

## Providing management options to control corn mouse (*Calomys musculus*) reservoir populations using a cohort structured model

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We evaluate several management options for *Calomys musculus* populations through the formulation and validation of a cohort structured model. Initially, a basic model was constructed and validated using field population data. Next, the model was altered to allow us to evaluate different management options. In general, basic model results were in agreement with field data, demonstrating that this model would be useful in describing aspects of corn mouse population dynamics. Restricting control measures to when mouse numbers reach high levels would be inadequate, because population numbers tend to increase in size after some years. In contrast, reducing vegetation cover in spring was more effective in reducing field population abundances. Despite some limitations, the model could be useful for evaluating the relationships between population dynamics and some biotic or physical environmental variables, and thus ensure more efficient use of resources in integrated pest management.

**Keywords:** Argentine hemorrhagic fever; *Calomys musculus*; integrated pest management; remote sensing; resource management; rodent ecology; rodent reservoirs; structured models

### 1. Introduction

Worldwide, rodents are the most important vertebrate pests (Singleton et al. 1999), and recently, increasing research attention has been given to rodent population dynamics associated to human diseases (Mills et al. 1992b; Engelthaler et al. 1999; Kuenzi et al. 1999; Jaksic and Lima 2003; Ylonen et al. 2003). In general, population dynamics are studied in order to predict or describe growth or decline of a population and to identify the underlying physical and biological mechanisms (Juliano 2007). Thus, the process of explaining and predicting population dynamics generally requires theoretical ecological models (Hastings 1997). These models are an important step towards a better understanding of dynamic systems and to the improvement of decision-making in pest population studies (Roughgarden et al. 1991; Lawton 1995; Hastings 1997; Lincoln et al. 1998; Calow 1999; Owen-Smith 2007).

The corn mouse, *Calomys musculus* (Thomas), inhabits Pampean agrarian ecosystems of central and northern Argentina (Redford and Eisenberg 1992). It exhibits different habitat associations within its distribution range. Several authors have carried out detailed studies of physical and environmental factors influencing its distribution and density (Crespo et al. 1970; Kravetz and de Villafañe 1981; Kravetz and

Polop 1983; Busch et al. 1984; de Villafañe and Bonaventura 1987; Polop and Sabbatini 1993; Busch et al. 2000). This rodent is particularly abundant in linear habitats that surround agricultural fields, presumably in response to the higher availability of agriculturally derived food resources and reduced competition or predation (Kravetz and Polop 1983; Mills et al. 1991a; Busch and Kravetz 1992; Polop and Sabbatini 1993; Busch et al. 2000).

*Calomys musculus* is mainly studied for its role as reservoir of Junin virus, the aetiological agent of Argentine hemorrhagic fever (AHF), a public health problem in Argentina (Sabbatini and Maiztegui 1970; Busch et al. 1984; Mills and Childs 1998). The endemic area of AHF encompasses more than 150,000 km<sup>2</sup> in northern and central Buenos Aires, southern Santa Fe, south-eastern Córdoba and north-eastern La Pampa provinces, with more than three million people at risk (Carballal et al. 1988; Mills et al. 1991b; Enria et al. 1998). The dynamics of AHF is closely related to population dynamics of *C. musculus* which exhibits a seasonal breeding pattern in the field. Reproduction, and consequently population density, increases from a minimum in spring to a peak in late autumn, then decreases during winter (de Villafañe et al. 1977; Kravetz 1977; Mills et al. 1991a, 1992a; Polop et al.

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2007). This pattern of annual fluctuation is in agreement with epidemiological characteristics of AHF, whose epidemics occur predominantly during autumn, coinciding with the major harvesting season in Argentina (Carballal et al. 1988; Mills et al. 1992b).

With the increase of ecological information on life history and habitat characteristics of the species, models have become more and more realistic. As most wild populations are subject to complex processes that cannot be described by simple models, understanding the dynamics of natural populations requires knowledge of demographic structure and its relation to physical environment (Deng and Hallam 2006; Sadhukhan et al. 2008). In general, small mammals have complex life histories, so they are not well described by simple models that do not consider age structure (Hastings 1997). Particularly for rodents, it is known that demographic parameters are highly dependent on functional categories like age or stage classes (Yoccoz and Stenseth 2000; Owen-Smith 2007). Several life-history studies have documented the dependence of life traits such as fecundity and survival, and the trade-offs between them, on current and previous environments (Lindstrom 1999; Beckerman et al. 2002). This dependence originates a "cohort effect", a phenomenon that occurs when the common conditions experienced by a group of individuals at time  $t$  generate differences in its future performance, which will be distinguishable from that of other groups (Beckerman et al. 2002; Lindstrom and Kokko 2002). Several studies have assessed the role of different cohorts in population dynamics of small mammals (Wiger 1979; Zuleta et al. 1988; Polop 1996; Provencal 2001; Nordahl and Korpimäki 2002; Polop et al. 2005). Castillo (2007) found that *C. musculus* exhibits a marked variation in its population structure over a year, with cohorts that have different number of individuals and distinct values of both survival and fecundity. However, cohort dynamics in *C. musculus* populations have been little studied. On the contrary, a more extensively studied species is *Calomys venustus* (Thomas), which has similar life history characteristics to corn mouse (Polop 1996; Provencal 2001; Priotto and Polop 2003; Polop et al. 2005; Gomez et al. 2007). In *C. venustus* populations, onset of the breeding period is produced by the overwintering cohort (C0). Individuals of this cohort belong to cohort 2 (C2) and cohort 3 (C3); they were born in the previous breeding period. This cohort shows the highest number of individuals in early spring and gives birth to cohort 1 (C1). After this, there are two abundance peaks; one produced by the recruitment of C1 individuals in early summer (December), and the second one produced by the recruitment of C2 individuals in late summer (Polop et al. 2005; Gomez et al. 2007). Cohort 2 and C3 are produced by C1 individuals. By the middle of summer, overwintering animals are no longer captured, and C1 individuals increase rapidly (Polop 1996) and

die within the same breeding period in which they were born (Priotto and Polop 2003). C1 exhibits the lowest average survivorship (Provencal 2001). An increase in the recruitment of C2 and C3 at the end of autumn causes the peak in annual population density (Gomez et al. 2007). In winter, after the breeding period, populations decline sharply, probably because of breeding interruption and mortality increase (Polop et al. 2005). Thus, this cohort effect could have an important influence on susceptibility, infectivity and the structure of the contact process (Heesterbeek and Roberts 1995) and, consequently, on the dynamics of host populations.

Our study attempted to extend a theoretical model of single population for *C. musculus* and viral infection which was built by Porcassi et al. (2005). Here, we aim to evaluate several management options of corn mouse populations through the formulation and validation of a cohort-structured population model. We consider that modelling population dynamics in this way can be very useful to understand the dynamics of rodent-borne diseases such as AHF. Moreover, control of *C. musculus* populations might be enhanced by a better understanding of population dynamics and the effects of environmental variability on it.

## 2. Methods

### 2.1. Model outline and form

The model structure presented here is based on the models proposed by Kirchner and Roy (1999) and Porcassi et al. (2005). These models considered the temporal dynamics of a single and genetically uniform host population infected by a single pathogen. As in May and Anderson (1983), the models assumed the existence of two population classes, "X" representing the susceptible rodent class and "Y" the infected rodent class. The abundances of both rodent classes are expressed as a fraction of the occupied carrying capacity. We used this as a measure of rodent relative density.

May and Anderson (1983) assumed that, in general, the susceptible host population will change at a rate determined by the balance among reproduction, infection and death rates:

$$\frac{dX}{dt} = \alpha(1 - N) * X - \beta XY - \frac{X}{\tau}.$$

Thus, susceptible hosts reproduce at a rate  $\alpha(1 - N) * X$ , where  $\alpha$  is the potential per-capita reproduction rate in the absence of carrying capacity constraints,  $1 - N = 1 - (X + Y)$  is the fraction of carrying capacity that is unoccupied. Furthermore, in this term,  $X$  is the total susceptible population and  $Y$  is the total infected host population. Susceptible hosts become infected at a rate  $\beta XY$ , where  $\beta$  reflects pathogen infectiousness and host susceptibility; and these hosts

die at a rate  $X/\tau$ , where  $\tau$  is the mean life-span in the absence of infection.

Pathogens cannot survive without hosts, so they do not need to be explicitly modelled; although their dynamics are represented by the infected host population. The models assume the pathogen to be transmitted only horizontally, so that all hosts are born susceptible. Like susceptible hosts, the infected population will change at a rate determined by the balance between infection and mortality:

$$\frac{dY}{dt} = \beta XY - \frac{mY}{\tau}.$$

Thus, hosts become infected at a rate  $\beta XY$  and die at a rate  $mY/\tau$ , where  $m$  is the ratio by which infection shortens life span (Kirchner and Roy 1999; Porcasi et al. 2005). Laboratory studies have shown that Junin virus does not exhibit apparent signs of lethality on *C. musculus*, regardless of the animals' age, inoculation route or dose (Sabattini et al. 1977). Therefore, we did not consider "m" as a parameter in the equation of the infected population.

We structured the population in four cohorts. Regarding the susceptible class ( $X$ ) and in agreement with the results shown by Polop (1996), Polop et al. (2005) and Castillo (2007), we considered the following relationships (Figure 1): cohort 1 (C1) is composed of animals born during September–December (spring and early summer), which gives birth to cohort 2 (C2) and cohort 3 (C3) animals; C2 is formed of animals born during January–March (summer) and gives birth to C3 animals; and C3 is formed of animals born during April–May (autumn). Cohort 0 (C0), or the overwintering cohort, corresponds to C2 and C3 to animals born in the previous breeding period that survived until

the following period to produce the first litters (C1). We considered that susceptible individuals of C3 do not breed until they are part of C0.

On the other hand, we considered that the susceptible cohorts lose individuals via mortality ( $x_n/t_n$ ) or infection ( $\beta x_n \cdot yt$ ), where  $yt$  is the total number of individuals of infected cohorts. Individuals lost by infection in each susceptible cohort become part of each infected cohort ( $Y$ ). These cohorts lose individuals only by mortality ( $y_n/t_n$ ). Thus, the rate of change of susceptible and infected hosts, structured by cohorts, was expressed as follows:

**Cohort 0:**

$$\begin{aligned} X0_{i+1} &= x0_i - \beta^*x0_i^*yt_i - x0_i/\tau0_i \\ Y0_{i+1} &= y0_i + \beta^*x0_i^*yt_i - y0_i/\tau0_i \end{aligned}$$

**Cohort 1:**

$$\begin{aligned} XI_{i+1} &= x1_i + (\alpha0_i^*\rho0_i^*(1 - Ni)^*x0_i) - \beta^*x1_i^*yt_i - x1_i/\tau1_i \\ YI_{i+1} &= y1_i + \beta^*x1_i^*yt_i - y1_i/\tau1_i \end{aligned}$$

**Cohort 2:**

$$\begin{aligned} X2_{i+1} &= x2_i + (\alpha1_i^*\rho1_i^*(1 - Ni)^*x1_i) - \beta^*x2_i^*yt_i - x2_i/\tau2_i \\ Y2_{i+1} &= y2_i + \beta^*x2_i^*yt_i - y2_i/\tau2_i \end{aligned}$$

**Cohort 3:**

$$\begin{aligned} X3_{i+1} &= x3_i + (\alpha2_i^*\rho2_i^*(1 - Ni)^*x2_i) + (\alpha1_i^*\rho1_i^*(1 - Ni)^*x1_i) - \beta^*x3_i^*yt_i - x3_i/\tau3_i \\ Y3_{i+1} &= y3_i + \beta^*x3_i^*yt_i - y3_i/\tau3_i \end{aligned}$$

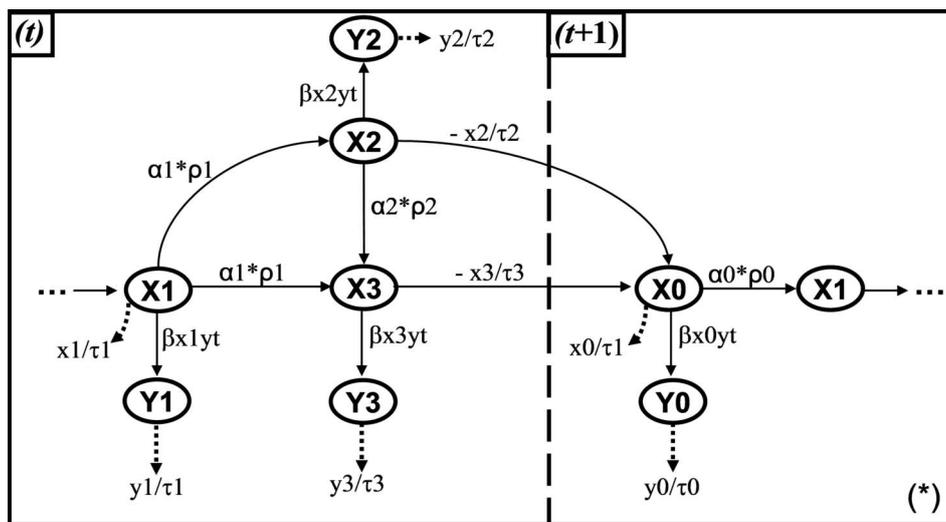


Figure 1. A schematic representation of the relationships among cohorts. Dashed arrows show outputs and full arrows exhibit inputs in each population class.  $X_n$  is the proportion of susceptible individuals of each cohort (0–3) and  $Y_n$  is the proportion of infected individuals of each cohort (0–3). Key: (\*)  $\tau$  = maximum mean lifespan;  $\alpha$  = potential reproductive rate;  $\rho$  = pregnancy prevalence;  $\beta$  = average number of non-infected hosts that an infected host can infect during its lifetime.

## 2.2. Parameter description

To parameterize our model, we used data extracted from our own database and from the literature. The values used to simulate population dynamics of *C. musculus* are shown in Table 1. The maximum mean life span “ $\tau$ ” (equal for both, infected and susceptible rodents) was obtained from Polop (1996). We considered that C0 could be present during September–December, C1 during November–March, C2 throughout January–June and C3 from April to June. The last two cohorts are also present in July and August to constitute the C0 of the following year.

As cohorts do not evidence the same  $t$ , they do not contribute with equal number of litters to the other cohorts, so we considered that the potential reproductive rate ( $\alpha$ ) was given by the relation between litter size and number of litters. Litter size was calculated from field data bases provided by Provencal (unpublished work) and Castillo (2007), and the number of litters was obtained from Polop (1996). As reproductive activity is different among seasons and consequently among cohorts, we included a new parameter “ $\rho$ ”. This parameter, linked to  $\alpha$ , is related to pregnancy prevalence of each susceptible cohort and was obtained from Mills et al. (1992a). We considered  $\rho$  from spring (C0), summer (C1) and autumn (C2).

The average number of non-infected hosts that an infected host can infect during its lifetime “ $\beta$ ” was taken from field experiences carried out by Sabattini et al. (1977). Due to the lack of information to discriminate this parameter among cohorts, we used the same value for all of them.

## 2.3. Environmental input data

We considered that the quality of the environment could be measured by remotely sensed data, and that it might influence both survival and fecundity of each cohort. As did Porcasi et al. (2005), we assumed a linear dependence of both reproductive rate “ $\alpha$ ” and the mean life span “ $\tau$ ” on Normalized Difference Vegetation Index (NDVI) data. Therefore,  $\alpha$  and  $\tau$  may rise if the NDVI shows high values (spring–summer), or they may decrease if NDVI has low values (autumn–winter).

NDVI data was derived from the Advanced Very High Resolution Radiometer (AVHRR) sensor on

board of the National Oceanic and Atmospheric Administration’s (NOAA) meteorological satellite, with a resolution of 8 km  $\times$  8 km. The data was obtained from decadal series available at NASA web page (daac.gsfc.nasa.gov). We considered that these values may describe environmental conditions of agricultural localities where the corn mouse reaches major abundance. To run the model for each locality we used NDVI data series of the single pixel representing that locality. An interpolation of decadal data was used in order to obtain an NDVI value for each time step (1 day). First, to evaluate the general performance of the model, we ran it for a period of six years (1988–1994) with the parameters and environmental conditions described above using a random pixel of endemic AHF zone (basic model). Then, we modified the basic model proposing different management options.

The model was programmed in IDL language and the time step considered was 1 day. Assuming that the breeding season of *C. musculus* may last from September to June (Mills et al. 1992b) model runs began in spring.

## 2.4. Model validation and field data

To validate our model we compared its outputs with field data of different data sets. Due to lack of data about wild infected populations, we could not verify the infected population outputs. To validate the model we ran it for a period of 3 years using pixels of three localities of AHF endemic zone: Máximo Paz, Alcorta, and Pergamino. In these sites, rodents were captured in weedy fencerows, roadsides and railroad rights-of-way. Ten removal trap lines consisting of 25 traps spaced at 5 m were placed in linear habitats in each sampling site. Rodents were trapped for three nights per season (spring, summer, autumn and winter) during a period of 3 years.

Relative *C. musculus* abundance in each locality for each season was estimated by the relative density index (RDI) and these values were used to evaluate the model results. The RDI was measured as:

$$RDI = \left( \frac{\text{number of captures}}{\text{number of trap} * \text{number of nights}} \right) * 100.$$

To validate the cohort structured model, we compared its outputs with a data set obtained from a capture–mark–recapture (CMR) field study carried out in a rural zone, near the AHF endemic zone. In this study, *C. musculus* abundance was registered in 9 weedy fencerows. In each weedy fencerow, 20 Sherman live traps were placed with an inter-station interval of 7 m. Seasonal censuses were carried out for three consecutive nights and traps were checked each morning. Captured animals were collected and their body length, weight, sex and reproductive condition were registered. Each rodent was marked with numbered ear tags.

Table 1. Parameter values used to simulate population dynamics of *Calomys musculus* with the basic model.

Parameter <sup>a</sup>		C0	C1	C2	C3
$\tau$		122	152	244	153
$\alpha$	Litter size	6	8	8	–
	No. of litter	1.6	2.3	1.8	–
$\rho$		0.5	0.75	0.6	–
$\beta$			12/7		

<sup>a</sup>Key:  $\tau$  = maximum mean life span in days;  $\alpha$  = potential reproductive rate;  $\rho$  = pregnancy prevalence;  $\beta$  = average number of non-infected hosts that an infected host can infect during its lifetime.

The classification of captured animals into cohorts was performed using measures of individuals from a semi-captivity study (Castillo 2007). According to the birth date of these rodents, we were able to know which cohort they belonged to. We used average body length and weight of these cohorts to classify field-captured animals. Then, seasonal abundance of each cohort was used to compare the pattern observed at the field with model outputs.

We used the Coefficient of Model Determination (CD; Tedeschi 2006) as a measure of how well the field data fitted the models for both total population and cohort dynamics. This coefficient is the ratio of the total variance of observed data to the squared of the difference between model-predicted and mean of the observed data ( $CD = 1$ , perfect fit;  $CD > 1$ , low prediction and  $CD < 1$ , overprediction).

### 3. Results

#### 3.1. Model performance

When the basic model was run, we observed that the total population showed a cyclic pattern, with years of

high and low carrying capacity occupied fraction (Figure 2). In a period of 1 year, the population showed a seasonal variation with the highest values in autumn and the lowest in winter and spring. However, we observed that NDVI reached an annual maximum in summer, previous to the total population peak. When we modified the parameters of the basic model and it started to run with harder conditions (NDVI reduced to a half), we observed that the simulated population reached lower values than the basic model but the overall shape and trend were similar (Figure 3). However, when the model was run with a third of life span, the population oscillated during the first years, as in the basic model, but then it decreased to values near zero.

All cohorts were present throughout the year, including C0, but in different proportions (Figure 4). We observed that C0 and C1 were more abundant in spring and summer while C2 and C3 reached higher values in autumn and winter. The autumn population peaks were predominantly composed of C2 and C3 individuals, and in some years C1 registered similar values to C3 in this season. Regarding the infected and non-infected cohort fractions, we observed that they

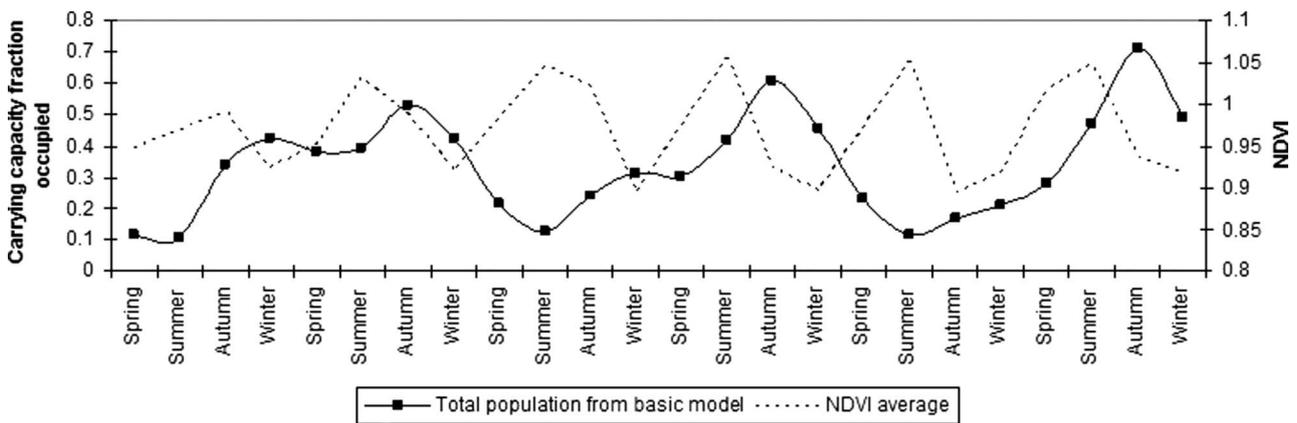


Figure 2. Total population dynamics of *Calomys musculus* in relation to Normalized Difference Vegetation Index (NDVI) values simulated for a 6-year period for a pixel corresponding to the endemic zone of Argentine hemorrhagic fever.

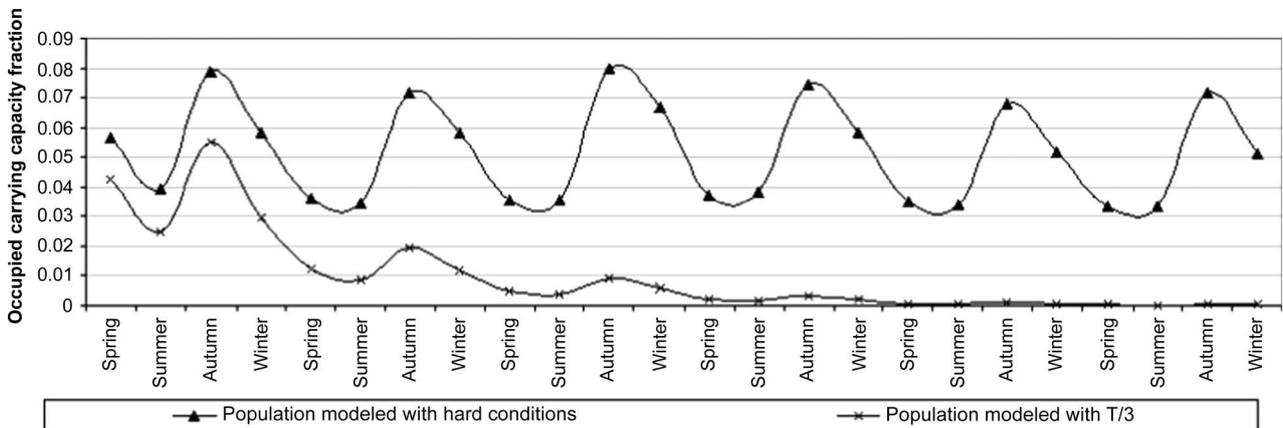


Figure 3. Model outputs for total population dynamics simulated with life span reduced to a third and Normalized Difference Vegetation Index conditions reduced to the half (hard environmental conditions).

showed different proportions according to the fraction and year (Figure 5). In general, non-infected cohorts peaked earlier than infected cohorts.

When C0 and C1 life span was artificially reduced to a quarter, we observed that the total population tended to decrease to very low values of abundance. On the other hand, when C2 and C3 life span was reduced to the same proportion, the total population oscillated

among low values the first years but then it started to increase (Figure 6a). When we simulated harder conditions in NDVI for C0 and C1, total population reached very low values and tended to zero (Figure 6b). In contrast, when hard environmental conditions were simulated for C2 and C3, total population had lower values at the first years but reached similar values to those of the basic model in subsequent years (Figure 6b).

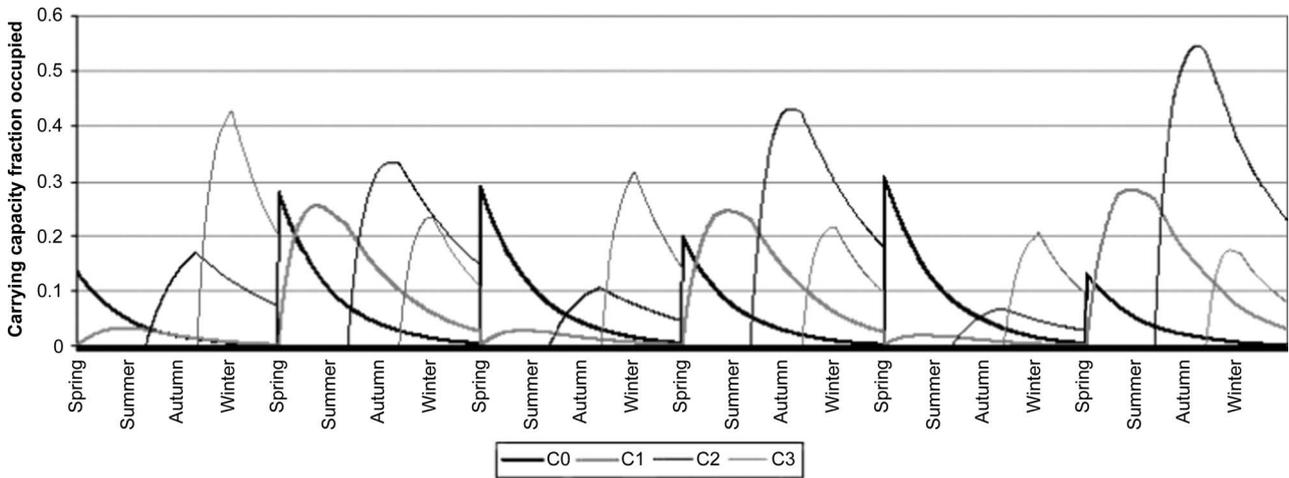


Figure 4. Model outputs for *Calomys musculus* cohort dynamics simulated for a pixel corresponding to endemic zone of Argentine hemorrhagic fever (C0: cohort 0; C1: cohort 1; C2: cohort 2; C3: cohort 3).

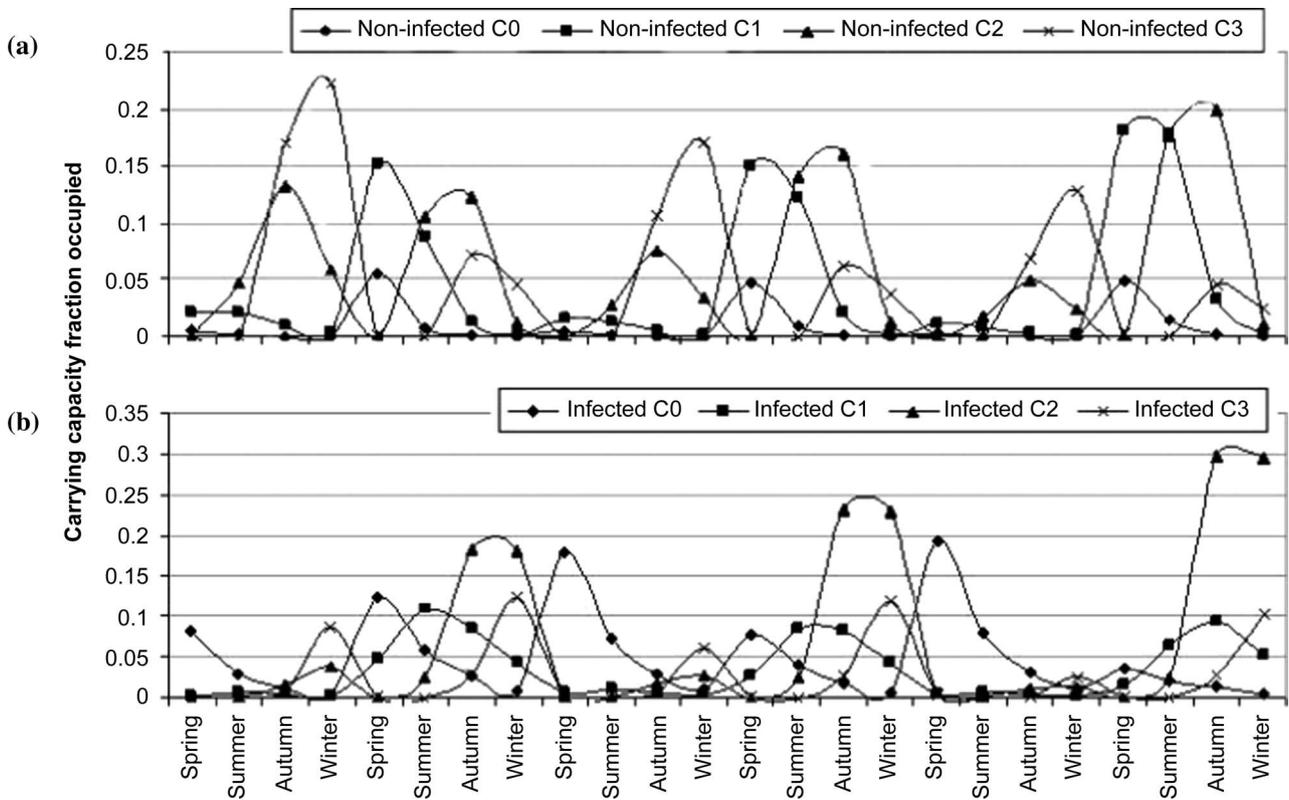


Figure 5. Model outputs for non-infected (a) and infected (b) *Calomys musculus* cohort dynamics simulated for a pixel corresponding to endemic zone of Argentine hemorrhagic fever (C0: cohort 0; C1: cohort 1; C2: cohort 2; C3: cohort 3).

3.2. Comparison between model outputs and field data

When the outputs of the modelled total population were compared with field data for three localities of endemic AHF zone, we observed that it was able to capture the general aspects of field data (Figure 7). The seasonal variation in population dynamics with low values in early seasons and high values in autumn were predicted by the model. Although the model followed the overall shape of the field population dynamics, it overestimated and underestimated some values. The model showed a good agreement (CD = 3.78) with Alcorta during the first two years but the abundance

peak in field population was registered earlier in time than the prediction of model in the last year. For Máximo Paz (CD = 4.21), the model predicted the highest abundance of the first year, but overestimated the abundance of the second year and delayed the peak of the last year. On the other hand, for Pergamino (CD = 9.15) the model predicted the abundance peak in the second and third year but not in the first year.

The outputs of the basic model for each cohort showed a general agreement with field data in years of low and high abundance (Figure 8). The model more accurately described the seasonal dynamics of C0 and

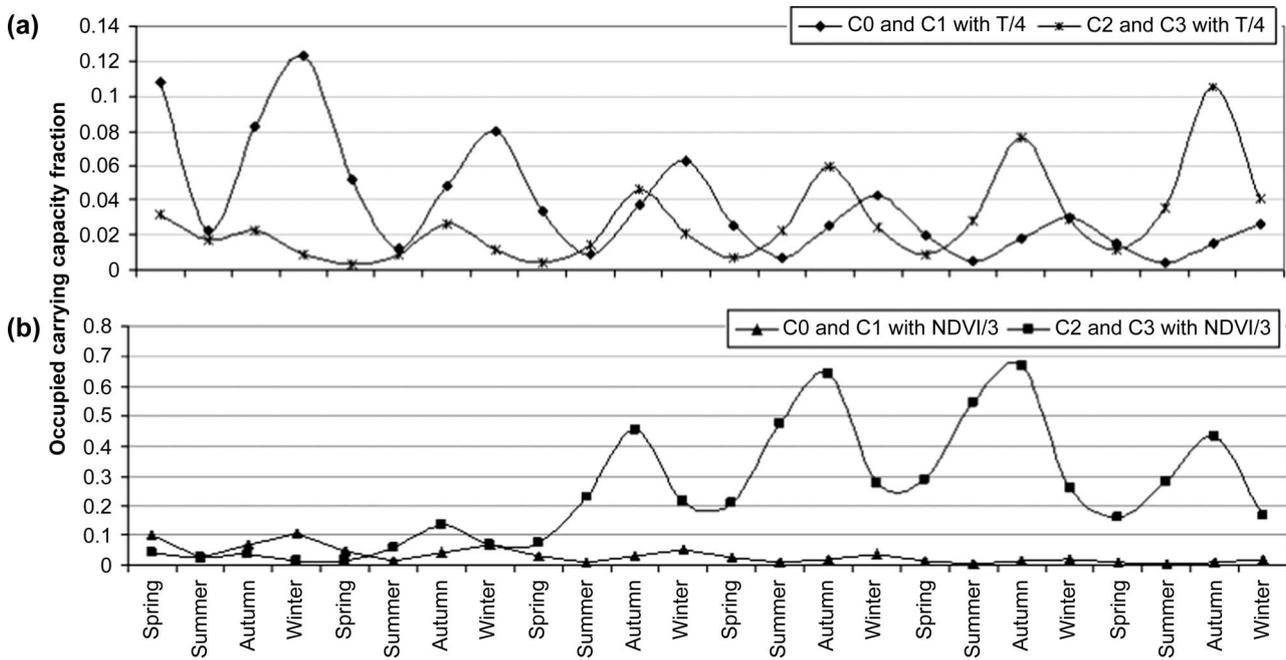


Figure 6. Model outputs for: (a) total population modelled with cohort mean life span reduced to a quarter; (b) total population modelled with Normalized Difference Vegetation Index values reduced to a third (C0: cohort 0; C1: cohort 1; C2: cohort 2; C3: cohort 3).

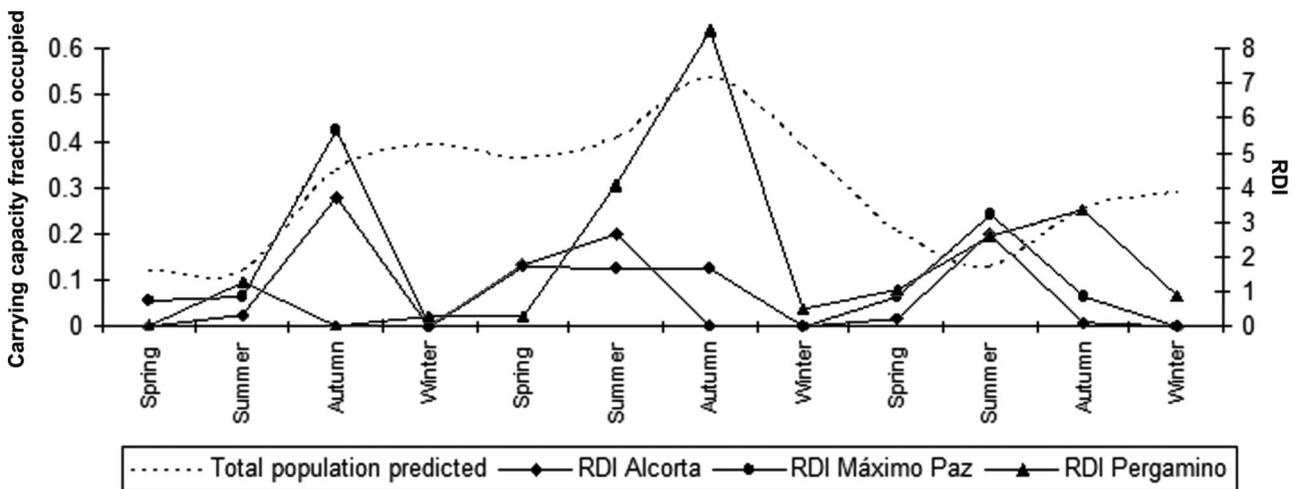


Figure 7. Total population predicted for three localities of the endemic zone of Argentine hemorrhagic fever (Máximo Paz, Pergamino, and Alcorta) compared with the relative density index (RDI) of the same places.

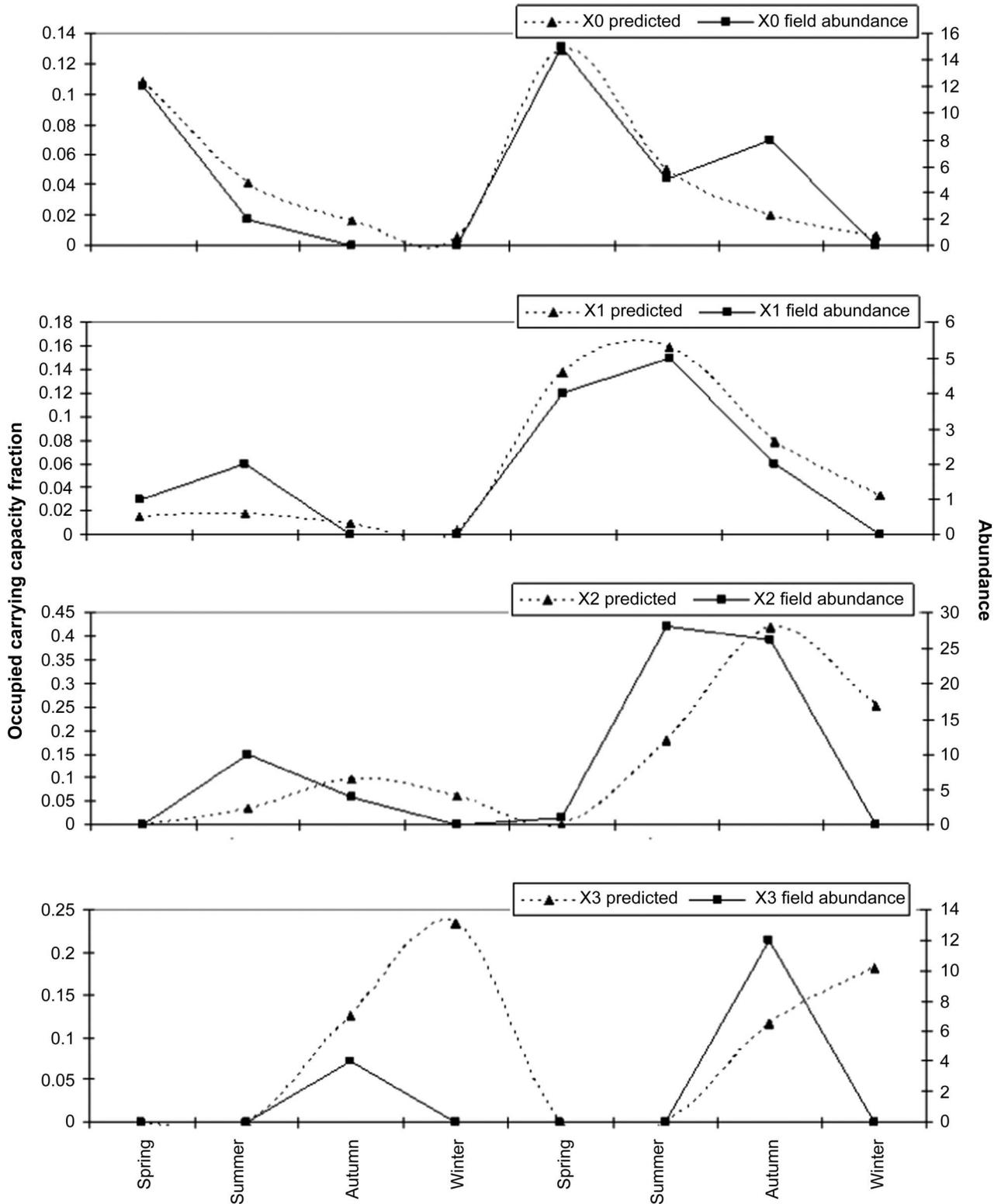


Figure 8. Model outputs for each cohort compared to field abundances of the same cohorts (C0: cohort 0; C1: cohort 1; C2: cohort 2; C3: cohort 3).

C1 (for both  $CD = 1.11$ ) were better described than C2 ( $CD = 1.70$ ) and C3 ( $CD = 4.34$ ). Particularly, the model delayed the season in which C2 and C3 peaked.

#### 4. Discussion

The most important practical application of studies of reservoir population ecology is to integrate and apply data from these studies into a model that would allow

public health practitioners to identify specific times and places where conditions may pose a threat to public health (Mills and Childs 1998; Mills 1999). Here, we have presented a new approach to a numerical model of corn mouse populations that incorporated more biological realism considering the population structured by cohorts.

Previous research on *C. musculus* populations (Sabattini et al. 1977; Mills et al. 1992a; Porcasi et al. 2005; Castillo 2007) has allowed us to create a model that, at least partially, captures the temporal variation of both total and cohort populations. The total population modelled by our basic model showed a seasonal fluctuation pattern throughout the years, with peaks in autumn and low numbers in spring and winter. These results are in agreement with the annual density oscillation previously reported by Porcasi et al. (2005) in their model, and with small rodents field studies from the Southern Hemisphere, where populations show seasonal changes in densities between the reproductive and non-reproductive seasons (Lima et al. 2002, 2003). Indeed, field studies of *C. musculus* populations showed that this species displays a strong seasonality and density fluctuations within and among years, registering years of very low densities and others of explosive increment (Crespo 1966; Crespo et al. 1970; de Villafañe et al. 1977; Kravetz 1977; Mills et al. 1991a, 1992a; Polop et al. 2007).

The population fluctuation has been reported as the result of the joint action of extrinsic and intrinsic factors and it is a widely studied phenomenon in many rodent species (Crespo 1966; Birney et al. 1976; Gards and Howard 1981; Getz et al. 1997; Mills et al. 1991a, 1992a). In *C. musculus*, this seasonal pattern of density fluctuation has been attributed to seasonal reproduction, climate and environmental disturbances (Mills et al. 1992a). An assumption of our model was that the seasonal fluctuation in rodent population density was modulated by the seasonal variation in NDVI as an extrinsic factor representing these environmental changes. Recently, Simone et al. (2009) observed that *C. musculus* evidenced a marked association with NDVI of field borders only in summer, reflecting the particular importance of this variable previous to the population peak. Similarly to Porcasi et al. (2005), we observed that the basic model outputs registered rodent annual maximum numbers in autumn, whereas NDVI has a maximum in summer, implying a lagged effect between simulated total population abundance and this environmental variable. Similar results have been obtained for other species of small rodents (Ernest et al. 2000; Stenseth et al. 2003; Zhang et al. 2003; Andreo et al. 2009a, 2009b). However, long-term studies establishing relationships between *C. musculus* field populations and this kind of variable have not been carried out yet.

The model showed a general agreement with the trends in total population and in temporal cohort

variation. However, model outputs differed from field observations in the timing of some seasonal peaks in total population (Figure 7) and C2 and C3 (Figure 8). Besides, it overestimated the mean life span of C0 (Figure 4). These inconsistencies could be due to three factors. First, the model might have a structural shortcoming; both the direct dependence of population parameters on NDVI and the relationships between these parameters should be carefully evaluated. Second, the spatial resolution of satellite images may have been large ( $8 \times 8$  km) and may have not accurately reflected the habitat requirements of *C. musculus*. Finally, differences between population peaks could be due to the fact that NDVI is not likely to be the unique variable that limits the population growth. Studies in field populations have demonstrated that several environmental factors affect the population density of *C. musculus* (Crespo et al. 1970; Kravetz and de Villafañe 1981; Kravetz and Polop 1983; Busch et al. 1984; de Villafañe and Bonaventura 1987; Polop and Sabattini 1993; Busch et al. 2000). Therefore, including other environmental variables (or a combination of them), or images with better spatial resolution, could improve the model results. In addition, these improvements may solve other limitations of the model, as the weak response of total population to NDVI, particularly at the third and fifth simulated years (Figure 2).

The application of rodent control strategies is often poorly timed or inadequate, so that populations recover quickly, or else control is performed in response to high rodent numbers, after the damage has been done (Stenseth et al. 2003). Despite its limitations, our model provides insights into the interplay between *C. musculus* populations and environmental variability, allowing the evaluation of different control strategies. When we simulated hypothetical scenarios varying both the environmental conditions and population parameters, the model outputs differed from each other. Indeed, when we applied measures tending to reduce the mean life span of those cohorts that are most represented in autumn (C2, C3), or the carrying capacity of the system in the same season (through vegetation cover reduction), the population recovered (Figure 6(a), (b)). Nevertheless, if we were interested in reducing total population of *C. musculus* to abundance values near zero, applying some strategy tending to reduce vegetation cover or the mean life span of C0 and C1 or total population could be a better management option (Figures 3, 6(a), (b)). Finally, considering that animal biodiversity is essential to support valuable ecological functions and ecosystem processes (Doak et al. 1998), it could be important to maintain the reservoir population in low levels of abundance, avoiding the extinction of local populations. Thus, managing total population reducing NDVI values through cleaning-vegetation actions from spring to winter would be a good control strategy (Busch et al. 1984; see also Figure 3).

The design of rodent control strategies has an ecological dimension related to the interaction of pest population and its resources and enemies (Singleton et al. 1999). Studies that contribute to understanding the dynamics of *C. musculinus* populations are useful toward a better comprehension of AHF dynamics. Moreover, understanding the population dynamics of any species is helpful, if not critical, to guide efforts for population control (Juliano 2007). Models such as the one presented here could be useful to assist in the control of rodent reservoirs through the evaluation of relationships between reservoir population dynamics and characteristics of biotic or physical environment, ensuring the efficient use of resources in integrated pest management.

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