# 11. A long-term study of rodent population dynamics in the Apennines

G. Amori[1]

[1]CNR-IRET, National Research Council, Research Institute on Terrestrial Ecosystems, Roma, Italy

**Introduction**

Understanding the fluctuations of natural populations is one of the classic themes in ecology. Both biotic factors, related to intra- and inter-specific interactions such as predation or parasitism, and external drivers such as climate variability and change and/or resource availability can generate population fluctuations. In extreme environments, such as those found in the mountains, in polar regions or in deserts, the impact of external forcing is especially important. To address the complex issue of population fluctuations, long-term observations are needed, accompanied by effective data analysis methods and modelling approaches.

One especially interesting behavior is the presence of similar variations in the population abundance of phylogenetically very different groups, a problem that has always stimulated the interest of ecologists (Krebs, 1994). This topic has been widely studied for a variety of reasons, such as intrinsic biological interest, relevance for game management, effects on pest species, conservation actions of threatened species, and the health status of habitats (Witmer, 2005). In particular, many studies have dealt with the population dynamics of rodents (Batzli, 1992). In fact, small rodents, due to their size, high reproductive rate and relatively short life cycle, are ideal subjects for this type of investigation (Delany, 1974). The specific focus on rodent populations is also motivated by several other factors, including the responsibility they can have as vectors of diseases (Hansson and Henttonen, 1988).

The role of rodents in ecosystems is much wider than usually thought. Rodents are mainly primary consumers and have a significant influence on the plant communities and on their predators such as birds of prey (Korpimäki, 1991), reptiles and mammals.

The custom of rodents to accumulate seeds in their burrows, sometimes at relatively large distance from the harvesting area, makes them good dispersal vehicles. In this way, they affect the vegetation structure, giving the possibility to different plant species to regenerate and settle in new places. In some habitats, rodents can have an overall impact on vegetation that is more significant than that due to large herbivores (Olofsson et al., 2004), and their consumption of seeds can exceed that of insects and birds (Kollmann and Buschor, 2002).

Rodents can ventilate and shuffle the land through the construction of burrows and tunnels, and they can affect the nitrogen cycle on both the short and long term (Galiano et al., 2014). In fact, rodent excrements allow a more rapid availability of nitrogen for plants and are distributed on the ground in a more homogeneous way than those of large herbivores (Bakker et al., 2004).

Different species of rodents show significant fluctuations in population abundance. Increments in the abundance of populations can be repeated over time in an approximately periodic way (in the case of the so-called cyclic populations, Krebs and Myers, 1974). Significant regional differences in cyclic populations have been found in a vole species, *Myodes glareolus* (Hansson and Henttonen, 1988).  Interestingly, this species shows cyclic populations in northern Sweden (with period of 3-4

years) and non-cyclic populations at lower latitude (Hansson and Henttonen, 1985). Many hypotheses have been formulated to explain this phenomenon. One possibility considers intrinsic factors such as physiological stress due to high density followed by intraspecific aggression, responsible for the reduction of reproduction and the survival rate of individuals (Krebs, 1978). Another hypothesis, based on extrinsic factors (cf. Hansson and Henttonen, 1988), identifies the availability of food, feeding strategies, climate and predators as the factors that influence population density and cyclicity. An important role can also be played by predatory specialists compared to generalists (Korpimäki et al., 2002; Hanski et al., 2001; Lambin et al., 2000).

Climate can also affect changes in population size in many different ways (Deitloff et al., 2010). Indeed, climate fluctuations can change seasonal breeding, reduce availability of food in winter and during the dry seasons, and reduce the amount and quality of the snow cover that can provide protection from predators.

Two species of forest rodents, *Apodemus flavicollis* and *Myodes glareolus*, have been thoroughly studied to determine what factors influence and potentially determine population size. These species display abundant fluctuations in central Europe, linked with forest productivity and masting, with a maximum density approximately every nine years, followed by a year with very low density (Pucek et al., 1983).

This chapter reports the results of a long-term study, partially funded by the NextData project, devoted to the population dynamics of *Apodemus flavicollis* and *Myodes glareolus* in a mountain area of central Italy. Aim of the study is to understand the ecological processes associated with density fluctuations, cyclicity, changes in recruitment, survival, sexual activity, intra- and inter-specific competition, habitat and the role of climate change.

More specifically, we address the following questions:

1) Are the density fluctuations of the two species mutually influenced by each other or do they respond to similar drivers?
2) Do the studied species coexist on a microhabitat scale?
3) Is there any evidence that interspecific competition may shape the fine-scale ecological distribution of these species?
4) How do environmental parameters affect the population dynamics of these species?

## 11.1 Geographical distribution of the two species

The distribution range of bank vole (*Myodes glareolus*) (Figure 1) extends from the forests of France and Scandinavia to lake Baikal, west and north Turkey, north Kazakhstan and the Altai and Sayan Mountains (Wilson & Reeder, 2005). In Italy, this species is present along the whole peninsula but, is absent in the islands (Amori et al., 2008).

The yellow-necked wood mouse (*Apodemus flavicollis*) (Figure 2) has a distribution from Great Britain across much of continental Europe to the Urals (Russian Federation). It also occurs through Turkey east to west Armenia, the Zagros Mountains of Iran and south to Syria, Lebanon and Israel (Wilson & Reeder, 2005). In Italy is present along the peninsula and it is absent in the islands (Amori et al., 2008). Forests are the preferred habitat of both species (Amori et al., 2008).

**Figure 1.** *Myodes glareolus*



**Figure 2.** *Apodemus flavicollis*

## 11.2 Study area

The long-term study reported here was carried out in the "Valle Orfento" oriented natural reserve (42°08' N – 14°05' E), located in central Italy, in the municipality of Caramanico Terme (Pescara, Abruzzo), which covers about 2600 hectares at 1100 m .a.s.l. The area is characterized by a thermophilus beech forest (*Fagus sylvatica*). The vegetation belongs to the association Geranio-Fagion. Data were obtained through capture-mark-recapture (CMR; Gurnell and Flowerdew, 1982) from spring to fall (April to October) in 1988–1995 and 2000–2005 for a total of 14 years. Each trapping session was 3-night-long, for a total of 1200-1500 trap nights per year. Rodents were live-trapped in a 1.44 ha square grid (100 home-made live-traps LOT, Locasciulli et al., 2015, spaced 12 m apart). The captured individuals were ear-tagged, measured for body length, tail length, hind-foot length and ear length, and weighed. The ecological structure of the populations was analyzed using the POPAN model.

## 11.3 Results

Overall, 960 individual rodents were captured (491 *M. glareolus* and 469 *A. flavicollis*), with about 2000 recaptures. The annual numbers of captured and recaptured individuals for the *A. flavicollis* and *M. glareolus* species are reported respectively in Figures 3 and 4.
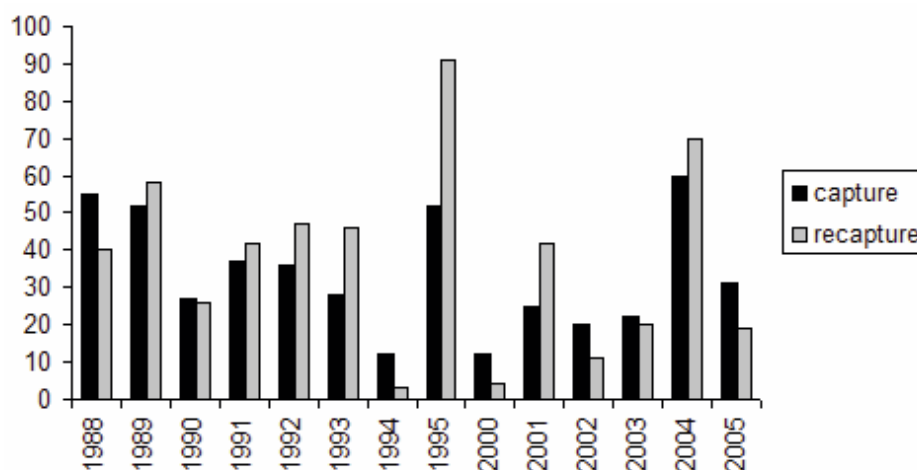


**Figure 3.** *Annual number of captured and recaptured individuals of A. flavicollis (from Amori et al., 2015).*
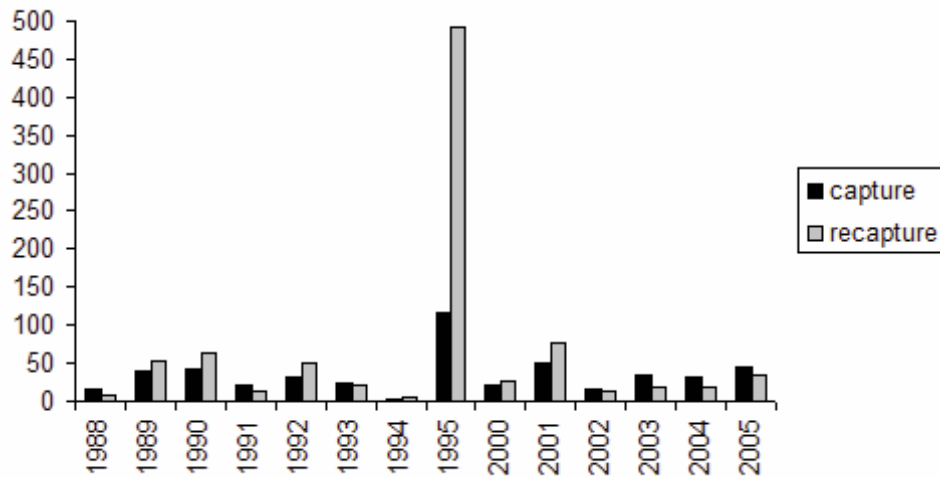
**Figure 4.** *Annual number of captured and recaptured individuals of M. glareolus (from Amori et al., 2015).*

The mean density of individuals was 8.24 ± 5.95 individuals per ha (median = 6.23) for *A. flavicollis*, and 8.59 ± 11.82 per ha (median = 5.56) for *M. glareolus*. The annual variations in the density are reported in Figure 5. Density of *M. glareolus* was significantly higher in comparison to *A. flavicollis* in 1995 and 2001 (Monte-Carlo ANOVA after 30,000 iterations, pseudo-F = 33.66, P < 0.001), the density of *A. flavicollis* was significantly larger, in comparison to *M. glareolus,* in 2004 and 2005 (Monte-Carlo ANOVA after 30,000 iterations, pseudo-F = 21.43, P < 0.001). Thus, for four years the assemblage structure seems to be compatible with a competitive structure, whereas for ten years it was not.
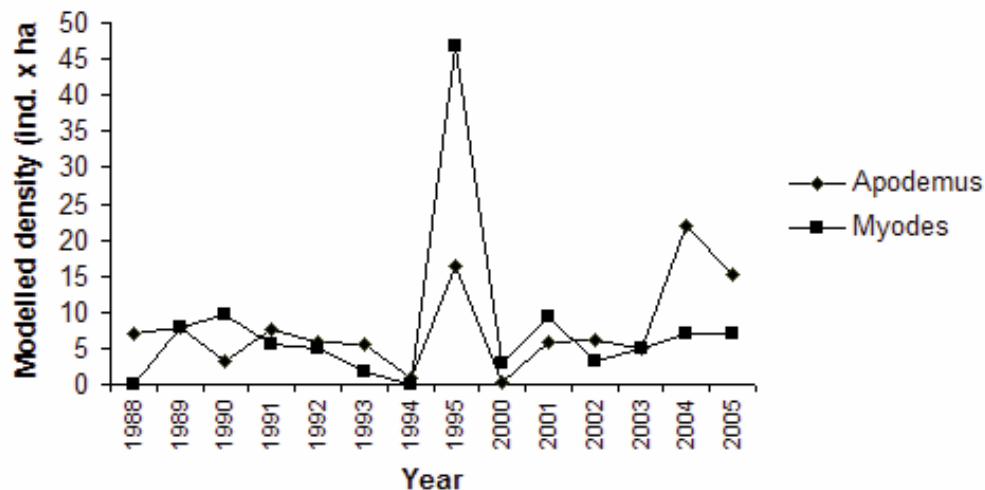


**Figure 5.** *Modelled annual density (ind. × ha$^{-1}$) of the two species (from Amori et al., 2015).*

According to the index defined by Henttonen et al. (1985), the two populations were not cyclic, in line what was found by Hansson and Henttonen (1985).

*Question 1: Are the density fluctuations of the two species mutually influenced by each other or do they respond to similar drivers?*

The average density (individuals/ha, Figure 5) was approximately similar in the two species. This means that, at the level of the grid scale, there was no clear dominance of one species versus the other, with population sizes changing in parallel for the two species. Parallel density fluctuations

between European sympatric rodents were also detected in Poland (Pucek et al., 1993). Obviously, these density estimates should be considered as the averages of the annual counts, given that both species showed clear seasonal (intra-annual) density fluctuations. In this system studied here, there was no competition between species at the landscape scale, since both species attained similar densities at the same time. However, interspecific competition could be more intense at the micro-habitat scale.

*Question 2: Do the study species coexist on a microhabitat scale?*

The frequency of capture of the two rodent species varied across traps (Table 1), thus showing a non-uniform and different distribution of the two species at the local scale.

|  | 1x | 2x | 3x | 4x | 5x | 6x | 7x | 8x | 9x | 10x |
|---|---|---|---|---|---|---|---|---|---|---|
| 1y | * |  |  |  |  | **Af |  |  |  |  |
| 2y |  |  |  | **Af | **Af |  | * |  |  | * |
| 3y |  | * | **Af | **Af |  |  |  |  |  |  |
| 4y |  |  |  |  |  | * |  | * |  |  |
| 5y |  |  |  |  |  |  |  |  | *Mg | *Mg |
| 6y | * | * | ** |  | ** | ** | *Mg | *Mg | ** | *Mg |
| 7y |  | ** |  | **Af |  | * | *Mg | *Mg |  |  |
| 8y |  |  | **Af | **Af | **Af | **Af | *Mg | *Mg | * | * |
| 9y | ** |  |  | **Af | **Af |  | ** | ** |  |  |
| 10y |  |  |  |  | **Af |  |  |  | * |  |

**Table 1.** *Spatial arrangement of trap grid with likelihood of capturing each of the two species.*
*\*= high likelihood of capturing Mg (M. glareolus) but not Af (A. flavicollis)*
*\*\* = high likelihood of capturing Af but not Mg*
*Cases with the symbols Af and Mg denote a multi-trap where one of the two species is dominant*
*(modified from Amori et al. 2015).*

From the spatial distribution of the traps, it is possible to identify two areas which were associated with high probability of capture for only one of the two studied species. One of these areas is associated to dominance of *A. flavicollis,* the other to *M. glareolus*. These differences revealed that micro-habitat played a crucial role in separating the ecological niche of the two rodent species, with *M. glareolus* preferring an habitat type with a vegetation component of rich underbrush, that was not relevant for *A. flavicollis*.

*Question 3: Is there any evidence that interspecific competition may shape the fine-scale ecological distribution of these species?*

The results obtained in the studies reported here suggest, on the whole, that interspecific competition should be present at the local micro-scale, because if a given trap was highly successful in capturing one species, it was also quite unsuccessful in capturing the other. If this is not merely an outcome of the different microhabitat selection of these rodents, it suggests that there is a direct avoidance of one species by the other. Thus, it is possible that behavioural interactions between the two species may play a role in explaining the fine-scale (apparently competitive) pattern evidenced by this study.

*Question 4: How do environmental parameters affect the population dynamics of these species?*

In conditions of ongoing climate change, it is important to assess what control parameters affect the density fluctuations of the species of interest. The density of the yellow-necked mouse population has been reconstructed in the recent past (1965 – 2006) by analyzing climatic parameters (temperature, rainfall and snow cover) and linking them to density fluctuations through non-linear analysis and Neural-Network (NN) approaches (Pasini et al., 2009). NN is an alternative to traditional statistical forecasting methods. It is a learning approach (similar to neural networks found in humans and animals) capable of providing a diverse family of flexible nonlinear data (see Tealab, 2018 for a methodological review). In this way, once determined how climatic parameters affect population density in the period when both climatic data and species abundance records are available, the past density (when population abundance data are not available) could be estimated from the knowledge of the climatic parameters. In particular, the analysis of the links between climate and species abundance has indicated that the only relevant parameter having direct and indirect effects on the density of *A. flavicollis* is precipitation (Pasini et al., 2009) (Figure 6).
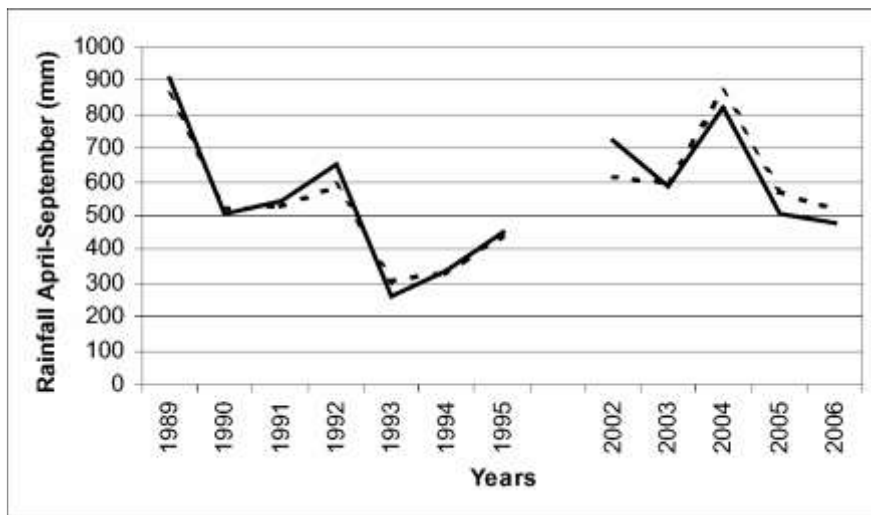


**Figure 6.** *Amount of rainfall measured at the study area (continuous line) and reconstructed at the same location (dashed line) via a NN model (from Pasini et al., 2009).*
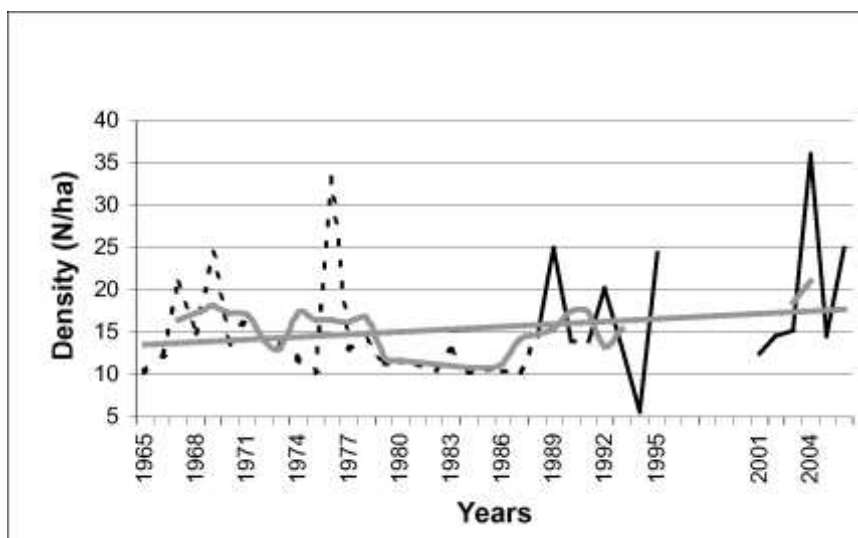


**Figure 7.** *Density of A. flavicollis obtained from data collected in the field (continuous black line) and reconstructed for the past via NN methods (dashed line) back to 1965. A linear fit (grey line) suggests an increasing trend; the grey curve indicates a 5-year moving average (from Pasini et al., 2009).*

**11.4 Discussion and conclusions**

The analysis of population dynamics reported in this chapter confirms the usefulness of exploring the information provided by spatial capture–recapture models. By evaluating the relationships between home ranges and population densities with different biological meaning (conspecifics vs. the density of the other co-occurring species vs. total density) it is possible to disentangle the relative importance of intraspecific vs. interspecific competition on space use patterns of two co-occurring rodent species, showing that the home ranges of both species are related to conspecific population density only.

The results obtained from this long-term study confirm the hypothesis of Hansson & Henttonen (1985), which suggests the presence of cyclic populations of small mammals in the northern part of their geographical range (about 60 ° N), and their absence in the southern part of the range.

A further peculiarity is that the populations of the species studied here are the most southern and peripheral and are also the only long-term data available for the Mediterranean environment.

The non-linear analysis performed here, based on Neural Networks, indicates the role played by environmental parameters such as rainfall in the density fluctuations of rodent species. This allowed to build a model for the inter-annual density fluctuations and trends. Future work will consider the response of these species to future climate scenarios. Knowing and predicting the density of rodent species populations in a woodland environment is also very important for a proper forest management and the functioning of the entire ecosystem.

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