992). To overcome this problem we instead looked at changes in weight over a fixed period (three weeks). We included an estimate of age in each of the models, but this was non-significant in all of them.

It is worth briefly considering the patterns that are observed both in the mean weights of individuals and the population densities for the woodland rodents in this study. Estimated population density from the Jolly-Seber open population model indicates an increase in density every two years, at the end of 2009, 2011 and 2013.

This pattern of increase is not mirrored in the weight of individuals even when juveniles are excluded, although there was an increase in mean weight during the breeding seasons. At high population densities we are not seeing large individuals that Chitty (1967) suggested would be present in his study of populations of *Microtus agrestis*. This is not to suggest that *A. sylvaticus* or *M. glareolus* don't self regulate, rather self-regulation may happen by a different method. Alternatively a high mortality rate could be keeping the population from achieving the densities where the large individuals would appear. The increase in density every two years is mostly likely driven by the masting of the native tree species, but unfortunately we did not have access to seed fall data for Silwood for this study, so we can not confirm this. Both species are known to change their breeding strategy based on the availability of resources (Watts, 1970), with up to 6 successive pregnancies being recorded in the wild for *A. sylvaticus* (Harris and Yalden, 2008). It is also possible for both species to breed through the winter (Montgomery et al., 1991) and this was observed in our study in the winter of 2013/14. This means that woodland rodents are able to increase in density fast in response to increased food availability. The pattern of mean weight through the year was in accordance with the published literature, an increase in weight at the start of the breeding season and a slow decrease into winter. Only female *A. sylvaticus* did not follow this pattern, but there was large variation in weight for this group.

The growth models indicate that *M. glareolus* females showed the largest growth between trapping sessions when other factors were not considered, they also showed the largest increase because of the breeding season of all the rodents. The increase in weight due to the breeding season is inline with what has been observed in previous studies (Gebczynska, 1983; Green, 1979), but it was not possible to detect

the differences between early and late breeding season for *M. glareolus* because we were unable to determine a suitable point to split the breeding season. The increase in growth of male *A. sylvaticus* when they were in breeding condition is also supported by previous studies (Baker, 1930). We did not detect any significant change in growth due to breeding condition in male *M. glareolus*, but with the difficulty of even sexing *M. glareolus* when not in breeding condition (Gurnell and Flowerdew, 2006), it is possible that breeding condition could have been mis-recorded in some cases.

Precipitation and temperature were not significant in most cases, with only female *A. sylvaticus* showing an increased growth rate with increasing temperature and male *A. sylvaticus* showing a slight decrease with increasing precipitation. Decreases in captures have been observed in other studies during cold wet weather (Gurnell, 1975), so the lack of the significance in this study may seem to be at odds with previous findings. But woodlands provide shelter for small mammals and can reduce the impacts of environmental factors, this could possibly explain why temperature and precipitation did not have a larger impact on *A. sylvaticus* and none on *M. glareolus*. A further explanation is that because *A. sylvaticus* are arboreal (Buesching et al., 2008) with males having larger home ranges during the breeding season (Corp et al., 1997), they are potentially more exposed to the effects of the environment compared to *M. glareolus* that prefer areas with dense ground cover (Mazurkiewicz, 1994).

Moonlight illumination level has been suggested to alter foraging behaviour of rodents (Orrock et al., 2004), rodents use the level of moonlight illumination as a indicator of predation risk. Although moonlight illumination only had an effect

on female *M. glareolus*, this does not mean that the other rodents are not altering their foraging based on moonlight, rather their calorific intake is not significantly altered. It was not possible to determine why only female *M. glareolus* are effected by moonlight illumination, but it may be related to the fact that *M. glareolus* preferentially choose areas of dense cover (Mazurkiewicz, 1994), so an increased illumination level may reduce the areas that *M. glareolus* prefers. Females also have an increased requirement for resources during the breeding season, to successfully raise young and compared to males have a smaller home range (Wolton and Flowerdew, 1985). Therefore any reduction in foraging, due to moonlight illumination, may possibly have a greater impact on their physical condition than males. One other explanation is that we are summarising to three week periods and moonlight illumination may operate at a finer scale. Trapping at a scale that may reveal the impact of moonlight illumination may not be possible with traditional trapping methodologies. As already mentioned capturing rodents can be stressful for them, and stress has been shown to potentially have an impact on growth (McLaren et al., 2004).

It may seem surprising that rhododendron cover was found to be non-significant for both species, as previous findings by Malo et al. (2013) has suggested that rhododendron cover not only increases density of *A. sylvaticus* but also that larger dominant individuals will be more numerous. But it is growth and not absolute weight that is being analysed; rather our results would suggest that rhododendron cover does not impact foraging success of individuals. It is known that rhododendron is able to out-compete native tree species, so in older patches of rhododendron, the amount of available native tree seeds will be reduced. This means that resident rodents will still need to utilise the edge and non-rhododendron areas of the wood-

land to forage for food, potentially being trapped in these areas. Rhododendron reduces the amount of ground flora and therefore the amount of food available to *M. glareolus*, so even though they are attracted to dense cover that rhododendron provides, *M. glareolus* would also need to forage outside the cover of rhododendron.

The increase in growth of *M. glareolus* with population density of *A. sylvaticus* seems to initially be puzzling, as the reverse is not observed. Other studies have found the removal of *A. sylvaticus* to positively impact the density of *M. glareolus* but again the reverse was found to be non-significant (Fasola and Canova, 2000). It is possible that the population density of *A. sylvaticus* effects individual *M. glareolus* differently. For example larger *M. glareolus* may be more resilient to increases in density of *A. sylvaticus*. Additionally the *M. glareolus* that remain, with increasing *A. sylvaticus* density, could potentially have access to more food resources leading to the increased growth rate observed in this study. Both species are known to increase in population density during the masting of native trees seeds (Mallorie and Flowerdew, 1994), but *M. glareolus* take more green leaf material (Watts, 1968). This may make them less dependant on seeds as a food source than *A. sylvaticus* but then again both species are able to utilise a wide variety food sources (Watts, 1968).

Both species and sexes saw a decrease in weight with increasing density of *A. flavicollis*. The dominance of *A. flavicollis* has been suggested by a number interspecific competition experiments (Cihakova and Frynta, 1996; Hoffmeyer, 1973; Montgomery, 1978); their presence in the woodland can delay the start of breeding for female *A. sylvaticus* (Montgomery, 1981) and reduce the number of male *A. sylvaticus* in breeding condition (Marsh, 1999).

Finally the effect of pregnancy was only found to be significant for *A. sylvaticus*, but this could be due to the low number of subsequent captures for *M. glareolus* after being pregnant. The decrease in weight at $t+1$ for pregnant *A. sylvaticus* is expected, as any individual detected as pregnant at time t would have given birth by time $t+1$ (Harris and Yalden, 2008).

Live trapping still remains the best method we have to collect data on woodland small mammals, but it has a number of inherent biases. Because we did not conduct repeat trapping, where traps are left in the woodland for a number of consecutive nights, we avoided the trapping bias from the previous occupant (Brouard et al., 2015). But biases such as the higher chance of trapping male *A. sylvaticus* than female (Crawley, 1970), and the hetergeneity of trap response between the different functional groups of the population (Jensen, 1975), could not be avoided. This means that certain groups are going to be under-represented in the data, in particular juveniles (Gurnell, 1978). As individuals do not enter the trappable population until after they have weaned (Harris and Yalden, 2008), we are missing this part of the life history. This life stage has been measured in captivity by Gurnell and Rennolls (1983), but even under controlled conditions, there was high mortality of the young when the mother was disturbed. It is also possible that differences would exist between the lab and wild rodents. We are not aware of any studies that have attempted to measure pre-weaned individuals in the wild, so this can not be confirmed.

In conclusion although environmental factors did impact growth in some cases, it is accepted that these will be different for other populations in other ecosystems.

The consistent effect of *A. flavicollis* density across the four models indicates the importance of inter-specific interactions and provides further evidence for the dominance of this species. We found no evidence for a conspecific density dependence effect on growth, although this has been suggested in a number studies (Kviljo et al., 1992). This does not mean density dependence does not exist, rather population density may have not been high enough to elicit the responses seen in other studies. Some studies have recorded densities up to 475 individuals per hectare for *M. glareolus* and over 200 per hectare for *A. sylvaticus* (Harris and Yalden, 2008). Finally we accept that we are limited by the current methodology of small mammal trapping. If a way can be found to identify and measure the individual rodents without having to capture them each time, thereby eliminating the stresses involved with frequent trapping, then it may be possible to get a even better understanding of what drives woodland rodent growth in the future.

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Supporting Information

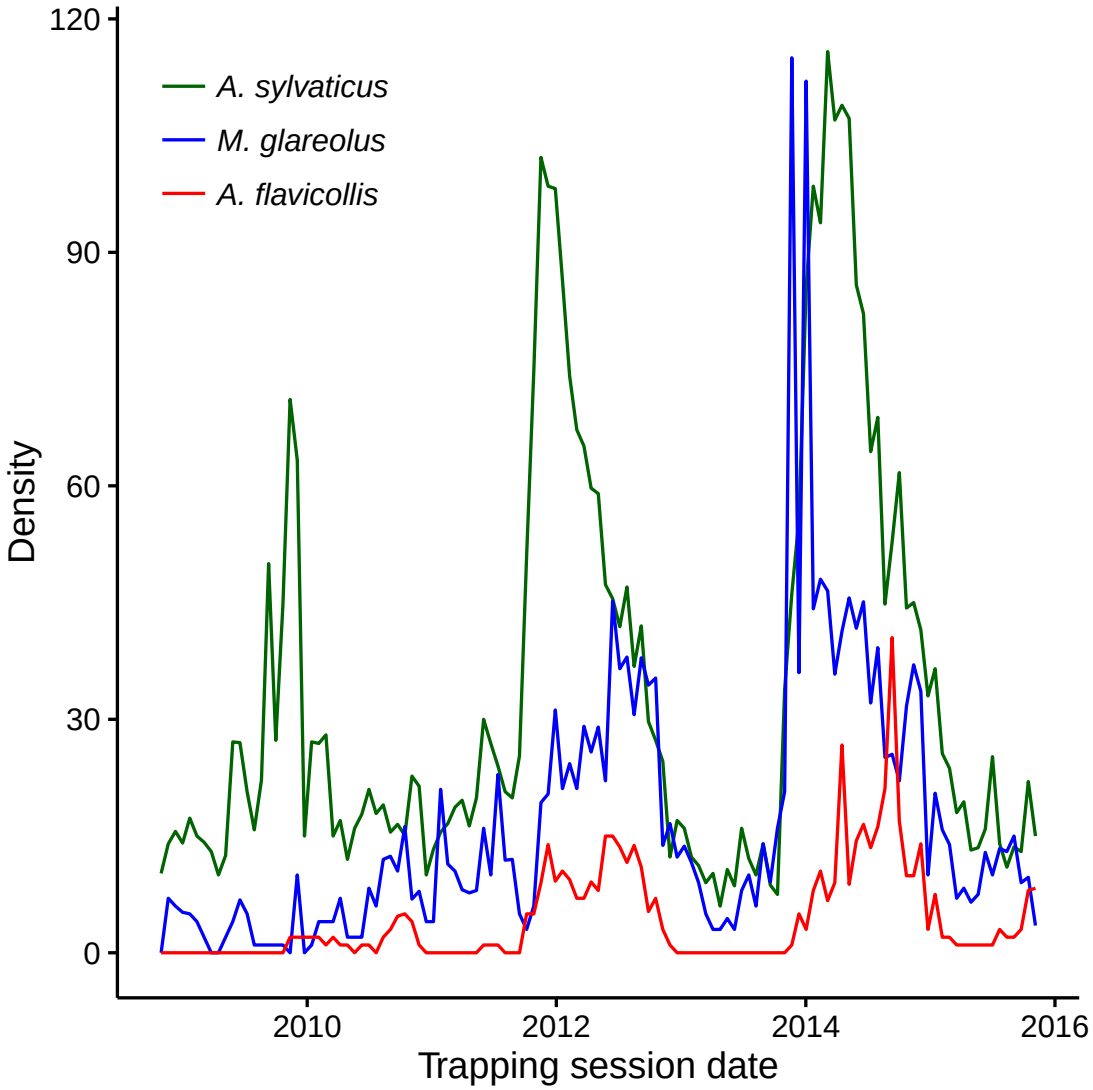


Figure S5.1. Population estimates at each three week period, for the three species *A. sylvaticus*, *M. glareolus* and *A. flavicollis*. The estimates were calculated using Jolly-Seber open population models (R package FSA (Ogle, 2016)).

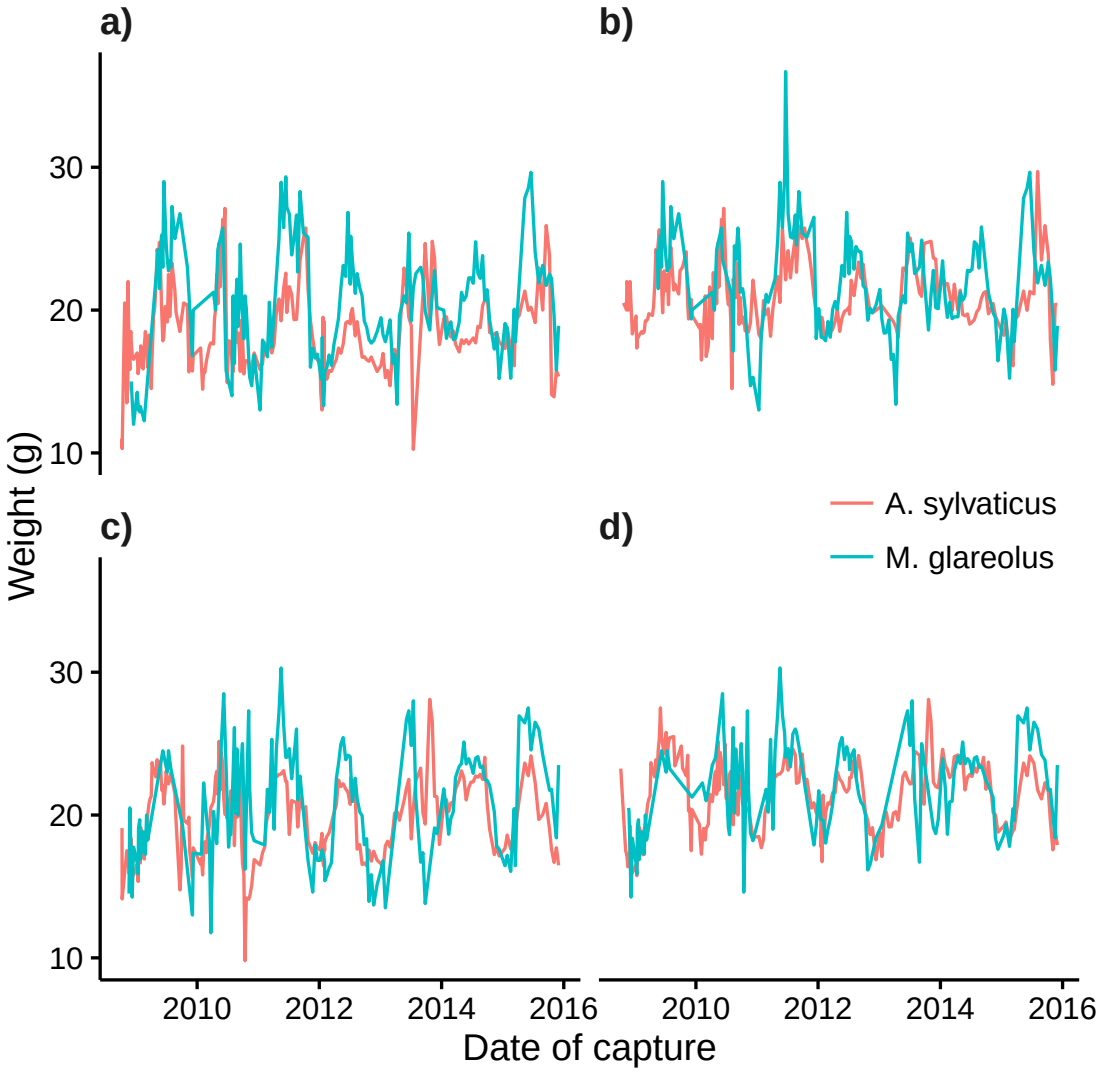


Figure S5.2. Mean rodent weight for trapping sessions. a) Females, all age classes, b) Females, adults only, c) Males, all age classes, d) Males, adults only.

Table S5.1. The variables used in the linear mixed effects models, with abbreviations.

Variable	Description
WN	The weight of the individual at the next trapping session ($t + 1$)
W	The weight of the individual at the current trapping session (t)
A	The age of the rodent ("J" for juvenile, "SA" for sub-adult and "A" for adult).
B	The breeding season of the current trapping session ("NBS" for non-breeding season, "BS" for breeding season, for *A. sylvaticus* the breeding season is split into early "EBS" and late "LBS")
M	The mean percentage of the moon that is illuminated, for the three week period from t to $t + 1$. Moon illumination percentage was calculated using the method described by Meeus (1991)
Ra	The sum of precipitation (in mm) during each night (17:00 to 06:00) for the period t to $t + 1$
T	The mean temperature for the nights during the period t to $t + 1$. The temperature for each night was calculated as the mean of the maximum and minimum temperature measured every hour from 18:00 to 06:00.
Rh	If the quadratic the rodent was caught in, was covered by rhododendron (logical)
P	If the rodent was pregnant at time t (only used in female models) (logical)
BC	If the rodent was in breeding condition at time t, testicules visible (only used in male models) (logical)
As	The population estimate for *A. sylvaticus* at time t
Af	The population estimate for *A. flavicollis* at time t
Mg	The population estimate for *M. glareolus* at time t
RID	The unique ID for the each rodent
S	The trapping session ID at time t
Y	The year of the capture at time t

Table S5.2. The linear mixed effect models fitted to the Silwood data for female *A. sylvaticus* determining the change in weight over a three week time step. The abbrevations for the terms in the models are detailed in table S5.1

	Model	df	AIC	delta
11	WN ~ W + P + T + Af + (1 | Session)	7	3288.7394	0.0000
10	WN ~ W + A + P + T + Af + (1 | Session)	8	3288.9536	0.2142
8	WN ~ W + A + B + P + T + Af + (1 | Session)	10	3291.7839	3.0445
7	WN ~ W + A + B + P + M + T + Af + (1 | Session)	11	3293.0193	4.2799
5	WN ~ W + A + B + P + M + Ra + T + Af + (1 | Session)	12	3295.0191	6.2798
3	WN ~ W + A + B + P + M + Ra + T + As + Af + (1 | Session)	13	3296.5485	7.8091
2	WN ~ W + A + B + P + M + Ra + T + As + Af + Mg + (1 | Session)	14	3298.4457	9.7064
9	WN ~ W + A + B + T + Af + (1 | Session)	9	3299.8095	11.0701
1	WN ~ 1 + W + A + B + P + M + Ra + T + As + Af + Mg + Rh + (1 | Session)	15	3299.9443	11.2049
4	WN ~ W + A + B + P + M + Ra + T + As + (1 | Session)	12	3300.2091	11.4697
6	WN ~ W + A + B + P + M + Ra + Af + (1 | Session)	11	3308.7080	19.9686
12	WN ~ P + T + Af + (1 | Session)	6	4045.1527	756.4133

Table S5.3. The linear mixed effect models fitted to the Silwood data for male *A. sylvaticus* determining the change in weight over a three week time step. The abbrevations for the terms in the models are detailed in table S5.1

	Model	df	AIC	delta
12	WN ~ W + B + BC + Ra + Af + (1 | Session)	9	3731.3001	0.0000
8	WN ~ W + A + B + BC + Ra + Af + (1 | Session)	10	3731.6975	0.3974
6	WN ~ W + A + B + BC + M + Ra + Af + (1 | Session)	11	3733.6274	2.3273
3	WN ~ W + A + B + BC + M + Ra + T + As + Af + (1 | Session)	13	3734.7245	3.4243
5	WN ~ W + A + B + BC + M + Ra + T + Af + (1 | Session)	12	3734.9414	3.6413
7	WN ~ W + A + B + BC + M + Af + (1 | Session)	10	3736.0628	4.7627
9	WN ~ W + A + B + Ra + Af + (1 | Session)	9	3736.5232	5.2230
2	WN ~ W + A + B + BC + M + Ra + T + As + Af + Mg + (1 | Session)	14	3736.7157	5.4156
1	WN ~ 1 + W + A + B + BC + M + Ra + T + As + Af + Mg + Rh + (1 | Session)	15	3738.6398	7.3397
4	WN ~ W + A + B + BC + M + Ra + T + As + (1 | Session)	12	3742.2997	10.9995
10	WN ~ W + A + BC + Ra + Af + (1 | Session)	8	3747.5195	16.2194
11	WN ~ A + B + BC + Ra + Af + (1 | Session)	9	4722.0164	990.7163

Table S5.4. The linear mixed effect models fitted to the Silwood data for female *M. glareolus* determining the change in weight over a three week time step. The abbrevations for the terms in the models are detailed in table S5.1

	Model	df	AIC	delta
12	WN ~ W + B + M + As + Af + (1 | Session)	8	1035.4209	0.0000
9	WN ~ W + A + B + M + As + Af + (1 | Session)	9	1037.3097	1.8888
7	WN ~ W + A + B + P + M + As + Af + (1 | Session)	10	1037.4143	1.9934
6	WN ~ W + A + B + P + M + Ra + As + Af + (1 | Session)	11	1039.3252	3.9043
8	WN ~ W + A + B + P + As + Af + (1 | Session)	9	1040.9465	5.5255
3	WN ~ W + A + B + P + M + Ra + T + As + Af + (1 | Session)	12	1041.0713	5.6504
4	WN ~ W + A + B + P + M + Ra + T + As + (1 | Session)	11	1042.2451	6.8242
2	WN ~ W + A + B + P + M + Ra + T + As + Af + Mg + (1 | Session)	13	1042.7905	7.3696
5	WN ~ W + A + B + P + M + Ra + T + Af + (1 | Session)	11	1043.1085	7.6876
10	WN ~ W + A + M + As + Af + (1 | Session)	8	1043.1620	7.7411
1	WN ~ 1 + W + A + B + P + M + Ra + T + As + Af + Mg + Rh + (1 | Session)	14	1044.7163	9.2953
11	WN ~ A + B + M + As + Af + (1 | Session)	8	1215.3089	179.8880

Table S5.5. The linear mixed effect models fitted to the Silwood data for male *M. glareolus* determining the change in weight over a three week time step. The abbrevations for the terms in the models are detailed in table S5.1

	Model	df	AIC	delta
12	WN ~ W + B + As + Af + (1 | Session)	7	867.1335	0.0000
9	WN ~ W + A + B + As + Af + (1 | Session)	8	868.4531	1.3196
10	WN ~ W + A + As + Af + (1 | Session)	7	869.8688	2.7353
8	WN ~ W + A + B + BC + As + Af + (1 | Session)	9	870.0949	2.9614
7	WN ~ W + A + B + BC + M + As + Af + (1 | Session)	10	870.4496	3.3161
6	WN ~ W + A + B + BC + M + Ra + As + Af + (1 | Session)	11	872.2252	5.0917
3	WN ~ W + A + B + BC + M + Ra + T + As + Af + (1 | Session)	12	873.5891	6.4556
2	WN ~ W + A + B + BC + M + Ra + T + As + Af + Mg + (1 | Session)	13	875.5382	8.4047
4	WN ~ W + A + B + BC + M + Ra + T + As + (1 | Session)	11	877.2471	10.1136
1	WN ~ 1 + W + A + B + BC + M + Ra + T + As + Af + Mg + Rh + (1 | Session)	14	877.3806	10.2471
5	WN ~ W + A + B + BC + M + Ra + T + Af + (1 | Session)	11	878.1736	11.0401
11	WN ~ A + B + As + Af + (1 | Session)	7	1048.4562	181.3227

6

Discussion

In this thesis we wanted to consider if the population dynamics of different populations of the same species differ, when they are located in similar habitats. If they do differ then we wanted to quantify which factors could be driving the differences. Building on this we then considered the effect that species have on each others' population dynamics when they are living in sympatry.

In our first chapter we considered if there were any differences in the life history and population dynamics between three populations of Columbian ground squirrels. Using Integral Projection Models (IPMs) to calculate population level estimates from trapping data of individuals revealed considerable differences between the three populations. The populations were located within 3km of each other at similar altitudes, so we could reasonably expect similar environments and climate. There were small differences in the management of the sites and the data were collected at different times but this did not account for the large differences. The three populations differed in population growth rate (λ), mean weight of both the adults and the offspring, survival rate and reproduction. For reproduction there were differences in the weight at which adults reproduced, the chance of re-

producing and the litter size.

When constructing an IPM it is important to consider the methods and protocols used to censor the data. In particular the structure of the data used in the statistical models is different depending on the timing of census, if it was conducted before breeding or after breeding (Ellner et al., 2016). In the Columbian ground squirrel data the adults (yearlings and older) were censused at first emergence from the hibernation, so before breeding. But there was an issue with the offspring, they are censused at a later date, when they emerged from the natal burrow about the same time they are weaned. Columbian ground squirrels emerge from the hibernation in the spring and are active for about 103 days in our study sites (Neuhaus, 2000, table 1). Breeding commences shortly after the emergence of the adult females and last for about three weeks (Elliott and Flinders, 1991), with offspring emerging from the natal burrow approximately 51 days after mating (Murie, 1992; Murie and Harris, 1982; Shaw, 1925). We were able to account for this by having separate development and survival functions for the offspring (Ellner et al., 2016, Appendix 2.10). This had the additional advantage of allowing us to provide estimates for the offspring separate from the adults. Previous studies exclude individuals that have not reached maturity, so the development of the young does not obscure the impact of the environment and climate on the condition of the individuals (Neuhaus, 2017), this has further ramifications which are discussed below.

IPMs are normally constructed against the females of the population, as identification of parentage, in most cases, is simpler. This is the approach that we took, as we wanted to understand what insights simple IPMs are able to provide when

comparing populations; two sex IPMs can be very complicated (Schindler et al., 2015). Because of the high certainty in the data we were able to use simple linear and generalised linear models to calculate the parameters for each of the IPM functions, with model reduction being conducted using AIC to determine the most parsimonious model. The most surprising result from the statistical analysis is the lack of significance for weight on litter size. This contradicts what other studies have found (Dobson and Kjelgaard, 1985a,b; Murie and Dobson, 1987), but those studies were looking at the total litter size, whilst our models are only interested in the female portion of the populations. As mentioned previously, previous studies have excluded juveniles from analysis; they additionally exclude yearlings and two year-olds from the analysis as Columbian ground squirrels do not reach full maturity until age 3. It is very rare for yearlings to breed and including yearlings and two year-olds with adults could be having a confounding effect on our analysis, in particular the reproduction functions (chance of reproduction, litter size and inheritance). There are two possible solutions to this. We are currently using a minimum weight limit for reproduction, to avoid have individuals that are unrealistically too light from breeding. This limit is currently set to the lightest individual that breed, taken from the raw data, increasing this limit would help to account for the rarity of the younger individual's breeding. The other option is to produce an age structure IPM (Childs et al., 2003; Ellner and Rees, 2006), which would increase the complexity, but would also mean interpretation of the results would be harder. Potentially the IPM would have at least four different values for each estimate, assuming that the age classification was limited to yearlings, two year-olds and adults in addition to the offspring. Finally it is possible to include a year random effect into the statistical models, but this would increase the complexity of the IPM and make analysis much harder. The suitability of the

IPMs were checked by comparing the IPM estimates against the values calculated directly from the raw data, even without the year random effect the IPMs provided estimates very close to the raw values.

The estimates from the three IPMs showed considerable differences between the three populations of Columbian ground squirrels. With the estimates for λ, adult survival, offspring weight and litter size all showing significant differences. Due to the populations being within 3km of each other we would not expect these large differences. Some of the differences may be due to the climate, as the population data were collected at differing times, but it is unlikely to explain it all. But what was driving these differences? In our 2nd chapter we took the IPMs produced in the 1st chapter and conducted a form of perturbation analysis first described by Ozgul et al. (2010). This allowed us to quantify the contribution of each of the demographic and trait transition functions to the IPM estimates. From the perturbation analysis it was clear that the survival function for the adults (yearlings and above) was a major driver for the differences between the three populations. It accounted for a large proportion of the differences observed in λ, generation length and R_0, along with the mean weight and mean survival rate of adults. The differences in the offspring estimates were mainly driven by the inheritance function. Although it is not possible to equate the differences in survival between the three populations to any particular factor, previous studies (Dobson and Kjelgaard, 1985a,b) have found that the availability and quality of food resources to be a major factor along with predation. Low availability of food can increase the chance of predation (Neuhaus and Pelletier, 2001), due to increased foraging time and distance.

As most species do not exist in isolation, we wanted to investigate how species

living in sympatry interact and how this effects the life history and population dynamics of both species. To this end we setup a new trapping grid in Wytham Woods building on the protocols previously used at another site in Silwood Park, Imperial College. Having access to data from more than one site would make the estimates and predictions more robust. Unfortunately a number of issues were encountered during the analysis of both the Silwood data and the newly collected Wytham Woods data, that meant we could not correctly estimate the required parameters for the IPMs. Below I will detail why this was the case and what we did to try and address the situation. This is important as it provides insights into the limitations of the techniques that we are using.

Limitations of the Silwood and Wytham data

As with any data collected on wild populations, the risk is run that the collected data will not adequately represent the population and individual dynamics that are being studied. Although the initial trappings had around a 40% capture rate this decreased during 2015 and kept below 20% for much of 2015 and 2016. We were also getting a high proportion of new adult captures during the non-breeding seasons and during the breeding season we had very low capture rates for juveniles. For the wood mice (*Apodemus sylvaticus*) we were also getting considerably more males than female captures. At the end of 2016 going into 2017 the percentage of bank vole (*Myodes glareolus*) increased and started to dominate the captures. We were also not detecting pregnant or lactating females that would have been expected from previous studies (Green, 1979). There is a number of reasons for the observed capture patterns. It is well known that small mammal population density varies considerably both in time and space (Flowerdew and Ellwood, 2001; Flowerdew et al., 1985). Wood mice populations are dependant on the masting of

native trees, being able to increase their reproduction during mast years (Harris and Yalden, 2008). Although we did not collect any data for seed fall from the trees in the trapping plot, we did not observe any signs that the trees masted during 2015 or 2016. The high number of new adult captures could be due to juveniles showing an aversion to our traps or it could be due to a high number of immigrants into the Wytham plot. The sex ratio for wood mice at birth is 1:1 (Crawley, 1970; Gurnell, 1982), but there are a number of reasons why the trapping ratio could be biased. Females could be showing an aversion to our traps or females could have higher mortality after leaving the nest. Previous studies have also found trapping to have a male bias (Crawley, 1970; Gurnell, 1982). One other explanation is that males travel further and have larger home ranges during the breeding season (Attuquayefio et al., 1986; Korn, 1986), meaning they would have a higher chance of encountering open traps. Female pregnancy can be hard to detect unless the female has recently bred or is in the later stages of the pregnancy, (Flowerdew et al., 2004). But the lack of pregnant females in our data could also be due to them showing an aversion to the traps. Finally the increase in the proportion of bank voles caught can be attributed to a change in the management strategy of Wytham Woods. Previously bank vole numbers had declined and this had been linked to increase in the three species of deer present in the woodland. The deer remove the understory and ground flora cover that bank voles preferred (Buesching et al., 2011; Bush et al., 2012; Flowerdew and Ellwood, 2001). As deer numbers are now being controlled the ground cover has returned and it looks like we are seeing a return to previous bank vole numbers. This all meant we had concerns about biases in the collected data and when using the data to generate the parameters required by an IPM, we calculated a population growth rate or λ that indicated a very fast declining population. Further investigation revealed this was due to low

survival and reproduction estimates.

We also had concerns about the validity of the Silwood data for parameterising an IPM. Although the IPM estimates for wood mice were more representative of what we would expect from previous studies (Harris and Yalden, 2008), the bank vole estimates still indicated a fast declining population. The emphasis of the data collection at Silwood was on the wood mice, so the traps were placed after twilight and collected in before dawn. This meant that the captures favoured wood mice and yellow necked mice (*Apodemus flavicollis*). Bank voles are crepuscular animals having their peak periods of activity at dawn and dusk, whilst wood mice and yellow necked mice are nocturnal (Harris and Yalden, 2008). This is not a criticism of the Silwood data rather an acknowledge of the methods are not a perfect fit for the analysis we attempted. The timing of trap placement and retrieval was changed at the Wytham Woods site to avoid this bias.

A number of modifications of the trapping protocols and analysis were looked at, but none provided an suitable solution to the issues. These are very briefly discussed here. Increasing the trapping grid size would allow for more individuals to be trapped, also the larger size would completely cover a larger proportion of home ranges. The current trapping grid covers 1 hectare with 100 traps, this is the maximum size that one person can process comfortably without resulting in the animals being left for long periods in the traps in the processing room. Extending the trapping grid would require additional resources in terms of both additional equipment and personnel that were just not available. Increasing the trapping frequency to every week from the fortnightly schedule may have increased the number of animals caught and the recaptures, but the increase in workload would

be considerable. The traps were cleaned and autoclaved to avoid olfactory cues and contamination of bacteria. This was important not only to avoid trapping bias but the scats were being collected for DNA analysis for another project. Autoclaving the traps on a weekly basis would have not been possible. Historically, trappings have been conducted for periods greater than one night, with traps being left out for multiple days and checked at regular intervals. But this introduces a number of biases, which is the subject of the third paper in this thesis (see chapter 4 and below). For the survival function, it would have been possible to use advance Mark-Recapture software. The Bayesian survival trajectory analysis (BaSTA) package (Colchero et al., 2012) allows the analysis of data with low recapture probability, unknown ages, unknown birth and death times and include the effect of continuous and categorical covariants. But this would have only provided a partial solution, and would have not accounted for the low reproduction estimates we were getting. Including functions for immigration and emigration may have helped, but detecting which individuals were immigrating or emigrating is problematic. Immigrants could possibly have been identified by using genetic methods and looking at parentage, but of course this assumes that the parents have been caught. Emigrants would require a buffer zone around the site to trapped, the distance of the buffer would have to be the distance an emigrant rodent would travel. This would expand the trapping effort considerably and would have all the problems described above for expanding the trapping grid. Finally one possible solution that would help to account for the low detection of reproduction is to use a method described by Smallegange et al. (2016), which uses Dynamic Energy Budget (DEB) theory to construct the IPM. The DEB model describes growth and reproduction using life cycle information making it suitable for data-deficient species. Unfortunately this paper was released too late for the methods to be utilised.

Previous trap occupant

The biases that affect live captured woodland rodents have been studied extensively (Montgomery, 1979; Stoddart and Smith, 1986; Tanton, 1965), but surprisingly little has been studied with regard to the effect of the previous trap occupant. Recent advances in modern statistical techniques offer possible new insights into the issue. Additionally we wanted to check if the methods we proposed to use in the new Wytham Woods site were efficient. Previous studies have used trapping sessions that ran continuously for a number of nights (Krebs, 2006; Strachan, 1995) whilst the Silwood site, on which we planned to base the trapping protocols for Wytham Woods, had trapping sessions that ran for only a single night. For the continuous trapping there were concerns that a number of biases could impact the data collected. We wanted to use modern statistical techniques to test if these concerns were warranted. If not we could possibly optimise our trapping protocols to improve the data collected in Wytham.

As we did not have access to trapping data that trapped over multiple continuous nights, we collaborated with WildCRU, who have been conducting ad-hoc trapping in Wytham Woods over the past 13 years. The data did not identify individuals, rather rodents were marked to identify recapture only. The chance of a capture in a small mammal trap can be divided into three components (Stoddart, 1982), how effective the trap is, the chance of encountering the trap and the behavioural response of the individual to the trap. It is this third effect that we were interested in. As individuals were not uniquely marked we could not investigate differences at the individual level but we could still investigate the differences between species and sex based on what had previously been caught.

We initially wanted to look at the biases due to combinations of species, sex, breeding condition and age (juvenile, sub-adult, adult) for the chance of capturing an individual with those attributes based on the previous trap occupant's attributes. Although the data were composed of 8,115 trap nights, it became clear that certain combinations of previous occupant and current caught individual were under-represented in the data. For this reason we limited the main statistical analysis to species and conducted a proportion test to assess sex differences within species. Even doing this we could not include age or breeding condition into the models, mainly due to the low capture rate of juveniles (Gurnell, 1978). The data were also limited to interactions between wood mice and bank voles and wood mice and field voles (*Microtus agrestis*). This made biological sense as field voles are rarely found in woodlands and bank voles rarely in grasslands. Wood mice on the other-hand are found in both habitats. Yellow necked mice were excluded from the study as only one individual was caught during the 13 years of the trapping.

Trapping studies rarely consider the behavioural aspect of trapping bias, it is clear from this study that it can have a large impact on subsequent captures. We therefore decided to limit the trapping sessions in Wytham Woods to one night every two weeks. Although continuous trapping over a number of nights could possibly allow us to investigate changes in individual traits over a short period (daily changes), the biases would have been prohibitive. As already mentioned this study had a number of limitations. We could not include all the factors in a single model and the effect of age and breeding condition could not be analysed at all. This emphasises the importance of long term studies when trying to analyse behaviour that is rarely captured. Additionally it is impossible in this study to disentangle the bias due to the same individual visiting a trap from the effect of

the conspecific olfactory cues. Disentangling this effect would require individuals to be uniquely marked, which is currently done in the Wytham Woods site and was also previously done in the Silwood Park site.

Factors affecting woodland rodent growth

As mentioned above a number of issues meant that the IPMs we constructed did not accurately represent the populations of small mammals in both the Silwood Park and Wytham Woods site. But during the construction of the IPMs, the analysis for the growth function did offer potentially interesting insights into the population dynamics of woodland mammals. I am aware of only one other study that has looked at woodland rodent growth (Amori and Luiselli, 2011a,b). Although the study ran for 12 years, the trapping was only conducted during the breeding season, so did not include the non-breeding season. We planned to conduct the analysis across both the Silwood Park and the Wytham Woods sites, but at the time of the analysis not enough trapping sessions had been conducted at the Wytham Site to provide meaningful results, so the analysis was restricted to the Silwood Park site.

Analysing woodland small mammal growth has a number of specific problems. As both mice and voles give birth in burrows, obtaining accurate weights at birth is near impossible, and even if we could, interference at this stage has been proven, in lab experiments, to cause the mother to commit infanticide (Gurnell and Rennolls, 1983). We are therefore dependant on obtaining the measurements when the individual enters the trappable population. This also raises the problem of ageing the individuals caught, although methods do exist to age rodents, most require the rodent to be dead (Frynta and Zizkova, 1992). Most small mammal trapping stud-

ies rely on the experience of the researcher to make an estimate of age based on the size, form and weight of the individual, into three categories, juvenile, sub-adult and adult. Juveniles were rarely caught (Gurnell, 1978) and the difference between sub-adult and adult can be very subjective. This may explain the reason why age was not found to be significant in this study. The Silwood Park data also presented an additional problem; for IPMs the interval between census periods needs to be a consistent length. As the period between trapping session changed during the project, the data needed to be summarised to a three week period.

In conclusion this study highlights several interesting changes in the growth of small mammals that are missed by models that only consider population density. Unfortunately it was not possible to include the complete life cycle of the rodents and it may never be possible, although advances in technology may offer hope in the future. Also if a way can be found to measure rodents without having to live trap them, additional understanding of these species may be revealed. As live trapping is stressful for small mammals, it is possible that this can have an effect on the condition of the individuals (McLaren et al., 2004). Finally this study highlights the importance of long term studies of populations in understanding their ecology, interactions with other species and population dynamics.

Conclusion

In conclusion the four studies highlight the differences and variation that can occur between populations of the same species. Interactions between species are also important, even when they are not physically interacting. But the studies also highlight the difficulties that are involved in obtaining suitable data for IPMs. If only part of a life cycle of a species can be observed, e.g. burrow-dwelling species,

or if certain subsets of individuals of a population are under represented in the data, then the IPM estimates may not accurately represent the population. Taking into account the methods used to collect the data and using suitable methods to generate the parameters used by IPMs will provide estimates that can provide useful insights into the life histories and population dynamics. Although the estimates that an IPM produces can be gotten in most cases directly from the data, by using an IPM we can understand the contributions of the different demographic and trait transition functions. This thesis highlights the importance of considering the variation between populations, even when the occupy similar habitats. When making comparisons between species using single population data, extreme care will be needed when interpreting the results.

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A
Site design

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Introduction

This chapter describes the setup of the trapping grid in Wytham Woods. A grid setup was chosen as this would allow the study of the populations of small mammals and possibly later the movements and home ranges of individuals (Gurnell and Flowerdew, 2006). Wytham Woods was identified as the most suitable location for the small mammal trapping grid, with a long history of small mammal trapping. Wytham Woods is located 5 km North-West of Oxford city, with the woodland and grassland covering an area of 415 hectares (Savill et al., 2010) (figure A.1).

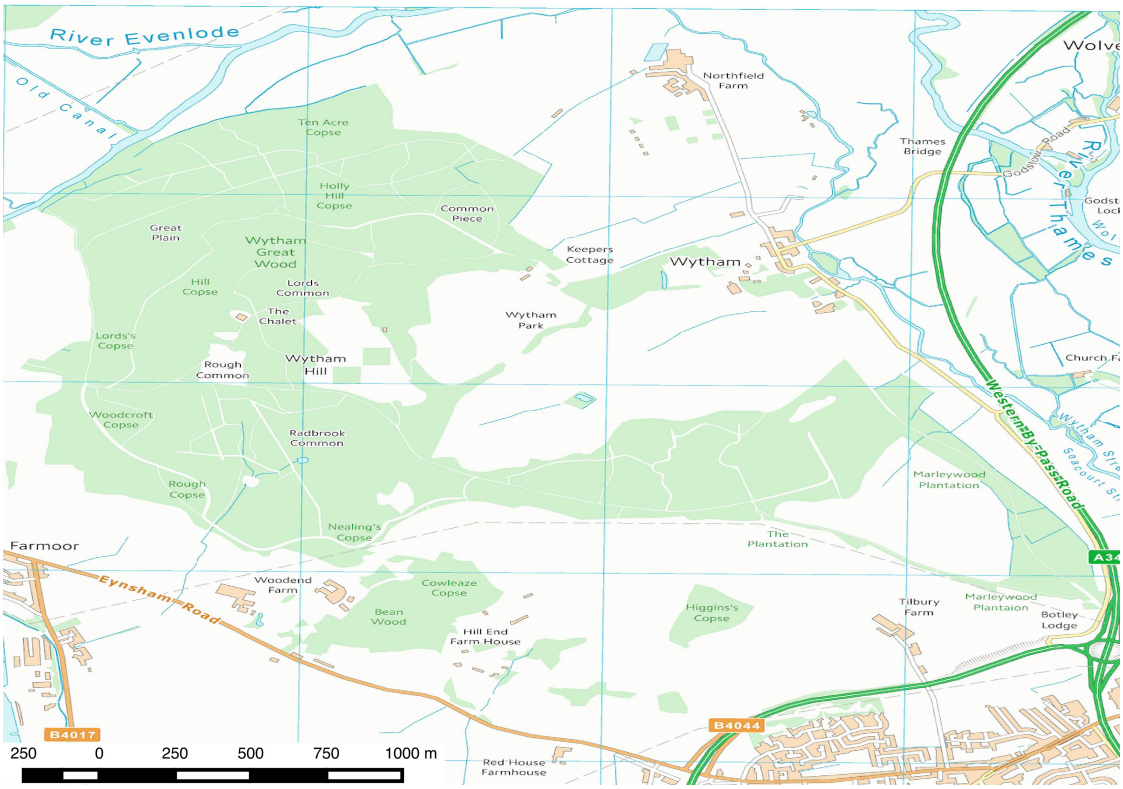


Figure A.1. Wytham Woods, located 5 km from Oxford city, (National Grid Reference SP 462083). The woodland and grassland areas cover an area of 415 hectares. VectorMap District Raster [TIFF geospatial data], Scale 1:25000, Tiles: sp40, Updated: 4 June 2014, Ordnance Survey (GB), Using: EDINA Digimap Ordnance Survey Service, `http://digimap.edina.ac.uk`, Downloaded: Wed Oct 08 11:28:50 BST 2014. © Crown Copyright and Database Right 2018. Ordnance Survey (Digimap Licence)

Trapping grid

The design of the trapping grid is based on the grid at Silwood Park, Imperial College London just outside Ascot. The Silwood trapping grid covers 2.4 ha and is made up of 10 metre by 10 metre cells, each with a trapping point. The Wytham Woods trapping grid has a similar configuration but will eventually cover 4 hectares; the current size of the Wytham Woods trapping is 1 hectare. The Smithsonian plot was chosen as the location of the trapping grid as it offers a number of advantages over other areas in Wytham Woods. The Smithsonian plot has been mapped, so the vegetative structure is known. Additionally the plot is close to the Chalet allowing for the processing of the capturing in a dry secure environment (figure A.2). Each cell in the trapping grid has an unique id that is determined from the row and column ids. The rows ids are numeric starting at zero and the column ids are alphabetic starting at "A". The corner of each grid cell is marked with a bamboo cane that is labelled with duck tape. The duck tape

label indicates the grid cell that is North-East of the cane.

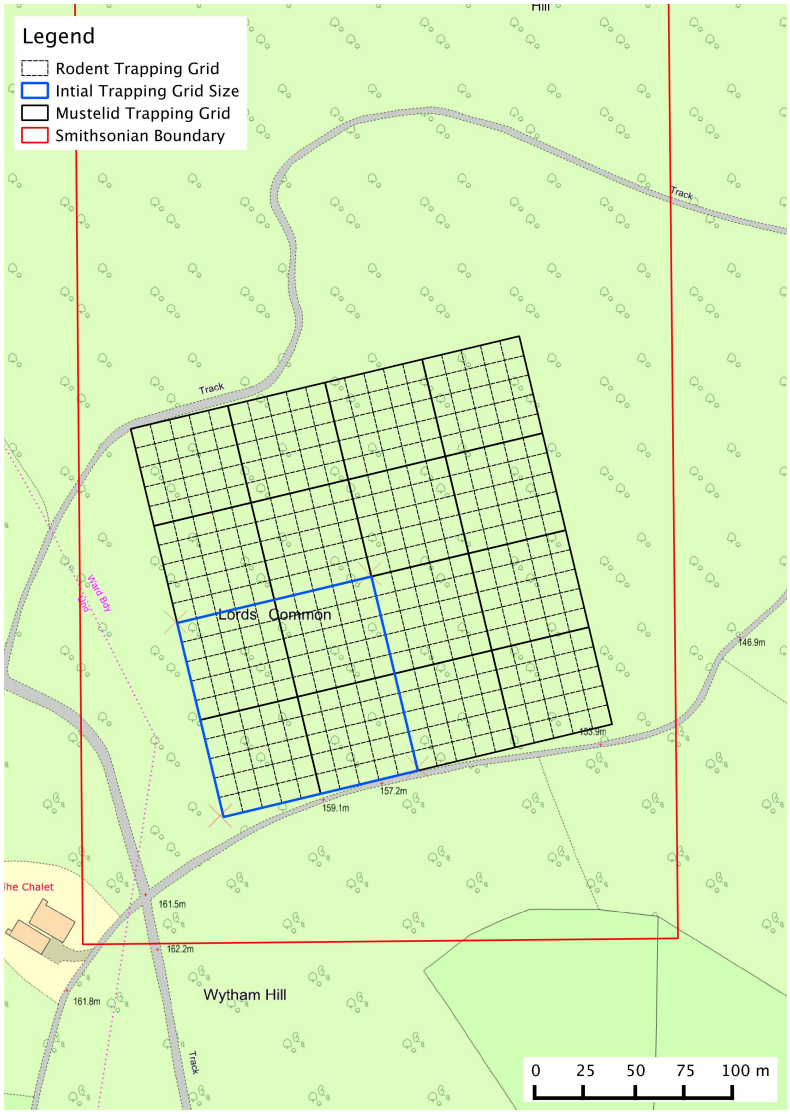


Figure A.2. The Wytham Trapping Grid, located near the Chalet in the Wytham Great Wood on Lords Common. The Smithsonian plot is designated by a red box. The full 4 ha grid is shown in black with the initial 1 ha grid outlined in blue. © Crown Copyright and Database Right 2018. Ordnance Survey (Digimap Licence)

Trapping points

One trapping point is installed in each of the grid cells. The placement of the trapping point is at the spot that contains the highest chance to capture a rodent. The choice of location was determined from the following list, with preference given to the former locations first.

1. Tree stump

2. Large fallen branch or trunk.
3. Small fallen log
4. Wood pile
5. Area of dense low cover
6. Open area

At each trap point a protective wooden box (Trap box) is installed.



Figure A.3. The protective trap box installed at a trap point in Wytham Woods. The box is mounted on a metal rod so that it can be raised off the ground to reduce degradation and extend their lifetime.

Trap box

A wooden box provides protection for each trap both from severe weather conditions and from other physical sources, for example, badgers (*Meles meles*) which have been known to damage or destroy small mammal traps (Christina Buesching & Chris Newman, personal communication, Aug. 14, 2014). The trap boxes have been designed to allow for the use of both the Longworth and Sherman design of trap. The back of the wooden box has a small hole drilled to allow the escape of shrews from the trap, if the trap is fitted with a shrew hole. To reduce the degradation of the wooden box and extend their lifetime, the boxes are mounted on a metal rod that allows the box to be lifted off the ground when not in use.

Traps

Many designs of small mammal traps are available, but for live trapping, the two most common are Longworth and Sherman traps. The Longworth trap has a separate nest box and entry tunnel and allows for the trap to be locked open or closed. The Sherman on the other hand is simpler with a combined entry tunnel and nest box. The capture assumptions of the two traps types differ slightly and are summarised by Anthony et al. (2005). The protocols detailed in the Trapping protocols appendix assumes that Sherman traps are being used, as this is what we are currently using. If Longworth traps are used in the future, then protocol to extract the individuals from the traps will need modification. It is not possible to first extract the bedding and food from the Longworth trap without having a high risk of the rodent escaping.

Sherman traps

The Sherman Folding Trap is the Small Galvanised version (5.1 x 6.4 x 16.5cm)(figure A.4). The traps are modified to allow more space for bedding and food. This is achieved by bending the last 2 cm of the trigger plate back on itself. To reduce the chance of wood mice trapping their tails when the door closes, the edges at the entrance of the trap and on the door are bent back using a pair of snub nose pliers. The edges are then covered using electrical tape. Each trap is assigned an unique number, this allows for the performance of the trap to be monitored.

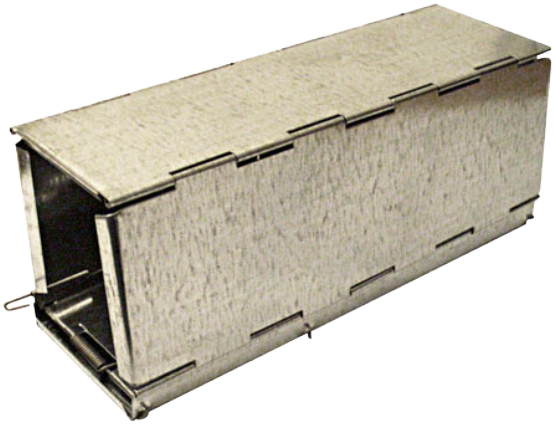


Figure A.4. Sherman Folding Trap, small folding galvanised (5.1 x 6.4 x 16.5cm). Image source `http://www.nhbs.com/title/183648/sherman-folding-trap-small-folding-galvanised`

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B
Trapping protocols

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Introduction

The following section contains information about the protocols used during the setup, trapping, processing and release of small mammals in Wytham Woods. It is important to note that this document is only a representation of the protocols at a particular point in time, the protocols can and will change depending on the aims of the research conducted. Additionally it is a requirement of the Home Office licence that the protocols are constantly reviewed, and changes made if it will improve the welfare of the animals. The information provided here, when combined with the information from the Site design appendix, should be detailed enough to allow the replication of the research conducted in Wytham Woods. At the time of writing, trapping was being conducted every two weeks through out the year, this allowed for life history data to be collected on individuals in the population.

Trapping considerations

The following points should be considered before trapping is conducted

1. Check the weather with a reliable source, e.g. Met Office
2. If the weather is going to be cold (<3°C) and wet, it is best to postpone the trapping. This is the worst time to trap, as the animals will be wet going into the traps and will have a hard time warming themselves, which combined with the stresses of being trapped will possibly cause a high mortality rate.
3. Cold weather, if it is dry, does not necessarily mean trapping should be postponed, but researcher comfort should also be considered.

Trapping sheet

The trapping sheet (figure B.1) details where each trap should be placed on the trapping grid; in which grid cell. It is produced from the database, using the New Day function. The New Day function will allow for the trap position to be rotated each trapping session, reducing the effect of trap differences on trapping success. If any traps have been retired and/or new traps brought into service then the database will need to be updated with the trap details before running the New Day function.

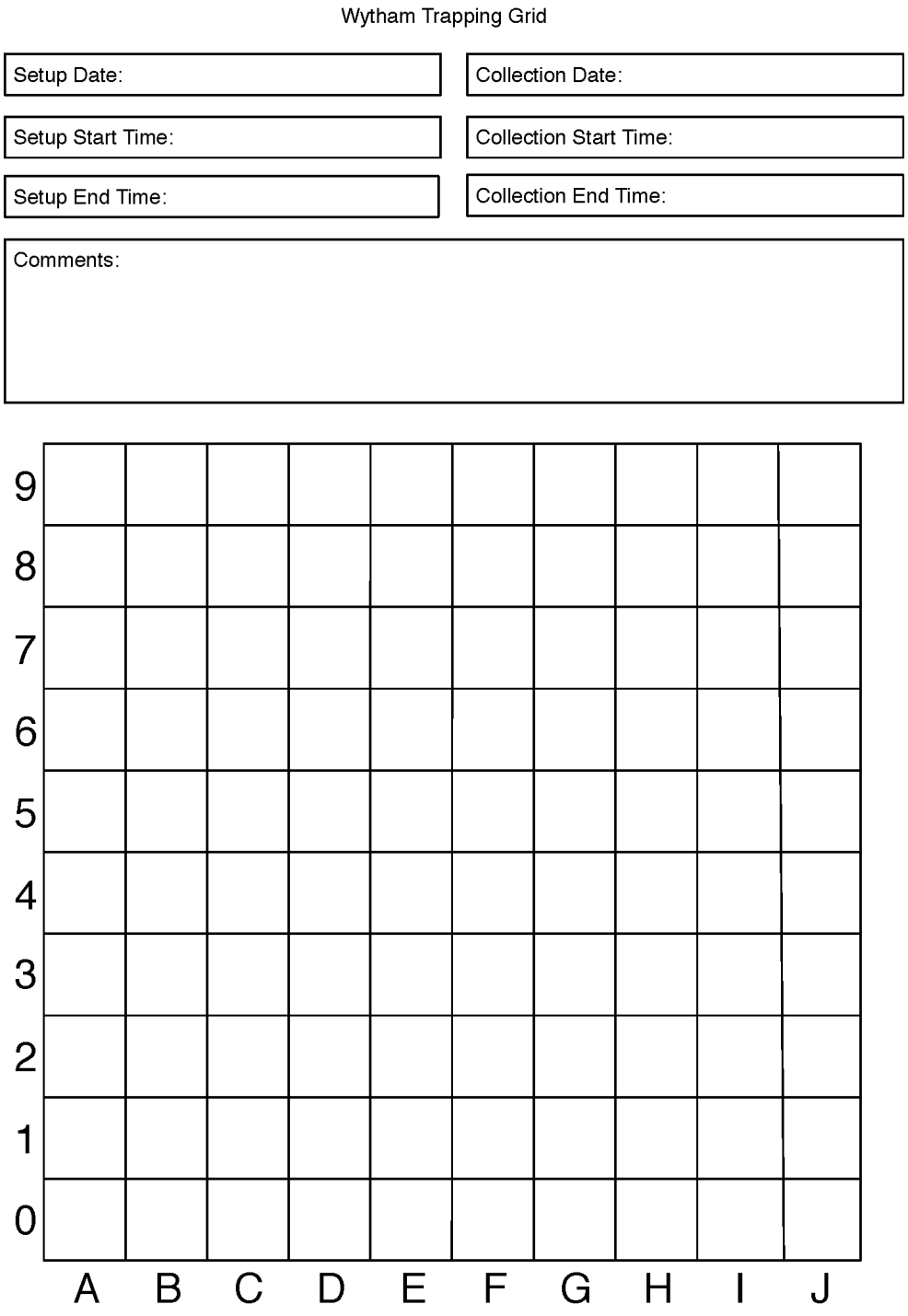


Figure B.1. Trapping sheet. The blank template trapping sheet used by the database. The database will populate the trapping dates and each grid cell with a trap number.

Trap setup

Traps from the previous trapping session, that have been known to have contact with rodents, will have been cleaned and autoclaved. Traps with no known contact with rodents will still have the cotton wool and peanuts from the previous trapping session. The following procedure is used to organise the traps and place them in the bag in order they are to be placed in the trapping grid.

1. Group the traps into transects using the shelves (A,B,C..J), using the trapping sheet as reference.

2. Cut up an apple into quarters or eighth's length ways and then slice these pieces into slices about 2-3mm width

3. Starting with transect A, prepare the traps with peanuts, apple and cotton wool bedding.
   - Organise the traps into order they are in the transect, using the trapping sheet
   - For traps with no cotton wool or peanuts
     - Add six peanuts to the bottom of the trap
     - Using a piece of cotton wool approx 15cm x 10cm (varying depending on the time of year), fold so that it will fit into the trap and cover all the peanuts.
   - For traps with cotton wool and peanuts
     - Check that the wool or peanuts are not mouldy, if in any doubt remove and replace both with new.
   - Slide a slice of apple down the side of the cotton wool. It is suggested that the same side is always used, as this makes removing it easier and faster.

4. Test each trap for the operation of the trigger. The trap should trigger if the treadle is lightly touched by the probe, but not go off when the trap is just moved. It is possible for peanuts to become lodged under the trigger. Sometimes it may be possible to remove these by tapping the trap on the desk. Otherwise the trap wil need to be dismantled to remove them.

5. Make sure the bedding or the apple does not interfere with the correct operation of the trigger.

6. Place the traps into the bag starting at the bottom left, when the Ikea bag is viewed from the top. The traps are placed in the bag in such a way that they can placed in the correct grid cell without having to refer to the trapping sheet.

Trap deployment

The order in which the grid cells are populated with traps should be kept the same. This helps with memorising the locations of the trapping points in the grid cells, speeds up deployment and reduces impact of the researcher in the woodland.

1. Locate the protective wooden trap box in the required grid cell.
2. Lower the protective wooden trap box.
3. Retrieve the trap from the IKEA bag starting at the top left of the bag.
4. Arm the trap and check that the treadle works using the probe.
5. Place the trap inside the wooden trap box (figure B.2). Making sure that it slides all the way to the stop in the back of the wooden box.



Figure B.2. Deploying trap in woodland. Picture credit Sarah Knowles

Trap recovery

The traps should be recovered in the same order that they were placed. This again helps with memorising the location of the trap points and speeds up their retrieval.

1. Traps are retrieved from the wooden protective boxes.
2. They are checked for one of four different outcomes.
    - CAPTURE The door is closed and an animal is caught in the trap
    - MIS-FIRE The door is closed but there is now animal in the trap
    - TRIGGER FAILURE The door is open but the bedding is disturbed and food has been taken
    - NO CAPTURE The door is open and the bedding and food is intact

3. If an animal is in the trap it is visually checked to make sure it is fit. If the animal is not visible because it is buried in the bedding, use a probe to gently move the bedding aside.
    - If the animal is a shrew and still alive it is released immediately.
    - If the animal does not look well then the researcher needs to make the decision to release it immediately or take it back to the processing room.
    - It is not always possible to tell if the animal is just sleeping or is unwell in the field, this is why a subsequent check back in the processing room is important.
4. The traps will be placed in the bag, so traps with different outcomes are kept separate.
    - The most important traps are those with captures and these should be placed into the box that is in the bag for this purpose.
5. Raise the protective wooden trap box. The wooden boxes are raised off the ground to increase their life (if they are not resting on the ground the speed of deterioration (rotting) is reduced).
6. Upon returning to the processing room, put the traps with captures on the table. Keep traps which you are sure the animals are ok separate from those you have concerns or are unsure about.
7. It is important to get all the traps in as fast as possible, so don't start dealing with the potentially sick animals, unless you have enough people available, before all the traps are in.
8. Separate out the NO-CAPTURE, TRIGGER FAILURE and MIS-FIRE traps into different bags.
9. Do not leave traps, with captures sitting in a bag in the woodland. If you can not get all the traps in without doing this then make multiple trips to the processing room. Whilst a trap is in the wooden protective box it has some protection from the elements, but sitting in a bag it is a great deal more vulnerable to extremes of cold and heat.

Pre–Trap processing

1. One person deals with any animals that you have concerns about. Unless there is only one person present, in which case do item 2 first. See Dealing with injured or sick animals section for details.
2. Sort through the traps with captures making sure the animal is fit.
    - Give the animal a slice of apple as this helps keep it hydrated.

- Check the trap with the large PIT tag reader, to see if it is a recapture and new capture
- Put the trap on the shelf for the transect it came from.
  - It is suggested that you keep suspected new captures and recapture separate. Previously LEFT of the shelf has been used for recaptures and the RIGHT for new captures.
- Record on trapping sheet which traps had a capture as you check them. This has been done by writing a capital C in red ink, in the corresponding grid cell.

3. Once all the CAPTURE traps have been checked and placed on the shelves and any traps of concern dealt with. Deal with the MIS-FIRE and TRIGGER FAILURE traps. This is to ensure that a capture has not been put withn the MIS-FIRE or TRIGGER FAILURE traps by mistake.
   - Remove all the bedding and any remaining food from the trap.
   - Mark on the trapping sheet, TF for trigger failure and MF for misfire in blue ink.
   - Put all the traps into a bag, so they can be taken back for washing
4. For the NO CAPTURE traps, remove just the apple.
   - Mark on the trapping sheet a tick in black ink in the relevant grid cell.
   - Put all the traps into separate bag as they do not need washing.

Dealing with injured or sick animals

It is inevitable that the traps will catch at some point a sick or injured animal. The project licence requires for any animal that is suffering to be put out of it's misery quickly and in the most humane way possible. Please refer to the Project Licence and other relevant material for advice. A brief summary is included here for ease of reference.

1. At least one person that is trapping needs to have been trained in Schedule One procedures.
2. It is best that more than one person conducts the trapping. This allows one person to deal with sick or injured animals whilst the other ensures the rest of the caught individuals are fit and well.
3. Although Schedule One details a number of methods, the one that is mostly commonly used during small mammal trapping is cervical dislocation. It is also important to confirm death with another method, in this case it is suggested that rigor mortis is used as an indicator of death.

4. It may be possible to get a dehydrated animal to drink by using a small amount of apple juice in a teaspoon. But extreme care must be taken ensure the suffering of the animal is not being extended.

5. It may be that an animal is just inactive due to being cold. Warming the animal can counteract this, but again extreme care must be taken to not extend any suffering.

Trap processing equipment

It is important to have all equipment for processing of the rodents ready and laid out before starting. Table B.1 lists the equipment used during the processing of the animals.

Table B.1. Trap processing equipment. Does not include equipment that is used for PIT tagging, which is detailed below in section B

Item	Notes
Large forceps	Used to extract the cotton wool from the trap.
Paper towel	To put bedding on, if poo samples are being taken and for cleaning equipment.
Clip	Used to hold door open.
Plastic wallet	Used to temporally hold the rodent until it is released.
Recording sheet	The recording information about the capture, see figure B.4
Clinical waste bag	All bedding and animal waste must be disposed of using clinical waste bags.
Cotton bag	Used to hold the animal whilst it is measured, PIT tagged and genetic samples taken.
Small scissors	Used for fur clipping if the animal is too small for PIT tagging.
Small scissors	Used during ear clipping, to retrieve the genetic sample.
Long arm ear punch	Used to ear clip the animal as an alternative form of ID and also for a genetic sample.
Ethanol 100%	For the genetic samples.
Ethanol 70%	Used for cleaning equipment.
Cyotube	For storing the genetic samples.
Tick removal tweezers	Ticks are removed for study by other groups.
Nitrile gloves	All processing, handling and poo sampling must be done whilst wearing gloves.
Lab scales	Accurate to 0.1g
Weighing clip	Fold back clip from a stationary store. It is important that the same one is used each time.
Trap clip	Fold back clip used to secure the trap door open.

Trap processing

It is suggested that trap processing starts with the J transect, as this is the furthest transect from the processing room. Then process traps from J transect back through the transects with the last transect being processed being transect A. Doing this means that animal releases are mostly in the same part of the woodland, reducing impact on the woodland and speeding up the release. It is important that any handling of the animals is down with gloves on.

1. Weigh an empty plastic wallet with the weighing clip and make a note of this weight. It would also be possible to zero the scales with this empty wallet and weighing clip.

2. Double check that the animal is fit and well.

3. Sterilise large forceps used to remove cotton wool between traps by wetting thoroughly with 70% Ethanol and wiping with paper towel.

4. Mark on the trapping sheet that the trap has been processed, by drawing a red box around the grid cell.

5. Mark on the plastic wallet, with the grid cell reference.

6. Record the following details on the recording sheet (figure B.4).
   - Grid cell reference.
   - Trap number.
   - Trap event number. This starts at one for the first animal processed and increments by 1 for each subsequent animal. This is used more to know how many captures there have been rather than as a index in the database.
   - Date

7. Start by removing the cotton wool and food from the trap.
   - If a poo sample is being taken put the bedding onto a paper towel.
   - If no poo sample is being taken the bedding can be put directly into the clinical waste bag.

8. Once the bedding and the food is removed from the trap, the animal can be extracted.
   - Place the lip on the bottom lip of the entrance of the trap.
   - Put the front of the trap into the plastic wallet.
   - Using one hand, start to open the entrance of the trap.

- Using the other hand hold the plastic wallet around the trap and your hand.
- Before opening the entrance of the trap all the way, make sure the rodent is not hiding under the door.
  - If the animal is hiding under the door, gently nudge the rodent to the back of the trap, by gently moving the trap.
- Open the entrance door of the trap fully and secure the door with the clip.
- If the animal does not exit immediately into the plastic wallet, give the animal some time to exit. It can be encouraged to exit by gently tapping the rear door.
- If the animal is refusing to exit, gently but firmly pull the trap and wallet towards you, ejecting the animal into the wallet.

9. If any stray bedding or food got into the plastic wallet with the animal, it needs to be removed.
10. If collecting poo samples, put the bedding back into the trap.
11. Put the trap to one side.
12. Check the animal in the wallet for any injuries and general fitness (figure B.3).
13. Record the following on the recording sheet
    - Species
      - For voles, nearly all individuals are going to be bank voles (*Myodes glareolus*). It is possible to catch field voles, but over the three years the project has run, only one has been caught in the wooland plot.
      - For mice, it is possible to catch two different species. Wood mice (*Apodemus sylvaticus*) and yellow necked mice (*Apodemus flavicollis*). Yellow necked mice tend to be larger, the yellow patch on the chest is much more pronounced and goes all the way across and their tail is a lot longer. Yellow necked mice also tend to be a great deal hard to process, struggling even when restrained in the bag, whilst wood mice tend to freeze once restrained.
    - Use the PIT tag reader to check the animal for a PIT tag. Record the number if a PIT tag is detected, and circle "WAS".
    - New or Recapture. The easiest way is to tell by if the animal has been ear clipped. As it is possible for the PIT tag to fall out this is the most reliable method to determine a new or recapture. Care most be taken though to make sure that ear damage is not mistaken for an ear punch.

- Sex, This may be hard to determine if the species is a vole and it is not in breeding condition. If unsure make note of it in the comment field.
- Reproductive condition, very important to record.
  - For female: Imp = Imperforate, Perf = Perforate, Preg = Pregnant, Lact = Lactating but not pregnant, Nips = Nipples clearly visible but not lactating or pregnant. It is possible for a female to have more than one of these characteristics. The most important to record is if the animal is pregnant as these is used in many of the mathematical models for the population.
  - For male: TA = Testes abdominal, TS = Testes small, TL = Testes large, TL+ = Testes very large. Unlike the females the males will only have one characteristic recorded.
- Age: Juv=Juvenile, SA=Sub-adult, A=Adult. To determine age use a combination of the following:
  - Weight, less than or near to 14 grams it may be a juvenile. But it is possible for adults to be around this weight during the spring or winter, if the proceeding autumn was not a mast year and food is scarce.
  - Pelage, juveniles tend to have a darker coat than adults. For details check Harris and Yalden (2008).
  - Size combined with body condition. If the animal has very little fat stores then it's weight is a bad indicating of age, but it skeletal size will not change.
  - Capture history of the animal, if available.

14. Record the time on the recording sheet
15. Visually inspect the animal for any external parasites and record the counts
16. Weigh the animal.
    - Encourage the animal into one corner of the bag.
    - Fold up the ag so the animal is temporally restrained. Secure the bag with the weighing clip. It is important that the same clip is used to weigh the animals.
    - Place the animal on the scales and record the weight along with the bag weight (figure B.6).
    - It is important that this is done fast but carefully to reduce the stress to the animal.
17. Transfer the animal to a cotton bag.

18. Restrain the animal with the cotton bag.
    - Position the animal into the corner of the cotton bag, so it's nose is pointing into the corner.
    - Secure the animal in that position with the first and second finger of your off-hand.
    - Roll back the ag to reveal the back and hind quarter of the animal.
    - It should then be possible to use the rest of the bag to secure the animal in place, with the least amount of discomfort for the animal.
19. Both voles and mice have a body condition estimate taken
    - Gently rub the spin and hips of the rodent, feeling for the vertebrate and hip bones. Use the body condition table (table B.2) and body fat score (figure B.5) to estimate the amount of body fat (figure B.7). Record the estimate.
20. For mice the rear right foot length is measured.
    - With the mouse in the palm of your hand
    - Position the mouse in your off-hand so it's rear is facing up near your first finger and it's head is near you little finger.
    - Open the calipers slightly, revealing the measurement bar.
    - Gently tease out the mouse's right rear leg with the caliper measurement bar.
    - Measure the foot of the mouse with the calipers, from the heel to the longest toe minus the nail (figure B.8).
    - Take three or more measurements, resetting the calipers between each. Record all measurement.
21. For mice measure the anal genital distance
    - With the mouse in the palm of your hand.
    - Adjust the mouse's position so it is on it's back with its rear showing.
    - Make sure that the mouse is relaxed as it can be and is not hunching.
    - Measure from the genitals to the middle of the anus (figure B.9).
    - Take at least three measurements. Record all measurements.
22. If the animal has not been PIT tagged then PIT tag or fur clip the animal and ear clip them.
    - As a guide an animal can be PIT tagged if it is >=14 grams. It is possilbe for smaller animals to be PIT tagged, but it depends on the expertise of the field worker. See PIT tagging section.

- Lower than this it may need fur clipping. See Fur clipping section.
- Record either the PIT tag number of the fur clipping on the recording sheet.
- No matter the weight of the animal, a new capture is ear clipped for identification purposes, with the by-product of the clipped skin being used for DNA analysis.
- Record the ear clipping number on the recording sheet, under ID#

23. Get the animal ready for release.
    - Transfer the mouse back to the plastic wallet.
    - Make sure the plastic wallet has the grid cell reference written on it.
    - Put two peanuts and a slice of apple in the bag.
    - Close the top of the bag with a clothes peg, but make sure there is enough air in the bag for the animal.
    - Put the animal in the release box, ensure that it has enough space. If there are other animals in the box, take the opportunity to check that they are fit and not too stressed.
    - Animals should not be left in the plastic wallets, in the release box, for any length of time and should be checked regularly. Amount of time depends on the conditions in the processing room, but 30 minutes should be seen as an absolute maximum between checks and refreshment of air.

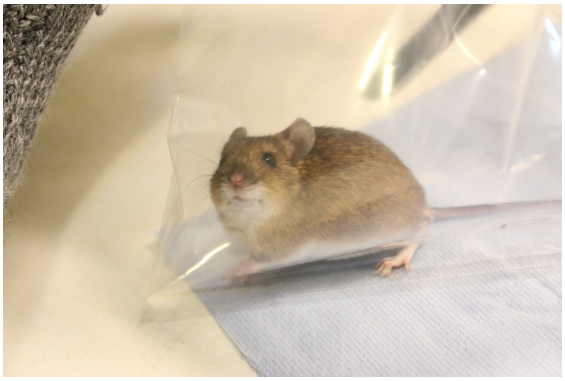


Figure B.3. Wood mouse in plastic wallet Picture credit Sarah Knowles

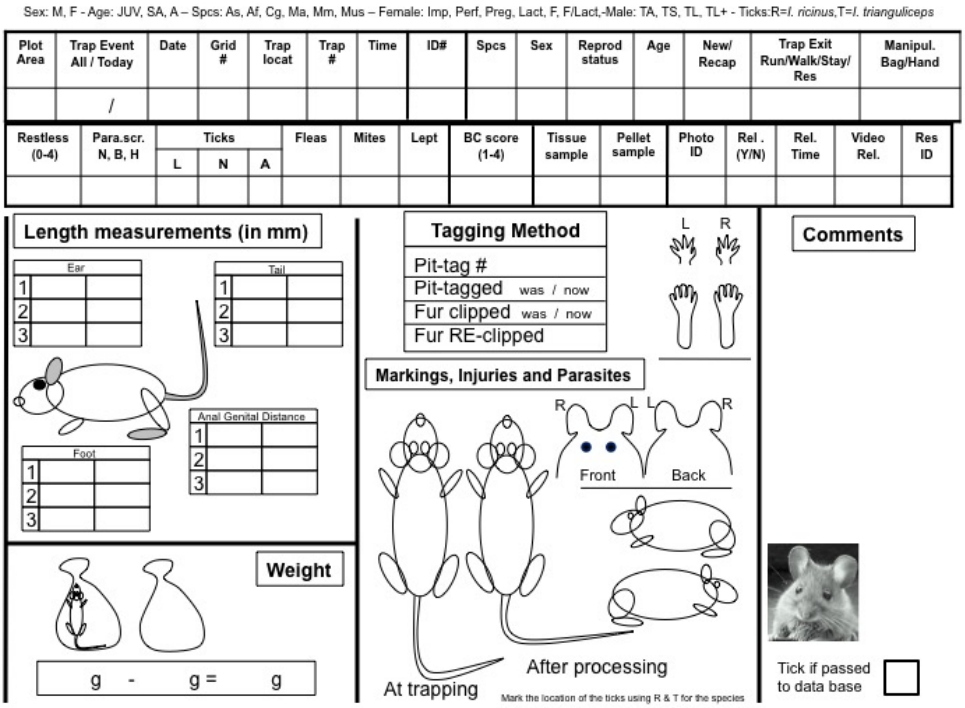


Figure B.4. Rodent recording sheet

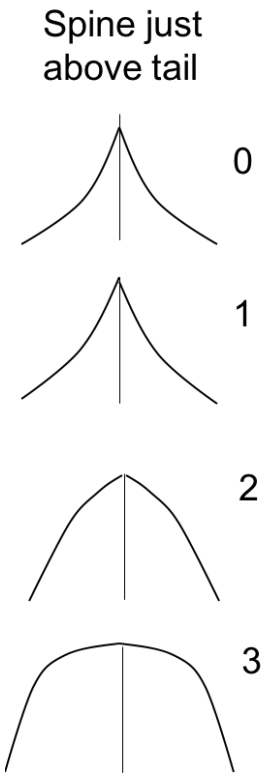


Figure B.5. Body fat score. Picture credit Sarah Knowles

Table B.2. Body condition scores.

Score	Description
0.0	No Subcutaneous fat deposit Skin hanging from bones
0.5	Very little subcutaneous fat deposit Spine and hip bones very sharp and clearly felt
1.0	Minimal subcutaneous fat deposit Can easily feel spine and hip bones. Can easily detect ridges of individual vertebrae.
1.5	Some subcutaneous fat deposit. Can easily feel spine and hip bones. Can barely detect individual vertebrae.
2.0	Average subcutaneous fat deposit. Can easily feel spine and hip bones. Cannot detect individual vertebrae.
2.5	High levels of subcutaneous fat deposit. Can feel hip bones and spine. Cannot detect individual vertebrae.
3.0	Very high levels of subcutaneous fat deposit. Can detect hip bones. Can barely detect spine.
3.5	Extremely high levels of subcutaneous fat deposit. Can detect hip bones Cannot feel spine.
4.0	Maximal levels of subcutaneous fat deposit. Cannot detect spine or hip bones.



Figure B.6. Weighing a rodent. Picture credit Sarah Knowles



Figure B.7. Measuring body condition. Picture credit Sarah Knowles



Figure B.8. Measuring foot length. Picture credit Sarah Knowles

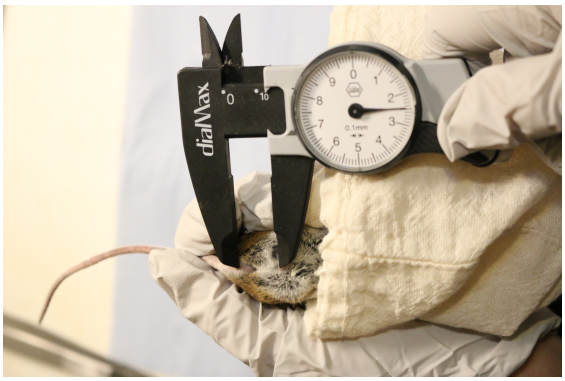


Figure B.9. Measuring anal genital distance. Picture credit Sarah Knowles

PIT tagging

Animals that have not been PIT tagged or have lost their tag need to be PIT tagged using the following procedure. As guideline use >=14 grams to determine if the animal should be tagged, less than this use a fur clipping to identify them.

1. Make sure a cannula (needle) is on the PIT tag gun. You can use one cannula for about three animals. Any more than this and the needle becomes blunt and PIT tagging becomes harder.
2. Clean the cannula by dipping in alcohol before PIT tagging and drying with a paper towel.
3. Check that the PIT tag is working, by using a PIT tag reader, note the number on the recording sheet and circle the "NOW".
4. Insert the PIT tag into the cannula. Ideally this should be done before the animal is removed from the trap.
5. If the animal is not already in a cloth bag from having it's measurements taken, transfer it to the cloth bag from the plastic wallet.
6. If the animal is not already restrained, then repeat the process as detailed in the Trap processing section.
7. Using a cotton flannel for padding, place the animal on the desk.
8. Roll back the bag to reveal the back of the animal. It is advised to cover the hind-quarters of the animal with the cotton bag, so that the animal is restrained by the head and the hind quarters.
9. Using your off-hand, place your second and third fingers down each side of the animal to secure it, palm facing up. It is also possible to use the little and ring finger to secure the animal, use whatever is most comfortable and allows you to get a good scruff.
10. Using your first finger and thumb, scruff the animal to create a fold of skin that you can insert the needle into.
11. Hold the PIT tag gun in your dominant hand. The barrel should be secured by most of your fingers, so that when the trigger is squeezed the needle does not move position and possible cause pain for the animal.
12. When injecting the PIT tag make sure the needle is laying flat or slightly point up and not point down into the animals body. The needle needs to go into the skin you are scruffing and not the body of the animal.
13. When injecting the PIT tag you should feel a slight bite as the needle penetrates the skin. It is necessary to push the needle in about two millimetres after this bite, before you pull the trigger.
14. It is important to try and to do the PIT tagging in an accurate way as possible. With practice it should be possible to PIT tag the animal with as minimal pain as possible and the least amount of stress.

Previously the area of skin, where the PIT tag was to be inserted, had fur removed. This was found to not be necessary and it could possibly cause the animal extra stress and reduce survival.

Fur clipping

If the animal can not be PIT tagged because it is too small, then fur clipping provides a temporary id solution.

1. Restraining the animal is similar to how it should be done with PIT tagging
2. Using a small pair of scissors, remove the guard hairs from the animal in the required pattern, leaving the base layer of hairs as this provides insulation for the animal (figure B.10).
3. A suggestion of patterns to use is shown in figure B.11. The database assumes that you will be using this notation.
4. Draw the location of the fur clippings on the recording sheet

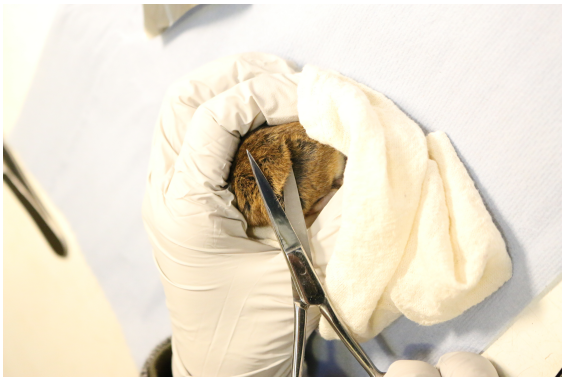


Figure B.10. Fur clipping a wood mouse. Picture credit Sarah Knowles

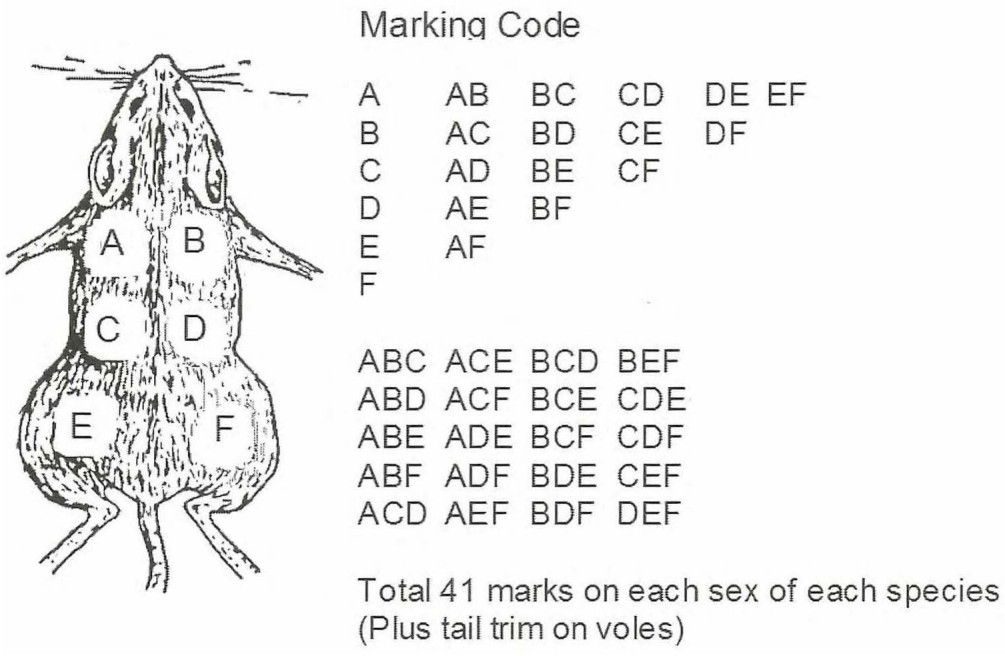


Figure B.11. Fur-clipping patterns. Taken from Gurnell and Flowerdew (2006)

Ear clipping

All rodents on first capture should have an ear clipping. The primary purpose of this is to identify rodents that have been caught before and as an alternative ID mechanism in case the animal loses or breaks it's PIT tag. The skin removed by ear clipping can also be used for genetic work. At least two ear clips should be taken to ensure enough material for DNA work.

1. Clean the Ear punch with alcohol and dry with a paper towel.
2. Restraining the animal is similar to how it should be done with PIT tagging.
3. Roll the bag back so that one ear is visible. As you roll the bag back to reveal the head you also want to roll it over to cover the back, this helps to restrain the animal.
4. Using the Ear punch clip the edge of the ear skin. Try to get the punch to be semi-circle and avoid holes in the middle of the ear, which can lead to the animal tearing it's ear.
5. If the animal is a mouse a pattern for unique id can be used, see B.12 figure.
6. Draw the location of the ear punches on the recording sheet.

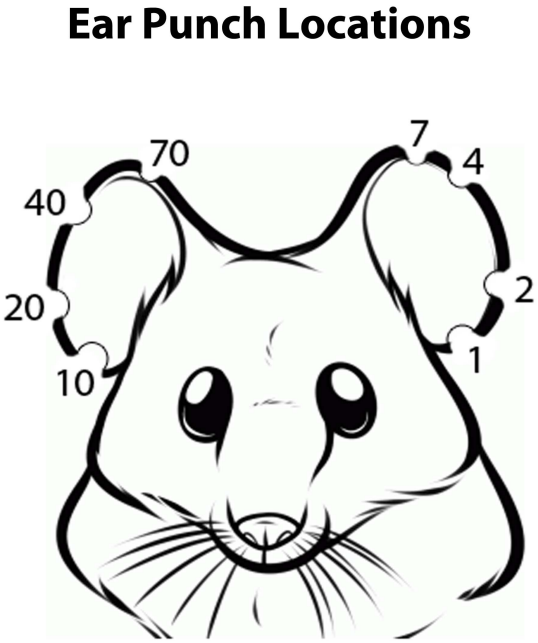


Figure B.12. Ear clipping locations

Waste disposal

All waste from trapping has to be disposed of in clinical waste bags.

1. Bags must be sealed with the provided tie.
2. Bags must be marked with the site code using a permanent marker.
3. In Wytham, the clinical waste bags can be taken to the field station and put in the shed for collection. It is important to inform Phil Smith, phil.smith@zoo.ox.ac.uk that you have left a bag in the shed.
4. In Zoology, the clinical waste bags are put down in the loading dock. A key for the cage is available from Intake.

Trap cleaning

It is important for traps to be cleaned between trapping sessions if they have come into contact with rodents. If microbiome samples are being taken then cleaning traps between trapping sessions is to remove any live bacterial cells and bacterial DNA.

Equipment

- Hot water
- Heavy duty washing up gloves
- Washing up brushes

- Bleach
- Autoclave (or Virkon powder if not possible)
- Yellow plastic bins (if sink not available / needed for Virkon).

All waste must be disposed of in clinical waste bags

Trap sterilisation

1. Wash all traps that had contact with an animal in bleach. Traps which have had captures should be scrubbed with washing up brush to remove poo (with the pin out / open flat) while for trigger failures the bottom of the trap can be brushed without removing the pin.
2. Re-assemble traps
3. Autoclave. Depending on what else is in the autoclave you may need different settings. The traps themselves can go on a quick cooling protocol, but if going in with waste etc usually the programme will be longer.
4. The zoology department has an autoclave on F level. The contact for this is William Volpato (william.volpato@zoo.ox.ac.uk)
5. If autoclave is not an option, leave traps to soak in 1% Virkon solution for several hours.

Faecal sample collection from rodents

The equipment used to take faecel samples from the traps is shown in table B.3. If you are short on time, assess what traps/samples you have and time available, and prioritize as follows.

1. Microbiome samples from all wood mice
2. Parasite samples from wood mice
3. First 3 microbiome samples from *A. flavicollis*
4. First 3 microbiome samples from bank voles
5. Parasite samples from first 3 *A. flavicollis*
6. Parasite samples from first 3 voles
7. Additional parasite samples from *A. flavicollis*
8. Additional parasite samples from voles

Table B.3. Faecel sampling equipment

Item	Description
Large forceps	For removing the cotton wool from the traps.
Nunc cryotubes	For the storage of the faecal samples.
Plastic storage boxes	For 1) microbiome samples 2) parasite samples
70% Ethanol spray bottle	For cleaning of equipment before and between traps.
Blue paper roll	For cleaning of equipment and to put bedding on whilst sampling.
10% Formalin	For storage of the parasite samples.
Flat-end tweezers	For the extraction of pellets from the bedding.
Scales	For weighing the samples, accurate to 0.001g.
Fridge	For storing the parasite samples. Currently using the one in EGI.
-80oC freezer	For storing the microbiome samples. Currently using the one in the Foster Lab.
-80-secure labels	(Starlab) if desired.
Permanent markers	For labelling the cyrotubes (Fine or Superfine).
Nitrile gloves	Must be worn at all times during faecal sampling.

Sample collection from traps

1. Remove pin from trap to open, and set aside pins in a pot where you won't lose them.

2. Pick the microbiome sample first. This is the priority – only take a parasite sample once you have the microbiome sample, if there is any poo left.

3. Microbiome sample should be ideally around 0.1g (0.05-0.2g; no more than 0.2g ideally, otherwise samples have to be split during DNA extraction). The number of pellets needed to achieve this weight will depend on the size and wetness of the pellets. Prioritise taking the darker pellets for this sample (rather than any that look like the result of eating peanuts!), and try to pull off cotton wool as much as possible.

4. In a second tube, pick the parasite sample. This is just whatever other poo you can gather, and can't really be too big! The only requirement is that some Formalin will be able to fit into the tube later. See below notes on what to do if short on time and prioritisation.

5. Label both tubes with the following information, as clearly as humanly possible (!): Trap number, Grid square, species initials (AS, AF, MG) and date. Separate information with space, do not use slashes or other notation.

6. While taking poo samples, note any extra ectoparasites observed and these can be added to the trapping data to increase accuracy.

7. Store microbiome samples in one plastic sample box, and parasite samples in another.

8. To avoid contamination between samples, it is VITAL that tweezers and your gloves (if pooey) are cleaned thoroughly with 70% ethanol and blue roll. Douse the blue roll with 70% ethanol spray, and then clean tweezers with this.

9. If gloves are very pooey on fingertips, change them.

Weighing and storing samples

1. Weigh each sample and record this in the lab book to 0.001g.

2. Freeze microbiome samples in -80°C ASAP, in labelled boxes. These samples should have nothing else added to them. Note the time samples were frozen in lab book.

3. After weighing the parasite samples, add 10% Formalin using the dropper, and shake. Store in the fridge. Make sure you wear gloves for this as Formalin is an irritant / potentially carcinogenic.

4. Mark "n/a" next to samples not taken in the lab, with a note why e.g. "not enough" or "no time"

References

Gurnell, John and John R Flowerdew (2006). *Live trapping small mammals*. Mammal Society.

Harris, Stephen and Derek William Yalden Yalden (2008). *Mammals of the British Isles: Handbook*. Mammal society.

C
Database design

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Introduction

Using a relational database has many advantages over a flat file method of storing data collected from ecological studies. A flat file can lead to missing information, for example in mark-recapture studies only the captures are normally recorded, this means that the information about the traps that did not catch an individual is missing. Data validation is also a problem with a flat file, whereas with a relational database, contents of a field can be checked using referential integrity. Flat files also have a lot of repeating data (increasing the chance of error) that is eliminated with a relational database.

To record the data for the Wytham Small Mammal project it was decided to use a relational database, in this case MySQL with an MS Access front-end. Although MS Access is far from the perfect solution and a web solution would be a better in terms of flexibility; using MS Access meant it was quick to implement and meets most of the requirements at the time of implementation. MySQL is an industry standard relational database; it is hosted by the Zoology IT department, which means the data is backed up on a regular basis. It is envisioned that the MS Access front-end will be replaced in the future.

Database structure

Figure C.1 shows the main structure of the database, the main tables and their relationships to each other. It does not include the lookup tables, which are detailed in Lookup tables section. It also does not include the tables that control how the grid is populated with traps, these tables are shown in figure C.2.

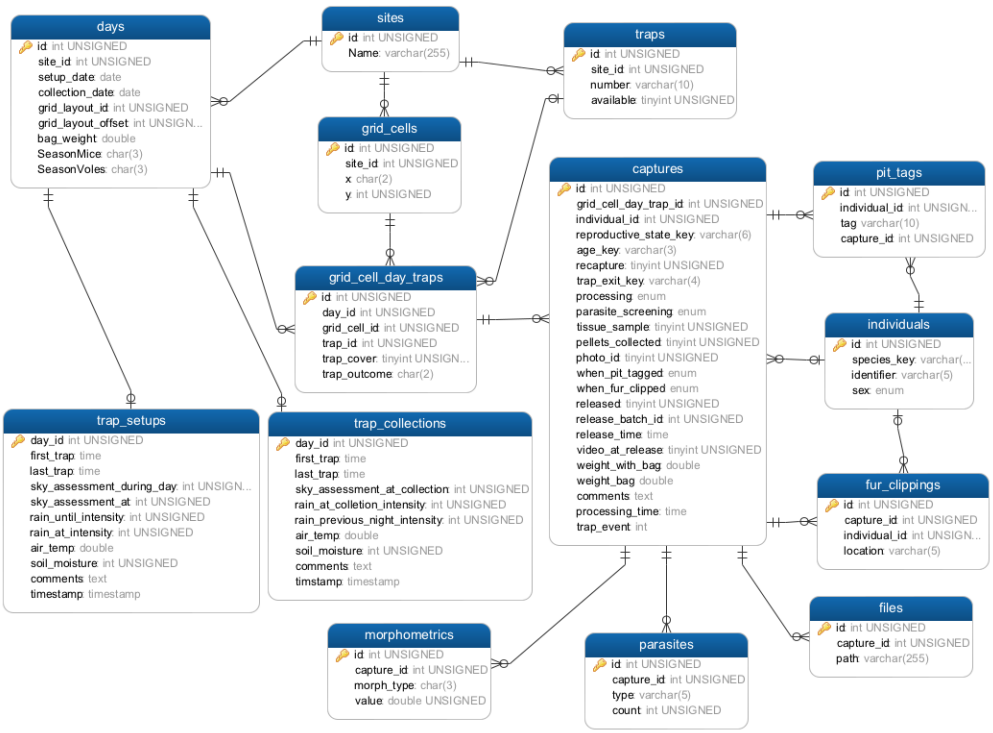


Figure C.1. Small recording database tables, does not include the lookup tables or the tables that control how the traps are placed in the grid for a new day.

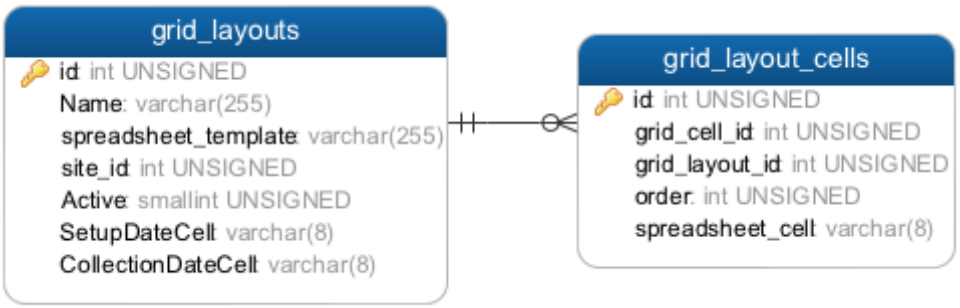


Figure C.2. Grid layout tables. Used to control how the traps are deployed in the grid when using the New Day function.

Main database tables

The design of the database reflects the "business" logic of the small mammal trapping conducted in Wytham Woods. The following details the main tables of the database with their structure. It does not include the lookup tables which are detailed in the Lookup tables section.

Sites table

Contains information about the different sites trapped. Currently there is only one site, but this table was included for future proofing, for example there may be the requirement for an experimental trapping grid to be created.

Table C.1. Definition of the sites table

Field	Type	Description
`id`	integer unsigned	Unique identifier for the site.
`Name`	string(255)	Name of the site.
Constraint field	Type	Description
`id`	primary key	

Days table

Contains information about each trapping session conducted. Links to the Site and the grid layout tables.

Table C.2. Definition of the days table

Field	Type	Description
`id`	integer	Unique identifier for the day record
`site_id`	integer	The site in which the trapping session was conducted
`setup_date`	date	The date which the traps were setup
`collection_date`	date	The date which the traps were collected
`grid_layout_id`	integer	The grid layout used for this trapping session
`grid_layout_offset`	integer	The offset used with the grid layout
`bag_weight`	double	The weight of the bag and clip used to weight the captures
`SeasonMice`	character(3)	The mouse breeding season for the trapping session BS=Breeding Season, NBS=Non breeding season
`SeasonVoles`	character(3)	The vole breeding season for the trapping session BS=Breeding Season, NBS=Non breeding season

Constraint field	Type	Description
`id`	primary key	
`site_id`	foreign key	Each trapping session has to be assigned a site
`grid_layout_id`	foreign key	Each trapping session has to be assigned a grid layout

Grid cells table

Holds the information for the grid cells for each site.

Table C.3. Definition of the grid cells table

Field	Type	Description
`id`	integer	Unique identifier for the grid cell record
`site_id`	integer	The site in which the grid cell is located
`x`	character(2)	The x cord of the grid cell
`y`	integer	The y cord of the grid cell
Constraint field	Type	Description
`id`	primary key	
`site_id`	foreign key	Each grid cell has to belong to a defined site

Traps table

Lists the traps that are used in each site, including those traps that have been retired.

Table C.4. Definition of the traps table

Field	Type	Description
`id`	integer	Unique identifier for the trap records
`site_id`	integer	The site to which the trap belongs
`number`	string(10)	Identifier written on the trap
`available`	boolean	If the trap is available to be currently deployed
Constraint field	Type	Description
`id`	primary key	
`site_id`	foreign key	Each trap record has to belong to a defined site

Grid cell day traps table

Holds the information for which traps where deployed in which grid cell on which day.

Table C.5. Definition of the grid cell day traps table

Field	Type	Description
`id`	integer	Unique identifier for the grid cell day trap records
`day_id`	integer	The day that the trap was deployed in the grid cell
`grid_cell_id`	integer	The grid cell that the trap was deployed
`trap_id`	integer	The trap that was deployed
`trap_cover`	boolean	Was a trap box used, defaults to TRUE
`trap_outcome`	character(2)	The outcome of the trapping for the deployed trap, defaults to 'NC' (No Capture)

Constraint field	Type	Description
`id`	primary key	
`day_id`	foreign key	Each record has to be assigned to a defined day
`grid_cell_id`	foreign key	Each record has to be assigned to a defined grid cell
`trap_id`	foreign key	Each record has to be assigned to a defined trap
`trap_outcome`	foreign key	Limits the entries in the trap_outcome field to those defined in the trap_outcomes table
`day_id, trap_id`	unique index	Only one record per trap per day

Trap setups table

Holds information about the setup of the traps, including general weather information. Wytham has a weather station so a lot of this information is potentially redundant. Kept for comparison with the Silwood site.

Table C.6. Definition of the trap setups table

Field	Type	Description
`day_id`	integer	The day that the traps were setup, only one record per day
`first_trap`	time	The time that the first trap was setup
`last_trap`	time	The time the last trap was setup
`sky_assessment_during_day`	integer	An assessment of the sky condition during the day
`sky_assessment_at`	integer	An assessment of the sky condition at the start of trapping

`rain_until_intensity`	integer	The intensity of the rain before the trapping
`rain_at_intensity`	integer	The intensity of the rain during the setup of the traps
`air_temp`	double	The temperature of the air at the time of trap setup
`soil_moisture`	integer	The soil moisture at trap setup
`comments`	text	Any comments about the trap setup
`timestamp`	timestamp	An internal value, holding when the record was last changed

Constraint field	Type	Description
`day_id`	primary key	
`day_id`	foreign key	Limits the values in the day_id field to those defined in the days table
`rain_until_intensity`	foreign key	Limits the entries in the rain_until_intensity field to those defined in the rain_intensity table
`rain_at_intensity`	foreign key	Limits the entries in the rain_at_intensity field to those defined in the rain_intensity table
`sky_assessment_during_day`	foreign key	Limits the entries in the sky_assessment_during_day field to those defined in the sky_assessment table
`sky_assessment_at`	foreign key	Limits the entries in the sky_assessment_at field to those defined in the sky_assessment table
`soil_moisture`	foreign key	Limits the entries in the soil_moisture field to those defined in the soil_moisture table

Trap Collections table

Holds similar details to the Traps setups table, but for the trap collection. Again this information may be potentially redundant, but kept for comparison reasons.

Table C.7. Definition of the trap collections table

Field	Type	Description
`day_id`	integer	The day that the traps were setup, only one record per day
`first_trap`	time	The time that the first trap was setup
`last_trap`	time	The time the last trap was setup
`sky_assessment_at_collection`	integer	An assessment of the sky condition at trap collection
`rain_at_collection_intensity`	integer	The intensity of the rain during trap collection
`rain_previous_night_intensity`	integer	The intensity of the rain the previous night
`air_temp`	double	The temperature of the air at the time of trap setup
`soil_moisture`	integer	The soil moisture at trap setup
`comments`	text	Any comments about the trap setup
`timestamp`	timestamp	An internal value, holding when the record was last changed
`tissue_sample`	boolean	Was a tissue sample taken
`pellets_collected`	boolean	Was a faecal sample taken
`photo_id`	boolean	Was a photo taken of the individual for identification purposes

Constraint field	Type	Description
`day_id`	primary key	
`day_id`	foreign key	Limits the values in the day_id field to those defined in the days table
`rain_at_collection_intensity`	foreign key	Limits the entries in the rain_at_collection_intensity field to those defined in the rain_intensity table
`rain_previous_night_intensity`	foreign key	Limits the entries in the rain_previous_night_intensity field to those defined in the rain_intensity table

`sky_assessment_at_collection`	foreign key	Limits the entries in the sky_assessment_at_collection field to those defined in the rain_intensity table
`soil_moisture`	foreign key	Limits the entries in the soil_moisture field to those defined in the soil_moisture table

Captures table

Lists the captures made in each of the traps. As it is possible to catch more than one individual in a trap on any given day, the relationship between Grid cell day traps table and the Captures table is a one to many.

Table C.8. Definition of the captures table

Field	Type	Description
`id`	integer	Unique capture identifier
`grid_cell_day_trap_id`	integer	The day, grid cell and trap that the capture was made in
`individual_id`	integer	The individual that was caught
`reproductive_state_key`	string(6)	The reproductive state of the individual
`age_key`	string(3)	The age of the individual
`recapture`	boolean	Had the individual been caught before
`trap_exit_key`	string(4)	How did the individual exit the trap
`processing`	enum('B','H')	How was the individual processed. 'B' bag, 'H' in hand (scruffed).
`parasite_screening`	enum('N','B','H')	How was the individual scanned for parasites. 'B' bag, 'H' in hand (scruffed), 'N' unknown what this value means, it was used in the Silwood trapping. It is kept only for compatibility with the Silwood dataset.
`when_pit_tagged`	enum('Before', 'Now')	When was the individual PIT tagged. 'Now' was PIT tagged this trapping session, 'Before' was already PIT tagged. NULL if not PIT tagged.
`when_fur_clipped`	enum('Before', 'Now')	When was the individual fur clipped. 'Now' was fur clipped this trapping season, 'Before' was fur clipped at a previous trapping session. NULL if not fur clipped.

`released`	boolean	Was the individual released back into the woodland. This is used along with the comments field to determine if the capture was a trap death.
`release_batch_id`	integer	In which batch was the individual released. Null if the individual was not released or the release time field is used.
`release_time`	time	The time that the individual was released. Null if the release_batch_id field is used or the individual was not used.
`video_at_release`	boolean	Was a video recorded during the release.
`weight_with_bag`	double	The weight of the individual in the plastic wallet with weighing clip attached.
`weight_bag`	double	Weight of the bag if different from the one held in the days table. Null if not used.
`comments`	text	Any comments about the capture. If the capture was a trap death, details should be recorded here.
`processing_time`	time	The time that capture was processed.
`trap_event`	integer	A number assigned by the researcher to identify the capture.

Constraint field	Type	Description
`id`	primary key	
`grid_cell_day_trap_id`	foreign key	Link to the grid_cell_day_traps table. As a trap can have more than one individual caught in it during a trapping session (although very rare occurance), this is a one to many relationship.
`individual_id`	foreign key	Link to the individuals table.
`release_batch_id`	foreign key	Link to the release_batch table
`age_key`	foreign key	Limits the entries in the age_key field to those defined in the age table
`reproductive_state_key`	foreign key	Limits the entries in the reproductive_state_key field to those defined in the reproductive_state table
`trap_exit`	foreign key	Limits the entries in the trap_exit field to those defined in the trap_exit table

PIT tags table

List of the PIT tags, that are used to uniquely identify individuals. Because it is possible for an individual to lose a PIT tag, the PIT tag information can not be

held in the individuals table. A link to the captures table is needed to work out an individuals current PIT tag on any particular date.

Table C.9. Definition of the PIT tags table

Field	Type	Description
`id`	integer	Unique PIT tag identifier
`individual_id`	integer	Each PIT tag record has to be assigned to an individual.
`tag`	string(10)	The PIT tag number in hexadecimal format.
`capture_id`	integer	Which capture was the PIT tag assigned to the individual.

Constraint field	Type	Description
`id`	primary key	
`capture_id`	foreign key	Link to the captures table.
`individual_id`	foreign key	Link to the individual table.

Individuals table

Lists all the individuals that have been caught during the project.

Table C.10. Definition of the individuals table

Field	Type	Description
`id`	integer	Unique individual id
`species_key`	string(3)	The individual's species
`identifier`	string(5)	An identifier for the individual assigned by the researcher. This is usually the ear clip number
`sex`	enum('M','F','?')	The sex of the individual. The '?' is included as voles are very hard to sex outside of the breeding season

Constraint field	Type	Description
`id`	primary key	
`species_key`	foreign key	Limits the values in the species_key field to those defined in the species table

Fur clippings table

Similar to the PIT tags table it is possible for an individual to have more than one fur clipping.

Table C.11. Definiation of the fur clippings table

Field	Type	Description
`id`	integer	Unique fur clipping identifier
`capture_id`	integer	The id of the capture that the fur clipping was done
`individual_id`	integer	The id of the individual that had the fur clipping
`location`	string(5)	The locations of the fur clippings, based on the technique describe by Gurnell and Flowerdew (2006)

Constraint field	Type	Description
`id`	primary key	
`capture_id`	foreign key	Link to the captures table
`individual_id`	foreign key	Link to the individuals table
`location`	foreign key	Limits the values in the location field to those defined in the fur_clipping_locations table
`capture_id, location, individual_id`	unique index	Only one record per capture pre individual per location

Files table

List files that are associated with a particular capture record.

Table C.12. Definition of the files table

Field	Type	Description
`id`	integer	Unique identifier for a file record
`capture_id`	integer	The id of the capture that file is associated with
`path`	string(255)	The file system path to the file

Constraint field	Type	Description
`id`	primary key	
`capture_id`	foreign key	Link to the captures table

Parasites table

Lists the count of each type of parasite found for the capture. Only one record for each type for each capture.

Table C.13. Definition of the parasites table

Field	Type	Description
`id`	integer	Unique identifier for the parasite count record
`capture_id`	integer	The id of the capture the parasite count was record for
`type`	string(5)	The type of parasite
`count`	integer	The number of parasites of that type found
Constraint field	Type	Description
`id`	primary key	
`capture_id`	foreign key	Link to the captures table
`type`	foreign key	Limits the type values to those defined in the parasite_type table
`capture_id, type`	unique index	Only one record for each parasite type for each capture

Morphometrics table

Lists the measured morphometrics for the capture, e.g. leg length. It is possible to have multiple measurements for each type for each capture. This is required as taking multiple measurements can reduce measurement error.

Table C.14. Definition of the morphpmetrics table

Field	Type	Description
`id`	integer	Unique identifier for each morphometric record
`capture_id`	integer	The capture id that the morphometric record was recorded for
`morph_type`	char(3)	The morphometric type
`value`	double	The measured value for the morphometric
Constraint field	Type	Description
`id`	primary key	
`capture_id`	foreign key	Link to the captures table
`morph_type`	foreign key	Limits the morhpometric types to those defined in the morphometrics_types table

Researchers table

Lists the researchers that work on the project. This information is required so that it is possible to account for differences between measurements taken by

different researchers.

Table C.15. Definition of the researchers table

Field	Type	Description
`id`	integer	Unique identifier for each researcher record.
`name`	string(255)	Name of the researcher
Constraint field	Type	Description
`id`	primary key	

Day researchers table

Which researchers were involved in the setup and the collection of the traps. Not really used, but kept for compatibility with the Silwood data.

Table C.16. The definition of the day researchers table

Field	Type	Description
`id`	integer	Unique identifier for each day researcher record
`day_id`	integer	The day identifier for the day that the researcher worked on
`researcher_id`	integer	The id of the researcher
`at_setup`	boolean	Was the researcher at setup
`at_collection`	boolean	Was the researcher at collection
Constraint field	Type	Description
`id`	primary key	
`day_id`	foreign key	Link to the day table
`researcher_id`	foreign key	Link to the researcher table
`day_id, researcher_id`	unique index	Limit one record per day per researcher

Capture researchers table

Which researchers were responsible for processing a particular capture. Used to account for differences between measurement techniques of the different researchers.

Table C.17. Definition of the capture researchers table

Field	Type	Description
`id`	integer	Unique identifier for each capture researchers record
`capture_id`	integer	The capture that the researcher worked on
`researcher_id`	integer	The identifier of the researcher that worked on the capture

Constraint field	Type	Description
`id`	primary key	
`capture_id`	foreign key	Link to the capture table
`researcher_id`	foreign key	Link to the researcher table

Grid layout table

List the grid layouts available for each site.

Table C.18. The definition of the grid layout table

Field	Type	Description
`id`	integer	Unique identifier for each grid layout
`Name`	string(255)	A Name for the grid layout
`spreedsheet_template`	string(255)	The Excel template to use for this grid layout
`site_id`	integer	The site identifier that the template is associated with
`Active`	boolean	Is the grid layout active (currently in use)
`SetupDateCell`	string(8)	Which cell on the spreadsheet should be populated with the setup date
`CollectionDateCell`	string(8)	Which cell on the spreadsheet should be population with the collection date

Constraint field	Type	Description
`id`	primary key	
`site_id`	foreign key	The link to the site table

Grid layout cells table

The cells of the spreadsheet that represents the grid layout. This table is mainly used to automatically population the spreadsheet with the trap numbers to produce the trapping sheet.

Table C.19. Definition of the grid layout cells table

Field	Type	Description
`id`	integer	Unique identifier for each grid layout cell record
`grid_cell_id`	integer	The grid cell that the grid layout cell refers to
`grid_layout_id`	integer	The grid layout that the grid layout cell belongs to
`order`	integer	The order that the grid cells should be populated
`spreadsheet_cell`	string(8)	The spreadsheet cell that represents the grid cell

Constraint field	Type	Description
`id`	primary key	
`grid_cell_id`	foreign key	The link to the grid_cells table
`grid_layout_id`	foreign key	The link to the grid_layouts table
`grid_layout_id, order`	unique index	Ensure that each order value is unique for a particular grid layout
`grid_cell_id, grid_layout_id`	unique index	Ensures that each grid cell is only represent once for each grid layout

Release batches table

Table C.20. Definition of the release batches table

Field	Type	Description
`id`	integer	Unique identifier for the release batch
`day_id`	integer	The day that the release batch is for
`number`	integer	The number of the release batch, assigned by the researchers
`start_time`	time	The time the first animal was released
`end_time`	time	The time the last animal was released

Constraint field	Type	Description
`id`	primary ley	
`day_id`	foreign key	Link to the days table

Lookup tables

Trap outcomes table

The outcome of the trapping session for the trap.

Table C.21. Definition of the trap outcome table

Field	Type	Description
`key`	character(2)	Unique key for the trap outcome
`description`	string(255)	Textual description for the trap outcome
Constraint field	Type	Description
`key`	primary key	

Species table

Holds information on the species caught during trappings.

Table C.22. Definition of the species table

Field	Type	Description
`key`	character(3)	Unique key for the species
`scientific_name`	string(255)	The scientific name for the species
`common_name`	string(255)	The common name for the species
Constraint field	Type	Description
`key`	primary key	

Moonlight table

Holds the moon illumination percentages for each day. Currently not linked to any other tables, but included as it is useful for analysis purposes to have this information.

Table C.23. Definition of the moonlight table

Field	Type	Description
`id`	integer	Unique identifier for the moonlight records
`date`	date	The date that the moonlight percentage is for
`illuminiation`	double	The moon illumination percentage
Constraint field	Type	Description
`id`	primary key	

Sky assessment table

The possible values for sky assessment fields

Table C.24. Definition of the sky assessment table

Field	Type	Description
`id`	integer	Unique identifier for the sky assessment
`description`	integer	Textual description for the sky assessment
Constraint field	Type	Description
`id`	primary key	

Rain intensity table

Possible values for the rain intensity fields

Table C.25. Definition of the rain intensity table

Field	Type	Description
`id`	integer	Unique identifier for the rain intensity
`description`	string(255)	Textual description for the rain intensity
Constraint field	Type	Description
`id`	primary key	

Soil moisture table

Possible values for the soil moisture fields

Table C.26. Definition of the soil moisture table

Field	Type	Description
`id`	integer	Unique identifier for the soil moisture
`description`	string(255)	Textual description for the soil moisture
Constraint field	Type	Description
`id`	primary key	

Control table

Holds system wide settings and generic lookup values.

Table C.27. Definition of the control table

Field	Type	Description
`control_type`	string(20)	The type of control value
`key`	string(20)	The key of the control type
`value`	string(255)	The value of the control type

Constraint field	Type	Description
`control_type, key`	primary key	

Control types table

The valid control types used in the control table

Table C.28. Definition of the control types table

Field	Type	Description
`control_type`	string(20)	Valid control type

Constraint field	Type	Description
`control_type`	primary key	

Morphometric types table

The valid morphometric types

Table C.29. Definition of the morphometric types table

Field	Type	Description
`type`	character(3)	Type code for the morphometric
`description`	string(255)	Textual description for the morphometric

Constraint field	Type	Description
`type`	primary key	

Parasite types table

The valid parasite types

Table C.30. Definition of the parasite types table

Field	Type	Description
`type`	string(5)	The parasite type code
`description`	string(255)	Textual description of the parasite type
Constraint field	Type	Description
`type`	primary key	

Fur clipping location table

Valid fur clipping location values.

Table C.31. Definition of the fur clipping location table

Field	Type	Description
`location`	string(5)	Fur clipping location code
`description`	string(255)	Textual description for the fur clipping location
Constraint field	Type	Description
`location`	primary key	

Age table

Valid values for age fields

Table C.32. Definition of the age table

Field	Type	Description
`key`	string(3)	Age code
`description`	string(255)	Textual description of the age
`order`	integer	The order of the ages, used when sorting by age
Constraint field	Type	Description
`key`	primary key	

Trap exit table

Valid values for trap exit fields

Table C.33. Definition of the trap exit table

Field	Type	Description
`key`	string(4)	Valid trap exit key
`description`	string(255)	Textual description for the trap exit
Constraint field	Type	Description
`key`	primary key	

Reproductive state table

Table C.34. Definition of the reproductive state table

Field	Type	Description
`key`	string(6)	Valid reproductive state key
`description`	string(255)	Textual description for the reproductive state
`sex`	enum('M','F')	The sex that the reproductive state is for
Constraint field	Type	Description
`key`	primary key	

Future work

Currently there is a number of enhancements planned to improve the storage of small mammal capture data. The first is to have a sex field added to the capture table. Although biologically the sex of small mammals does not change, the identification of sex, particularly for voles out of breeding is difficult. Having the sex information held in the capture table in addition to the individual table, would allow for a history of sex identification to be kept.

It is planned to implement electronic recording of capture information using tablets, such as Android. This would require an automated system to upload the information from the tablets and additional tables to handle the validation of the data.

Metabolic and genetic information (both from the mice and from faecal samples) is currently being collected for the small mammals. It would be useful to have this information added to the database. This would require the addition of additional tables to hold the information.

References

Gurnell, John and John R Flowerdew (2006). *Live trapping small mammals*. Mammal Society.