


# Factors affecting woodland rodent growth

M. J. Brouard<sup>1</sup> , S. C. L. Knowles<sup>2</sup>, S. Dressen<sup>3</sup>, T. Coulson<sup>1</sup> & A. F. Malo<sup>4</sup>

<sup>1</sup>E2D Ecological and Evolutionary Dynamics, Department of Zoology, University of Oxford, Oxford, UK

<sup>2</sup>Department of Zoology, University of Oxford, Oxford, UK

<sup>3</sup>DER GRÜNE ZOO WUPPERTAL, Wuppertal, Germany

<sup>4</sup>GLOCEE - Global Change Ecology and Evolution Group, Universidad de Alcalá, Madrid, Spain

## Keywords

*Apodemus sylvaticus*; *Myodes glareolus*; rodent growth; body size dynamics; mark–recapture; sympatry; population density.

## Correspondence

Marc J. Brouard, Department of Zoology, University of Oxford, Oxford OX1 3PS, UK.  
Email: marc.brouard@zoo.ox.ac

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## Introduction

Body size is an important phenotypic trait in ecology. For example, there are a number of general rules of ecology, including Cope's rule that states that individuals of a species will increase in size with evolutionary time (Stanley, 1973) or Foster's rule that states members of a species will get bigger or smaller depending on availability of resources in their environment (Foster, 1964). However, why we see such general rules is a bit of an enigma, particularly 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, Sheldon, & Kruuk, 2001). In order to gain insight into why body size behaves as it does, it is necessary to analyse data on individual growth trajectories. For many free-living species, including rodents, little is known about the dynamics of body size. Hone & Benton (2005) list the advantages and disadvantages of a large body size. The advantages include increased success in mating, increased intraspecific and interspecific competition success, increased defence against predation, increased predation success, a greater range of food choice, extended longevity and increased intelligence. Whilst the disadvantages include increase in resource requirements, increased risk of extinction, increased development time and lower fecundity. For rodents, there are advantages to having a

## 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. 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.

smaller size. They are able to increase their reproductive effort quickly when there are increases in food supply (Watts, 1970), by having more litters with more offspring in each litter. Also, in the specific case of wood mice (*Apodemus sylvaticus*) their small size allows them to utilize the trees in the woodland to avoid predation and conflict with other species (Buesching *et al.*, 2008). Understanding the development of individuals, and in particular how they grow and the factors that influence their growth rates, is a core component of mammal ecology.

Very little information exist for growth patterns of wild, free-ranging rodents, which is surprising given they are the group that contains Britain's most common mammals; 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 examine what drives the growth of rodents in native British woodlands. Rodents provide a good study system as they have short generation times, so in any given year the majority of individuals will have been reared under the same conditions. 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. Population density is known to be influenced by

food availability (Montgomery & Montgomery, 1990; Pucek *et al.*, 1993), vegetation cover (Mazurkiewicz, 1994), abiotic environmental factors (Brown, 1956; Orrock, 2004), biotic environmental drivers (Flowerdew, 1974) and density dependence (Watts, 1969; Flowerdew, 1985). All these factors could also potentially influence body size and growth of individuals.

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, 2009). Although high population densities have been shown to retard growth in *M. glareolus* (Kviljo *et al.*, 1992), 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). In this study, we look at the dynamics of rodent growth throughout the year, for two species, *A. sylvaticus* and *M. glareolus*, covering both the breeding and the non-breeding seasons.

As food availability is a major factor in determining the population density (Montgomery *et al.*, 1991), we would expect it to also have an impact on rodent growth. With larger individuals in the population with increased food availability, the population mean weight may actually decrease due to increased juvenile survival. Although we do not measure food availability directly, other factors we do measure can be considered as surrogates. We would expect areas of increased cover and nights with low moon illumination to have rodent populations with higher growth rates and survival, due to increased foraging activity. 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 heterospecifics, with increasing density of both reducing the growth of individuals. Particularly for females, as previously mentioned high densities can reduce the number of breeding individuals.

## Materials and methods

In this paper, we use change in weight of individuals through time. Weight is straightforward to measure and does not require the rodents to be anaesthetized; therefore, the impact on individuals is minimal. This is important when individuals are trapped at short regular intervals, as in this study (McLaren *et al.*, 2004). The use of animals and all procedures was in accordance with Imperial College London ethical committee and Home Office UK guidelines.

### 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 the site was dominated by birch (*Betula pubescens*), and the site is classified as W11 (*Quercus petraea*–*B. pubescens*–*Oxalis acetosella* woodland) using the National Vegetation Classification System (Pigott *et al.*, 2000). The understorey is composed of

hazel (*Corylus avellana*) and rhododendron (*Rhododendron 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 10 m × 10 m squares. Data were collected between 9 October 2008 and 1 December 2015. Trapping sessions were conducted weekly between 9 October 2008 and 10 November 2010, then fortnightly until 26 November 2014 and finally every 3 weeks until 1 December 2015. Full details of the trapping protocols used are detailed in Godsall, Coulson, & Malo (2013).

### Data preparation

All statistical analyses were conducted using R version 3.2.2 (R Core Team, 2015). The data were checked for consistency and validity, in particular for the ageing of individuals, as this can be subjective and depends on the experience of the researcher making the estimate. The onset of the breeding season, for each species, was determined when more than half the caught adult males in a trapping season 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 in diet for *A. sylvaticus* (Watts, 1969). Moon illumination proportion was calculated using the method described by Meeus (1991). The full Visual Basic for Applications code is included in the (Supporting Information Text S1). Precipitation and temperature data were taken from the MIDAS Land and Marine Surface Station Data produced by the Met Office (Met Office, 2012), provided at an hourly resolution. The capture data were summarized to 3-week periods. Some individuals were caught more than once during each 3-week period; the methods used to summarize the variables are detailed in Supporting Information Table S1.

### 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.*, 2015). 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  $t + 1$  (in g), with a Gaussian distribution and an identity link. The explanatory variables were weight at  $t$  (in g), breeding season, pregnancy or breeding condition, moon illumination proportion, precipitation (in mm), temperature (in °C), rhododendron cover and population estimates for *A. sylvaticus*, *Apodemus flavicollis* and *M. glareolus*. A random effect for trapping session was also included in the models. Because of the way that the data were collected, trapping session was independent of year, it was therefore not possible to include both year and trapping session in the models as a random effect. Model reduction was conducted using the comparison of AIC values, to find the best fitting model. For model comparisons, we fitted the models with ML, with the final

models being run with REML. Model fit was assessed using the `sem.model.fits` function from the R package `piecewiseSEM` (Nakagawa & Schielzeth, 2012), 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. This form of analysis was chosen as the data were being prepared to be used as part of an integral projection model (IPM), of which growth is one of the core functions. Population estimates were calculated using a Jolly–Seber open population model (R Package FSA (Ogle, 2020)).

## Results

There were a total of 6113 captures (4291 *A. sylvaticus*, 415 *A. flavicollis* and 1407 *M. glareolus*), with 1476 unique individuals (892 *A. sylvaticus*, 149 *A. flavicollis* and 435 *M. glareolus*). On average, each individual was caught 4.24 times (*A. sylvaticus* 4.92 times, *A. flavicollis* 2.91 times and *M. glareolus* 3.29 times). On trapping nights, the mean ( $\pm$ SE) moon illumination was  $0.49 \pm 0.02$ , the mean rainfall was  $0.44 \pm 0.09$  mm, the mean minimum temperature was  $8.27 \pm 0.34^\circ\text{C}$  and the mean maximum temperature was  $13.26 \pm 0.41^\circ\text{C}$ . 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*).

When summarizing the mean weight of individuals by month, males of 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 (Fig. 1a). This trend for males is not changed if only adults are considered (Fig. 1b). For female *A. sylvaticus*, there is little change in mean weight, although there is considerable variation if all age classes are included (Fig. 1c). In comparison, female *M. glareolus* mean weight shows an increase in May/June before decreasing again in September, even when only adults are considered (Fig. 1c,d). During this period of increase, the mean female *M. glareolus* weight is higher than mean female *A. sylvaticus* weight. If mean weight is summarized by trapping session, the increase in weight during the breeding season is evident, although there is variation between years (Supporting Information Fig. S1). In comparison, the estimated population density at 3-week intervals, estimated using Jolly–Seber open population models, showed a 2-year cycle in density (Supporting Information Fig. S2). Although this is not evident in all species for all years, it is particularly evident for *A. sylvaticus*. Other summary statistics for the captures are shown in Supporting Information Table S6.

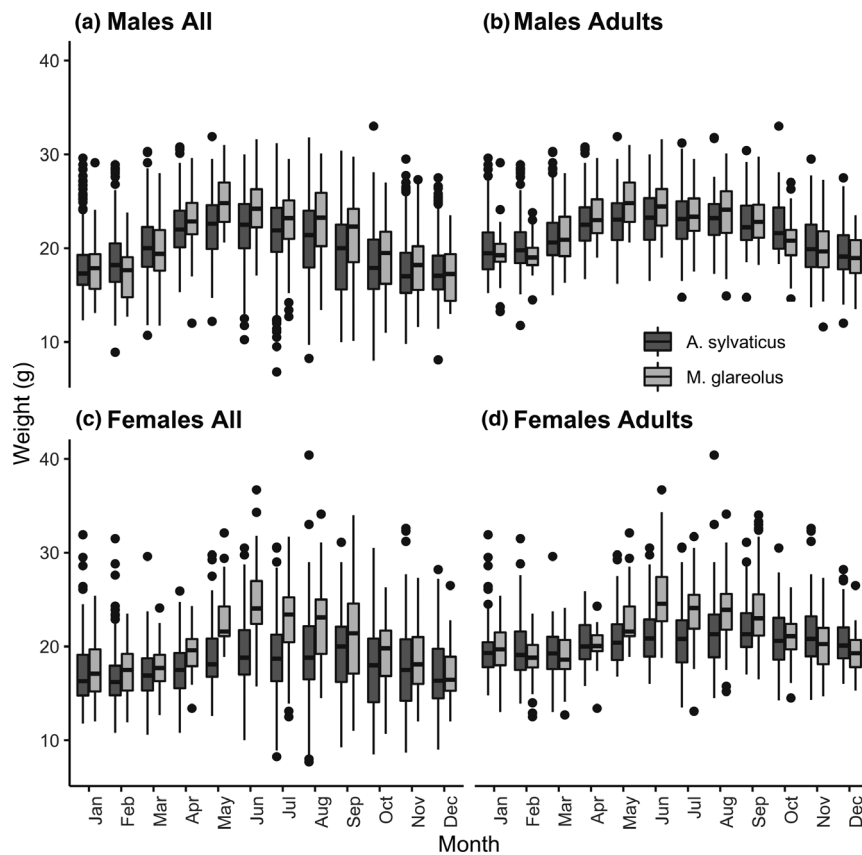
## Growth models

The number of observations used in each of the models was 778 for female *A. sylvaticus*, 1045 for male *A. sylvaticus*, 236 for female *M. glareolus* and 211 for male *M. glareolus*. After model reduction, the LME growth models (Table 1 and Figs 2

and 3) predict an increase in weight during breeding season for *A. sylvaticus* males and *M. glareolus* males and females, but not *A. sylvaticus* females. *Apodemus 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. Model reduction is detailed in Supporting Information Tables S2–S5 (for variable abbreviation, see Supporting Information Table S1). Finally, the full model details, before reduction, are shown in Supporting Information Table S7. The models were checked for multicollinearity, and in all cases, low correlation was found.

## Discussion

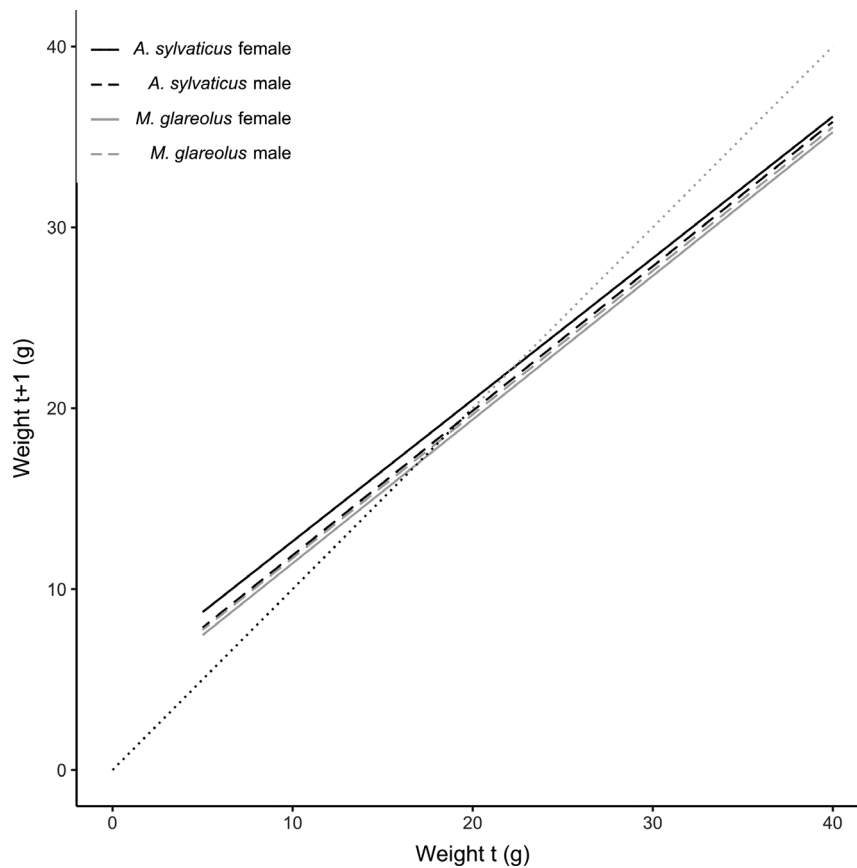
This study looks at the growth of two species of woodland rodents living in sympatry, *A. sylvaticus* and *M. glareolus*. Before discussing the growth, it is worth briefly considering the patterns that are observed both in the mean weights of individuals and the population densities for the woodland rodents in this study. Estimated population density from the Jolly–Seber open population model indicates an increase in density every 2 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 did not see the 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* do not 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 2 years is most 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 cannot confirm this. Both species are known to change their breeding strategy based on the availability of resources (Watts, 1970), with up to six 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 (Green, 2009), an increase in weight at the start of the breeding season and a slow decrease in winter. Only female *A. sylvaticus* did not follow this pattern, but there



**Figure 1** Rodent weight summarized by month. (a) Males, all age classes; (b) males, adults only; (c) females, all age classes; (d) females, adults only.

**Table 1** Comparison of the Silwood rodent growth linear mixed effect models after model reduction. Late and early breeding season apply only to *Apodemus sylvaticus* and breeding season applies only to *Myodes glareolus*

	<i>A. sylvaticus</i> ♀	<i>A. sylvaticus</i> ♂	<i>M. glareolus</i> ♀	<i>M. glareolus</i> ♂
(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)			
<i>Apodemus flavicollis</i> 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)	
<i>A. sylvaticus</i> density			0.02 (0.01)	0.02 (0.01)
AIC	3308.16	3762.29	1051.69	886.96
Num. of obs.	778	1045	236	211
Num. of 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
$R^2$ marginal	0.65	0.84	0.73	0.75
$R^2$ conditional	0.77	0.86	0.80	0.82



**Figure 2** Predicted rodent weight at  $t + 1$  based on weight at  $t$  in the non-breeding season for non-pregnant females and non-breeding condition males with a mean population density of *Apodemus flavicollis* (4.46) and *Apodemus sylvaticus* (35.30), mean temperature (10.86°C), precipitation (12.13 mm) and moonlight (0.49).

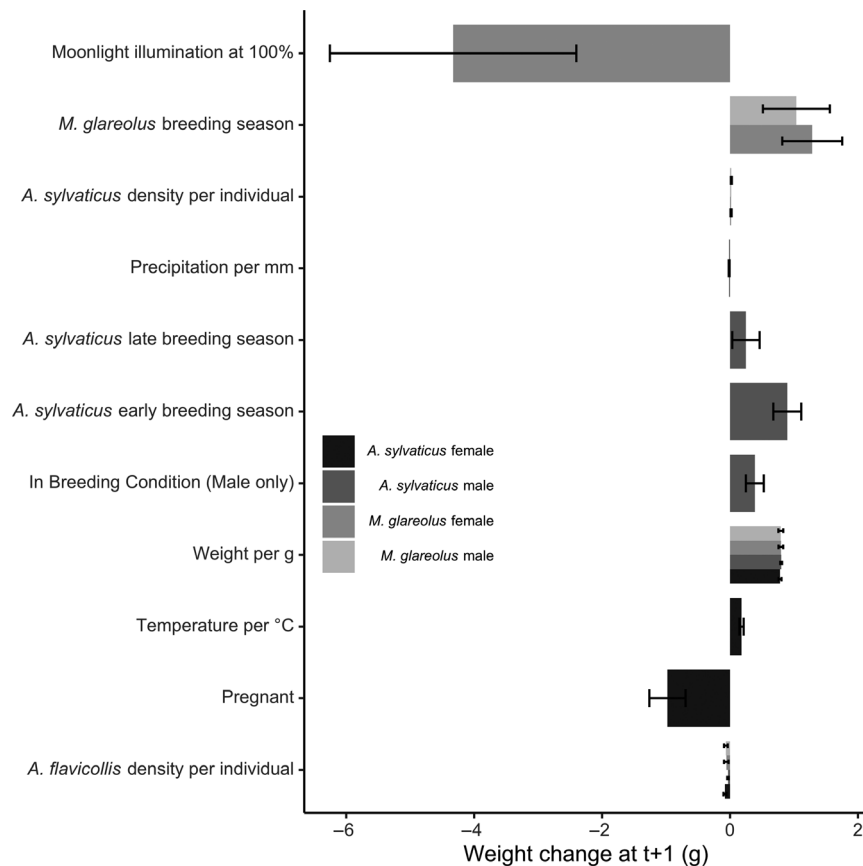
was large variation in weight for this group. This may be explained by changes in weight of individuals due to pregnancy. Although pregnancy was recorded in this study, it can be difficult to detect early pregnancies in captured individuals.

The growth models indicate that *M. glareolus* females showed the largest growth between trapping sessions when other factors were not considered, and they also showed the largest increase during the breeding season of all the rodents. The increase in weight due to the breeding season is in line with what has been observed in previous studies (Green, 2009), 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 & Flowerdew, 2006), it is possible that breeding condition could have been mis-recorded in some cases.

Precipitation and temperature did not predict changes in body mass 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. One possible explanation is that because *A. sylvaticus* are arboreal (Buesching *et al.*, 2008) with males having larger home ranges during the breeding season (Corp, Gorman, & Speakman, 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, 2004), and rodents use the level of moonlight illumination as an indicator of predation risk. Although moonlight illumination only had an effect on female *M. glareolus*, with a decrease in body mass with increasing illumination, this does not mean that the other rodents are not altering their foraging based on moonlight, rather their body mass is not significantly altered. It was not possible to determine why only female *M. glareolus* growth was affected 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



**Figure 3** The estimated effect size changes in weight from  $t$  to  $t + 1$  for the covariates of the models. The error bars denote the SE of the estimates.

during the breeding season, to successfully raise young and compared to males have a smaller home range (Wolton & 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 summarizing to 3-week periods and moonlight illumination may operate at a finer scale. Trapping at a scale that may reveal the impact of moonlight illumination was not possible in this study. 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.* (2012) have suggested that rhododendron cover not only increases density of *A. sylvaticus* but also that larger dominant individuals will be more numerous. It is known that rhododendron is able to outcompete 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 utilize the edge and non-rhododendron areas of the woodland 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* positively impacts the density of *M. glareolus* but the reverse was found to be non-significant (Fasola & Canova, 2000). It is possible that the population density of *A. sylvaticus* affects 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 & Flowerdew, 1994), but *M. glareolus* take more green leaf material (Watts, 1968). This may make them less dependent on seeds as a food source than *A. sylvaticus* but then again both species are able to utilize a wide variety of 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 (Hoffmeyer, 1973; Montgomery, 1978; Cihakova & Frynta, 1996); 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). 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  $t + 1$  (Yalden and Albarella 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, such as the higher chance of trapping male *A. sylvaticus* than female (Crawley, 2009) and the heterogeneity of trap response between the different functional groups of the population (Jensen, 1975). This means that certain groups are going to be under-represented in the data, in particular juveniles (Gurnell, 2009). Additionally, the impact of trapping on the body condition of individuals cannot be discounted. Lower temperatures, increased time spent in traps and the methods used to process the animals can all increase this impact (McLaren *et al.*, 2004).

In conclusion, the consistent effect of *A. flavicollis* density across the four models indicates the importance of interspecific 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 of 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* (Yalden and Albarella 2008). It is accepted that the availability of food resources will have a major impact on individual fitness and population density (Prevedello, *et al.*, 2013), and this is something we were unable to include directly in this study. 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 (McLaren *et al.*, 2004), then it may be possible to get an even better understanding of what drives woodland rodent growth in the future.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Mean rodent weight for trapping sessions. (a) Females, all age classes, (b) Females, adults only, (c) Males, all age classes, (d) Males, adults only.

**Figure S2.** Population estimates at each 3 week period, for the three species *Apodemus sylvaticus*, *Myodes glareolus* and *Apodemus flavicollis*. The estimates were calculated using Jolly-Seber open population models (R package FSA (Ogle, 2020)).

**Figure S3.** Predicted rodent weight at  $t + 1$  based on weight at  $t$  in the non-breeding season for non-pregnant females and



non-breeding condition males with a mean population density of *Apodemus flavicollis* (4.46) and *Apodemus sylvaticus* (35.30), mean temperature (10.86°C), precipitation (12.13 mm) and moonlight (0.49). The shaded area denotes the upper and lower 95% confidence intervals.

**Table S1.** The variables used in the linear mixed effects models, with abbreviations. Includes details on how the variables were summarized for the 3 week period.

**Table S2.** The linear mixed effect models fitted to the Silwood data for female *Apodemus sylvaticus* determining the weight at  $t + 1$  in grams over a 3-week time step. The abbreviations for the terms in the models are detailed in Table S1.

**Table S3.** The linear mixed effect models fitted to the Silwood data for male *Apodemus sylvaticus* determining the weight at  $t + 1$  in grams over a 3-week time step. The abbreviations for the terms in the models are detailed in Table S1.

**Table S4.** The linear mixed effect models fitted to the Silwood data for female *Myodes glareolus* determining the change in weight over a 3 week time step. The abbreviations for the terms in the models are detailed in Table S1.

**Table S5.** The linear mixed effect models fitted to the Silwood data for male *Myodes glareolus* determining the change in weight over a 3-week time step. The abbreviations for the terms in the models are detailed in Table S1.

**Table S6.** Summary statistics for the captures, overall totals and by species. Means are shown with  $\pm$  SE.

**Table S7.** Comparison of the Silwood rodent growth linear mixed effect models before model reduction. Late and Early breeding season apply only to *Apodemus sylvaticus* and Breeding season applies only to *Myodes glareolus*.

**Text S1.** The Visual Basic for Applications code used to calculate the illuminated fraction of the moon's disk.