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REVIEW

Rating the rat: global patterns and research priorities in impacts and management of rodent pests

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ABSTRACT

1. We report the results of the first systematic assessment of global patterns and research priorities emerging in the field of rodent pest management. We carried out an extensive literature review targeted towards identifying the most relevant rodent pests, their impacts and the most common methods used to control them.
2. We identified three disproportionally important pest species that are characterized by severe, generalist and geographically widespread impacts: the black rat *Rattus rattus*, the Norway rat *Rattus norvegicus* and the house mouse *Mus musculus*. Overall, only 7% of known rodent species may be considered pests. Scansorial (i.e. terrestrial and semi arboreal) and fossorial species are generally important as pests, while aquatic and arboreal species have only specific impacts.
3. Impacts of rodent pests on arable crops were studied most, followed by impacts on ecosystems. Studies on arable crops were typical in countries with low net income and health expenditure, while the opposite was observed for studies on ecosystems. Poisons were the most commonly used control method, followed by traps and habitat management. The need to control rodent species is expanding, especially to protect ecosystems and public health. Unlike in other fields of pest management (e.g. insect control), in rodent control we are approaching new problems with old solutions; control strategies and methods have not kept pace with emerging impacts.
4. The need to control a rodent pest species is higher when it is non-native than within its original geographical range. The impact of a rodent species in its native range is a good predictor of the impact it may have in areas of introduction.
5. Our review will contribute towards guiding researchers and stakeholders to focus research efforts and investments on a subset of species, and on new, less hazardous control techniques.

Keywords Eradication, invasive, non-native species, rodenticides, small mammals

Running title: Rating the rat

INTRODUCTION

Rodents are a unique order in the mammalian class, and their peculiarity goes far beyond the fact that they are the most species-rich order: 2277 of the 5419 mammalian species are rodents (i.e. 42% of all species; Carleton & Musser 2005). There is no other vertebrate order with such a high diversity of pest species, such a widespread range, and such variety of impacts, in agriculture, urban areas, ecosystems, forestry, public health, etc. (see Singleton et al. 1999). As an example, between 1998 and 2008, more than 23000 cases of human plague, an infectious disease caused by *Yersinia pestis* which is carried by *Rattus rattus* as intermediate host, were reported, including 2116 fatalities in 11 countries (Anonymous 2010a). The cost of rodent pests to agriculture is enormous (Singleton et al. 2010). In Asia, the preharvest loss of rice *Oryza sativa* due to rodents – either native or non-native – is estimated to be 5% of the production, or approximately 30 million metric tonnes: enough rice to feed 180 million people for a year; the postharvest losses are probably of a similar magnitude (Singleton 2003). The worldwide business activities associated with pest control is therefore huge, ranging from manufacturing of pest control products to highly qualified pest control services provided to e.g. householders and food industries in urban areas (Langton et al. 2001).

When introduced outside their natural range, many rodents such as rats, mice, squirrels and coypus may have a detrimental impact on native species and ecosystems, requiring the implementation of control or eradication programs (see Carter & Leonard 2002, Howald et al. 2007, Bertolino et al. 2008, Capizzi et al. 2010).

Due to the use of non-selective toxins and traps, rodent control activities have implications for other research fields, such as the study of impacts on non-target species (Brown 1994, Hoare & Hare 2006) and of animal welfare (Meerburg et al. 2008). Moreover, rodents exhibit both genetic and behavioural responses to control activities, which may result respectively in resistance (Pelz et al. 2005) and neophobia (Brigham & Sibly 1999, Clapperton 2006), two issues concurrently present, amongst vertebrates, only in rodents.

The richness and diversity of rodent pest species and impacts has led, over the centuries, to extreme diversification of control techniques and devices. Attempts to trap, repel and poison rodents have occurred throughout the centuries: as an example, the use of naturally-derived poisons (mainly based on hellebore, black henbane, hemlock, and wild cucumber) to kill rats and mice around houses and granaries were recommended in ancient Greece and Rome (Smith & Secoy 1975).

Despite this long history of fighting against rodents, no definitive solution has been found yet, and diverse control methods are currently used throughout the world (Buckle 1994, Smith 1994, Singleton et al. 1999 for reviews). The worldwide adaptive radiation of techniques, however, may determine a progressive lack of common ground in the various research lines.

Despite the fact that rodent control is routinely performed worldwide, most existing reviews focus on specific subjects (Clapperton 2006, Howald et al. 2007, Jacob et al. 2008, Meerburg et al. 2009, Banks & Hughes 2012, Bertolino & Lurz 2013, Tran & Hinds 2013). No study so far has addressed all species and all levels of information on impact, control and trends. Such a review would help researchers to prioritize future research on relevant species and impacts, and to develop more effective control techniques and materials. The goal of this work is therefore to contribute towards filling this knowledge gap by identifying the most relevant rodent pests, their impacts, and the most common methods used to control them. We searched for studies that were focused on rodent impact and control, assuming that the percentage of studies on each species or taxon, impact or control technique reflects the level of interest in it in each country or continent. In our paper, the 'pest' concept mirrors the terminology adopted by the Center for Biological Diversity and the International Union for Conservation of Nature for 'invasive species', and is based on any impact a species may pose (see Brunel et al. 2013). This definition is more appropriate for our purposes than the definitions proposed by Richardson et al. (2000) and Ricciardi and Cohen (2007). We identified five key questions that will help to frame a taxonomic and geographic identikit of the main issues in this research area: 1) Which are the main rodent pest species in the world? 2) What are their main impacts? 3) What are the main control methods adopted? 4) Are there temporal trends emerging in control methods and impacts? 5) Are rodent control activities correlated with the socio-economic conditions in the various countries? We finally provide a prospectus for future research, highlighting knowledge gaps and research priorities.

METHODS

We performed a review of scientific literature by adopting *a priori* defined criteria, so that the review process can be both repeated by others and updated in the future (Littell et al. 2008, Lowry et al. 2012). The literature search encompassed the period January 1990 - December 2010. We searched in Scopus for papers written in English with the following words in the title and/or in the abstract: *rodent(s*) and *pest* or *impact* or *control* or *management* or *eradication*. We extended our search to appropriate titles included in the various reference lists.

We also considered papers published in specific conference proceedings such as the Vertebrate Pest Conference (from 1990 to 2008), the European Vertebrate Pest Conference (from 2001 to 2007), and Rats, Mice and People (2003).

We included in the database case studies mentioned (even very briefly) in the papers, in which information on at least three of the following four points was reported:

1) Name of the pest species or, if the species was not determined, genus.

2) Control methods used: 1: trapping, 2: poisons, 3: habitat management, 4: fertility control, 5: barriers, 6: repellents (acoustic and olfactory), 7: behavioural mechanisms, 8: predator or parasites, 9: control of ectoparasites or pathogens, 10: damage prevention and forecasting, with a maximum number of five different methods for a single case study.

3) Specific impact on: 1: arable crops (defined here to include orchards and horticulture), 2: ecosystems, 3: livestock farming, 4: forestry, 5: public health, 6: urban areas. With the term 'impact on ecosystems' we refer to all impacts on native species and habitats. We also included studies on other subjects strictly linked to control activities, such as: 7: animal welfare, 8: behavioural aspects, 9: impact on non-target species, 10: resistance to rodenticides and 11: tests of the efficacy of various baits or traps.

4) Country and continent where the study was carried out. We considered North and South America as two separate 'continents', as the two areas are biogeographically distinct. Other continents were Africa, Asia, Europe and Oceania, the latter including

Australia. Islands were grouped with the closest continent (e.g. New Zealand with Oceania, Indonesia with Asia).

We found a total of 658 papers fitting our criteria, in which a total of 1850 case studies were described (see Appendix S1). A case study was defined a 'pest species-impact-control method' combination within a paper. Therefore, a single paper could include more than one case study if: 1) at least two species were controlled, in relation to the same impact (e.g. *Mus musculus* and *Rattus norvegicus* for public health purposes), 2) the same species was controlled, in relation to two or more different impacts (e.g. *Rattus rattus* in arable crops and livestock farming), 3) the same species was controlled with two or more control methods (e.g. *Mastomys natalensis* with poisons and habitat management). Most case studies (31%) came from Asia, followed by North America (26%), Oceania (16%) and Europe (16%); fewer were from Africa and South America (8% and 4% respectively). To assess the importance of taxa (mostly species), impacts and control techniques, we used a suite of criteria (three for impacts, six for species and control methods; Table 1).

RESULTS

Which are the main rodent pest species?

We found mention of at least 147 pest species, i.e. 7% of known rodent species (2277). If a species' identification was uncertain (e.g. *Microtus* and *Thomomys* spp.), we considered it as a pest taxon only if no species of the genus was already present in the database. The partial and the final rankings of the main pest taxa (mostly species) are presented in Table 2. Three species were always in the first three positions according to each criterion. These were the black rat *Rattus rattus* (first in criteria 1, 3, and 5; see Tables 1 and 2), the Norway rat *Rattus norvegicus* (first in 3 and 4) and the house mouse *Mus musculus* (first in 2, 3 and 6). The black rat is revealed as the main rodent pest species in the world. All the three species were cosmopolitan and were controlled in all six continents, but only *Mus musculus* was controlled for all impacts.

Other important species were the Pacific rat *Rattus exulans* and the grey squirrel *Sciurus carolinensis*. The first species controlled only in its native range was *Spermophilus beecheyi,* followed by the multimammate rat *Mastomys natalensis*, the rice-field rat *Rattus argentiventer* and the lesser bandicoot rat *Bandicota bengalensis*.

We stress that we recorded a high frequency of undetermined species for some taxa. Considering only the most important genera, this problem was especially evident in North America for the genus *Thomomys* (undetermined in the 55% of cases), *Microtus* (7%) and *Spermophilus* (6%) and in Asia for *Bandicota* (5%).

A crucial aspect determining whether a species is a pest or not may be its status, i.e. if it is native or alien to a given area: alien species are considered likely to become invasive out of their geographical range, since they may overcome potential competitors, and may not have natural predators or parasites (Mitchell & Power 2003, Torchin et al. 2003). In order to assess the influence of species' status on their level of impact, we selected the eight species which are non-native (alien) in at least one continent, without setting a temporal limit of the time of introduction of the species. The native and introduced range were here considered at the continent level: a species was considered non-native when it was encountered in a study carried out in a continent where it was non-native. For example, we considered *Rattus rattus* as native throughout Asia, but non-native elsewhere. We acknowledge that such an approach is quite coarse and therefore questionable, since, for example, if a species originated in north-west Asia it is considered native to the whole of Asia. However, this method may overcome the problems of establishing, at the country level, the native range of some species [see references and discussion in Carleton & Musser (2005) for *Rattus rattus*, *Rattus norvegicus* and *Mus musculus*, but also Aplin et al. (2011)]. For each of these eight species, we compared the proportion of studies in the continents where they were non-native with that in areas where they were native. We considered the average percentage of studies among five impacts, excluding only that on ecosystems which, by definition, deals almost exclusively with alien species. A repeated-measures analysis of variance between the status of the species (alien or native, within-subject factor) and type of impact (between-subject factor) showed that the percentage of studies in continents where the species was non-native was significantly higher than the percentage in continents where it was native (F= 12.097, df 1, P=0.001), but there was no difference between the various impacts (F= 0.115, df 4, P=0.98) (Fig. 1).

In order to assess whether the impact of a species in its original geographical range is a good predictor of its importance in its introduced range, we correlated the importance of the species in its native range with that in continents where it had been introduced. We observed a positive correlation between the average percentage of studies on the species in its native and non-native range (n=8, r=0.76, P=0.03, Fig. 2).

Such species-based analysis may underestimate the importance of groups of species causing similar damage patterns (e.g. those in the Arvicolinae subfamily), but which are much more restricted in their distribution than cosmopolitan rats and mice, because the effect of such species may be overlooked if they are considered separately. In order to highlight trends related to the species' lifestyle, pest species were split into four lifestyle groups: 1) strictly arboreal; 2) scansorial (terrestrial or semi arboreal); 3) fossorial or semifossorial; 4) aquatic. When in doubt, we assigned the species to one of the four groups following published accounts (e.g. Nowak 1999).

Relying on the criteria of Table 1, scansorial species were by far the most important as pests (sum of ranks: 6), followed by fossorial (12), arboreal (17) and aquatic (19). A saturated Poisson log-linear analysis was run to compare the contingency table of rodent pests' lifestyle vs. impact. A significant model was obtained (df 15, likelihood ratio 458.9, Pearson Chi-Square 448.9, P=0.000). Analysis of the deviance residuals revealed (Fig. 3a) that: 1) fossorial species were especially important in forestry and arable crops, and less important in ecosystems and urban areas; 2) scansorial species were studied more than expected in ecosystems, and less in forestry; 3) aquatic species were more important in ecosystems and less in public health, while arboreal ones were more studied than expected in forestry and less in arable crops.

In a second log-linear analysis, rodent pests' lifestyles were compared to control methods, considering only those taxa with at least 50 case studies. A significant model was obtained (df 15, likelihood ratio 136.8, Pearson Chi-Square 152.1, P=0.000), showing the lack of independence between the two factors. Deviance residuals (Fig. 3b) showed that: 1) scansorial species were controlled more than expected by poisons and less by traps, habitat management and repellents; 2) both arboreal and aquatic species were controlled more often by trapping and hunting and less often by poisons; 3) the use of repellents and habitat management to control fossorial species was reported more than expected, hunting less often. Fossorial species were the only group for which both traps and poisons were used less than expected.

What are their main impacts?

Impacts on arable crops were the most studied, followed by impacts on ecosystems (Table 3). Impacts on urban areas, forestry, public health and livestock farming were studied considerably less. However, impacts on arable crops were exceeded by impacts on ecosystems in Oceania and on livestock farming in South America.

Apart from the six impacts considered here, studies on rodent control were also focused on other topics closely related to rodent management. The most important subject areas were impacts on non-target species and resistance to rodenticides, followed by tests of efficacy (of either rodenticide baits or active ingredients), and behavioural aspects (e.g. behavioural resistance and neophobia; Table 3). Animal welfare and impact on humans were considerably less important.

What are the main control methods?

Poisons were by far the most widely used control method, followed by traps and habitat management (Table 4). Independent of the adopted criterion, these techniques were always within the first three positions of the six rankings; poisons were always the first method. Among poisons, 61% of cases dealt with anticoagulants.

Within a paper, a single species may be reported as being controlled by using one or more methods. We analysed the pattern of use of the different control methods by checking if a method was more likely be used alone or in integration with other techniques. The pattern of use differed between the various methods. A two by two contingency table was used to assess statistical significance in the differences between the frequency of use of a given control method alone, in respect to the cumulative frequency of all methods alone. Some methods were used preferentially in combination with others, e.g. hunting (searching for individuals with dogs, digging with the aim of capturing, killing by means of shooting $p<0.0001$), barriers ($p=0.05$) and traps ($p<0.0001$). Repellents ($p=0.005$) and damage prevention and forecasting ($p=0.007$) were disproportionately chosen as single control methods.

Through a one-way analysis of variance, we showed that the average number of control methods differed depending on the impact being controlled for ($F_{5,1589}=26.45$, $P=0.00001$, Fig. 4). A Tukey HSD post-hoc test indicated that these difference were accounted for by the lower number of methods used in relation to impacts on ecosystems and urban areas.

Relationships between species, impacts and control methods were examined by multiple correspondence analysis. The observed pattern of association among the categorical variables is presented in Fig. 5. The analysis extracted two dimensions (explained variance: dimension 1: 64%, dimension 2: 56%, mean: 60%). Impacts were well divided on the first dimension, while only forestry strongly departed along the second dimension. Arable crops was clustered with some specific control methods (fertility control, barriers, habitat management and hunting) and pest species. Impacts on ecosystems, urban areas, public health and livestock farming were clustered together, sharing a pool of generalist, cosmopolitan pest species and widespread control techniques (i.e. traps and poisons).

Are temporal trends emerging?

To address this question, we fitted the best regression models to the data, checking the validity of assumptions and the goodness of fit of the model. The predictor variable was time (years between 1990 and 2010), while response variables were the percentage frequency of the various impacts, continents and control methods. Among impacts, all the analyses revealed that data were best fitted by a linear model (Table 5). Studies focusing on both arable crops and forestry showed a significant decrease over time, while an opposite trend was recorded for those on ecosystems and public health (Table 5).

The only trend recorded for control methods was an increase in the use of damage prevention and forecasting, but none of the models attained statistical significance (linear model, P=0.08).

Are rodent control activities correlated with socio-economic factors?

We selected five socio-economic indicators (from the database of the World Bank; Anonymous 2010b) to relate with the impacts studied in the various countries (Table 6). Indicators are provided for each year until 2009, with a few missing data for some years and some countries. We fitted the best regression models to the data, checking the validity of assumptions and the goodness of fit of the model. As in the previous analysis, the response variable was the percentage frequency of the various impacts; the predictor variables were the socio-economic indicators for each country. For each indicator, we considered the average value during the period 1990-2009.

We recorded significant relationships for impacts on ecosystems, arable crops and forestry (Table 6). Studies on arable crops were typical of countries with lower net income and health expenditure, while exactly the opposite trend was observed for studies on ecosystems.

DISCUSSION

Our results reveal several clear patterns and trends in the field of rodent pest control: 1) the most important rodent pest species, *Rattus rattus*, *Rattus norvegicus* and *Mus musculus,* are characterised by strong, generalist and geographically widespread impacts; 2) the need to control a rodent pest species is higher when it is alien than in its native geographical range, and its impact in the native range is a good predictor of its importance in the introduced range; 3) impacts of rodents on arable crops are the most-studied impacts, particularly in relatively poor countries; however, a temporal trend is emerging in which studies on the impact on ecosystems are becoming increasingly important, especially in richer and more developed countries; 4) although the features of the rodent pest problem have substantially changed over the last twenty years, we still attempt to control rodents mainly by using poisons and traps, thus facing new problems with old solutions.

The main assumption of our work is that the percentage of studies on either a species, impact or control technique reflects actual interest in it in the country or continent. The percentage of articles is often used to assess trends and patterns in scientific interest within a subject (see e.g. Thill et al. 1991, Brown et al. 2008, and Lowry et al. 2013 for case studies on pest control and biological invasions). Nevertheless, we recommend caution in the interpretation of our results, since they may be biased towards the most scientifically relevant (or publishable) case studies. The reader should not assume that scientific relevance translates to economic or health relevance. Furthermore, we stress that we did not consider the ‘grey’ literature, and this may be a problem for countries where there is patchy documentation of rodent problems. At the same time, we stress that our approach may be the only way in which rodent control activities can be scientifically evaluated at the global level. An alternative approach would be to apply more subjective techniques such as a scoring system, an expert-based method that may be applied at the level of single continents (e.g. Nentwig et al. 2009); nevertheless, it would hardly be feasible at a worldwide scale, as experts would be required from all over the world. An additional source of bias may have been introduced because papers published in languages other than English could not be considered in this review. It is therefore possible that we may have overestimated the importance of rodent problems occurring in western countries, because that is where most of the literature emanates from. However, our study includes an extensive sample of the scientific literature on this subject. We are therefore confident of capturing patterns and trends in this sector of research, and thus believe that our findings should be considered as a reliable relative index of the importance of species, impacts and control methods. The latter hypothesis is corroborated by our analyses involving socio-economic indicators, which show a general accordance between our data and the real world.

A second caveat of our study relates to the approach we followed for computing rankings. We adopted a multi-criteria approach. In our opinion, a pest species is important (i.e. worth the investment of resources and research effort) if it has a wide geographical range, causes a high average incidence of damage, and is responsible for different impacts. Furthermore, a high incidence in either a single impact or continent is important (see e.g. Lowe et al. 2000, Long 2003). To make the analysis as objective as possible, we used the same weighting for each of the six impact criteria.

Rating the rat

Our analysis supports the general perception that three disproportionally important rodent species have severe, generalist and geographically widespread impact. Although Rodentia contains more than 2000 species (Carleton & Musser 2005), 44% of the papers published on rodent control deal with only three species, *Rattus rattus*, *Rattus norvegicus* and *Mus musculus*. Their importance is further enhanced by the number of impacts for which they have been responsible, and by the wide geographical range in which they have been controlled for. It is surprising to note that only a relatively small number of papers has been published in last decade on the basic ecology of these species (see Sutherland et al. 2005, Stokes et al. 2009, Ruscoe et al. 2011, Heiberg et al. 2012). Our results clearly suggest that carrying out basic research on the biology and ecology of top pest species should be a priority, in order to develop more effective techniques and control materials. Metaphorically, these three disproportionally important pest species could be compared to countries with high credit ratings in the global economy (the so-called "AAA countries"), as there should be great interest in investing money in them (to fund research on applied ecology and control techniques). Any innovation in this latter field would be especially important, as these species are not controlled by specifically designed techniques, and therefore would lead to higher returns on the investment.

It is noticeable that only 7% of known rodent species may be referred to as pests, a figure somewhat consistent with Singleton et al. (2007), who considered that in many regions of the world, less than 10% of the resident rodent species are significant agricultural pests.

The importance of pests may be viewed by adopting a functional rather than a taxonomic approach. We addressed this aspect by considering species' lifestyle, i.e. whether they were arboreal, scansorial, fossorial, or aquatic. From an applied point of view, species with the same lifestyle may cause similar damage and similar control strategies may be appropriate for them. Besides our basic findings (e.g. that arboreal species were most important in forestry, and that aquatic species were less important in livestock farming), we underline that fossorial and scansorial species, which were by far the most important functional groups, showed contrasting patterns, with regard to both impacts and control techniques. Allocation of species to one of four lifestyle categories is not always straightforward and is somewhat arbitrary (e.g. *Rattus norvegicus*, when outdoors, may be considered a semifossorial species; *Rattus argentiventer* is partly aquatic in rice fields). These findings suggest that a deep understanding of the biology of a pest species is a key factor in predicting its impact, as well as in achieving management objectives and in developing proper control techniques.

The importance of being alien

A noticeable finding of our research is that the need to control a rodent is higher when it is non-native than in its native range. We emphasise that we did not include in this analysis the impact on natural ecosystems, as it is quite obvious that in this context, an alien species may be controlled more often simply because of the precautionary principle (Brunel et al. 2013). Therefore, our results apply to ecosystems altered by humans and to human activities, and are in general agreement with the findings of Kumschick et al. (2011) and Simberloff et al. (2012), who found that introduced mammal and plant species are more invasive than native ones. This result clearly shows that the problem of biological invasions should not be considered only from a conservation perspective, and we are confident that this argument will help ensure that countries adopt a more stringent policy for monitoring and preventing the spread of non-native species (Pimentel et al. 2005, Vilà et al. 2010). Furthermore, the impact of an alien species is correlated with its impact in its native range. Due to difficulties in pinpointing the origin of rats and mice in Asia (see Carleton & Musser 2005, Aplin et al. 2011), we suggest caution in interpreting this result. However, we suggest that by gathering *ad hoc* data on potential pest species in their native ranges, we may be able to predict which species could have most impact when introduced elsewhere (Krivanek & Pyšek 2006, Nentwig et al. 2009). This latter consideration can be viewed in the light of the Early Warning and Rapid Response approach (see Brunel et al. 2013), a key pillar of action toward invasive species, which requires assessing potential impacts before they are recorded. Clearly, other parameters may also play important roles, nevertheless such findings warrant further investigation.

The power of money

Unlike individual taxa (mostly species), the impacts we studied were more diversified among continents; those on arable crops and ecosystems were the most important, depending on the continent. Relationships between the frequency of studies on impacts on ecosystems and arable crops showed opposite patterns of association with both socio-economic indicators and time. Studies on the impact of rodents on ecosystems are typical of countries with lower population growth rate and higher gross net income and expenditure on public health, and the relationship is exactly the opposite for studies on arable crops. However, it should be stressed that much of the global biodiversity, and probably many of the most severe impacts, occur in the developing regions of the world. This suggests that these differences do not reflect the actual impacts but may be due to different priorities. We caution the reader by stressing that the relationships were not always straightforward; in some cases non-linear models fit the data better than linear ones.

The relative importance of studies on arable crops and forestry decreased over the years, while the opposite was true for those on ecosystems and public health. It is difficult to understand whether this is due to a change in the impact of the species or in interest in the topic. The former is perhaps the case for arable crops, where increased mechanization and reductions in edge habitats may have caused a reduction in damage by some pests (e.g. voles, see Jacob 2003, Jacob & Tkadlec 2010). It is possible that the increase in studies dealing with impacts on ecosystems is connected with increasing attention for this topic by scientists and media (Simberloff 2004). A similar argument may apply to public health: though the impact of rodent-borne zoonosis such as plague have been mitigated (but not eliminated) in the last decades (Meerburg et al. 2009), this trend is not reflected in the scientific literature. There could be other reasons why the rate of publication for a certain topic increases or decreases over time, e.g. shifts in the policy of funding bodies such as governments and research councils. The increase in the overall level of economic parameters (e.g. Gross Net Income pro-capita) that occurred in the last twenty years may also have played a role. Whichever the reason, the linear trend we found suggests that, in the coming years, we should expect a further reduction of the gap between these subjects.

Other topics related to rodent management

Aside from the impacts, studies were focused on two main topics related to rodent management: non-target species and resistance to rodenticides. These results represent the flipside of the widespread and generalized use of rodenticides, the former reflecting concerns about the environmental risks associated with their use, the latter about their efficacy. The two aspects are related, since the recent advances in the genetic location of resistant populations (Pelz et al. 2005) offer the opportunity to limit the use of more hazardous substances to areas where they are really needed and effective. We found few studies on animal welfare and on the impact of rodenticides on humans. However, while the former aspect is still at an early stage and is expected to increase in the coming years, the latter was unimportant because, contrary to what was found for insecticides, rodenticides are unlikely to contaminate water or foods (Anonymous 1995, Nasreddine & Parent-Massin 2002, but see Brown 1994 for some problems with old acute rodenticides).

Main control methods

The analysis of control techniques allowed us to highlight some general trends. First, the simplest methods are the most widespread: poisons and traps accounted for over 60% of control techniques. These two methods may be preferred because they provide tangible results (i.e. death or captured individuals, or consumed bait) and relatively little expertise. Conversely, methods that require extensive research and expertise (i.e. fertility control, damage prevention and forecasting, behavioural mechanisms) are much less often used. Despite these results, as predicted in theoretical studies (see Singleton 1994, Krebs 1999, Shi et al. 2002, Arthur et al. 2007), lethal methods are intrinsically less effective on rodents than methods aimed at reducing carrying capacity or reproductive output, because rodents are highly fecund, short-lived species (i.e. extreme r-strategists). In this regard, it is emblematic that lethal methods (i.e. traps and poisons) are strongly underselected for use against fossorial species, a functional group including many r-strategists such as Arvicolinae, perhaps because of the difficulty of placing baits or traps inside tunnels. Another relevant issue is damage prevention and forecasting, where population or ecological niche models for predicting rodent outbreaks have been successfully applied (Leirs et al. 1996, Sanchez-Cordero & Martinez-Meyer 2000, Stenseth et al. 2001). As ecological studies focusing on rodent demography, movements and ecological niche are routinely performed on several non-pest species, we envisage that applying the same biological and statistical background to economically relevant species may offer promising perspectives.

Anticoagulants are the most widespread poison category, but many farmers in developing countries cannot afford anticoagulants, so their use is often limited (e.g. Stuart et al. 2011). Unlike in other fields of pest control (e.g. insect control), where in recent decades species-specific techniques have been developed and adopted on a large scale (such as pheromones for capturing and disruption of mating, species-specific parasitoids, see Jutsum & Gordon 1989, Arn 1990), the most commonly used techniques against rodents are largely non-selective.

In this respect, the lack of evident temporal trends in the control methods used suggests that the search for alternative techniques has lost momentum. This is somewhat at odds with the trends in legislation; for example, the increasing restrictions in the use of anticoagulants in Europe (i.e. Directive 98/8/EC and successive amendments and corrections, concerning the placing on the market of biocide products) further emphasize the need for new, environmentally safer methods of rodent control. Following the implementation of the EU directive, several widely used insecticides have been removed from the market, but no anticoagulant, despite concerns about environmental risks. The main reason for this is that there is no established alternative (Anonymous 2007). It is likely that, as soon as new techniques become available, the use of anticoagulants will be reviewed.

The latest innovation in the field of anticoagulants dates back to the late nineteen eighties (i.e. Flocoumafen and Difethialone, see Lund 1988, Nahas et al. 1989), thus highlighting the lack of interest in developing more powerful rodenticides. However, concerns about the effects of poisons on non-target species, and about resistance to anticoagulants show that the ideal rodenticide should balance effectiveness against target species and risks to non-target ones.

When the aim is to eradicate a species (a task typical of alien species management, but also in urban areas, where the goal is to eliminate rodents, or reduce as much as possible their density), we might intuitively expect the use of several combined methods. Our analysis showed in fact fewer methods are used. This may be due to the need to concentrate efforts in a restricted time-period, but psychological aspects may play a role too. Although we have no data on efficacy of the various methods, poisons seem to be the most trusted method; they are preferentially adopted when it is necessary to eliminate all individuals. This is confirmed by case studies of rodent eradication on islands, where the use of poison has been recognized as being by far the most effective technique to achieve the complete eradication of the populations (Howald et al. 2007, Pluess et al. 2012).

However, it is likely that such an approach was not able effectively to account for the implementation of ecologically-based rodent management, an important and emerging approach used particularly in Asia and Oceania. For example, smallholder farmers in Asia may use rodenticides, but studies have clearly shown that ecologically-based rodent management has led to a reduction by 50% in their use (see Brown et al. 2006, Jacob 2010).

Research priorities and perspectives

Our results should contribute towards directing and prioritizing research and marketing strategies by researchers and pest management stakeholders. One priority is the need to develop population models allowing the forecasting of rodent damage in time and space, which, in turn, will require long-term population studies targeted towards collecting ecological and demographic data (Leirs et al. 1996, Krebs et al. 2005, Brown et al. 2010). Our analysis narrows the number of candidate species for these long-term studies, and identifies those whose biology and ecology should be studied more thoroughly. Considering the grave concerns about environmental risks posed by the generalized use of anticoagulants, research should focus on new techniques, which should be more specific and less hazardous for non-target species. In theory, the most demanding control methods, in terms of research and expertise, such as fertility control and damage prevention and forecasting, may have the greatest potential for expansion. Fertility control, although rarely used to manage the impacts of rodent pests, has potential as a management technique and could be a good approach, especially to reduce the impact of rodent damage on farmland or in forestry (e.g. see Tran & Hinds 2013). Damage prevention and forecasting have potential for the control of rodent populations that show density fluctuations stimulated by specific factors like weather or food (Davis et al. 2004, Brown et al. 2010), but not for the control of commensal rats and mice where such fluctuations are uncommon, or in species where damage is not density-dependent.

Future research should be focussed on the development of poisons which are safer for non-target species, rather than on development of active ingredients that are more effective on target species, and on methods for site-specific, weighed decisions about the active ingredients, relying on genetic location of resistant populations (Pelz et al. 2005).

Investors should consider the emerging temporal trends, especially in the impacts we studied, as attention on ecosystems and public health is expected to become increasingly intense (Meerburg et al. 2009, Banks & Hughes 2012). Therefore, investments in those fields may offer a higher return.

The rodent species with most impact as pests are widespread and controlled in many continents, and have higher impact in their introduced ranges. Strategies implemented to reduce the damage caused by introduced species should thus involve the identification of rodent species known for their impacts in their native range as candidates for inclusion in black lists in other geographic areas.

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Appendix S1 Dataset of published papers used for all analyses.

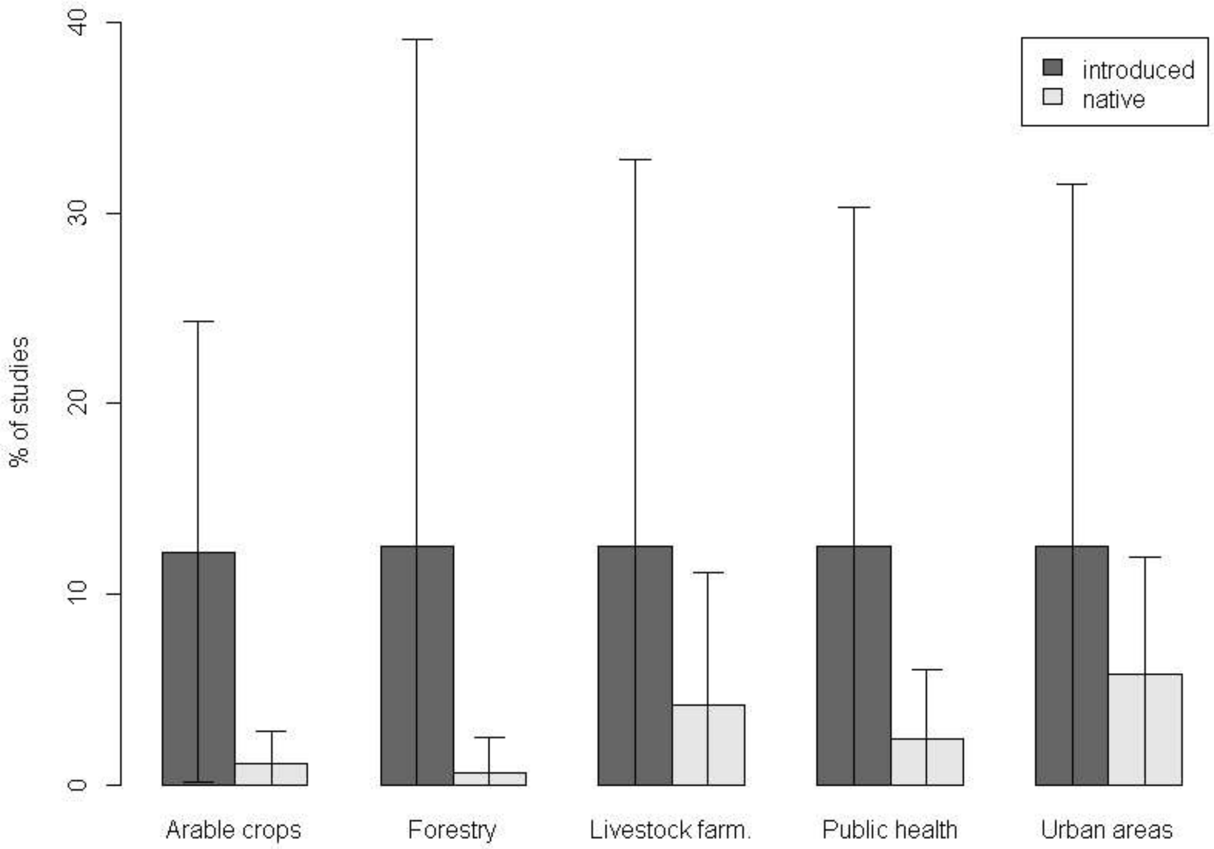

Fig. 1. The mean and standard deviation of percentages of studies focusing on the eight rodent species which were alien in at least one continent. Impact on ecosystems was not included in the analysis as it relates almost exclusively to alien species.

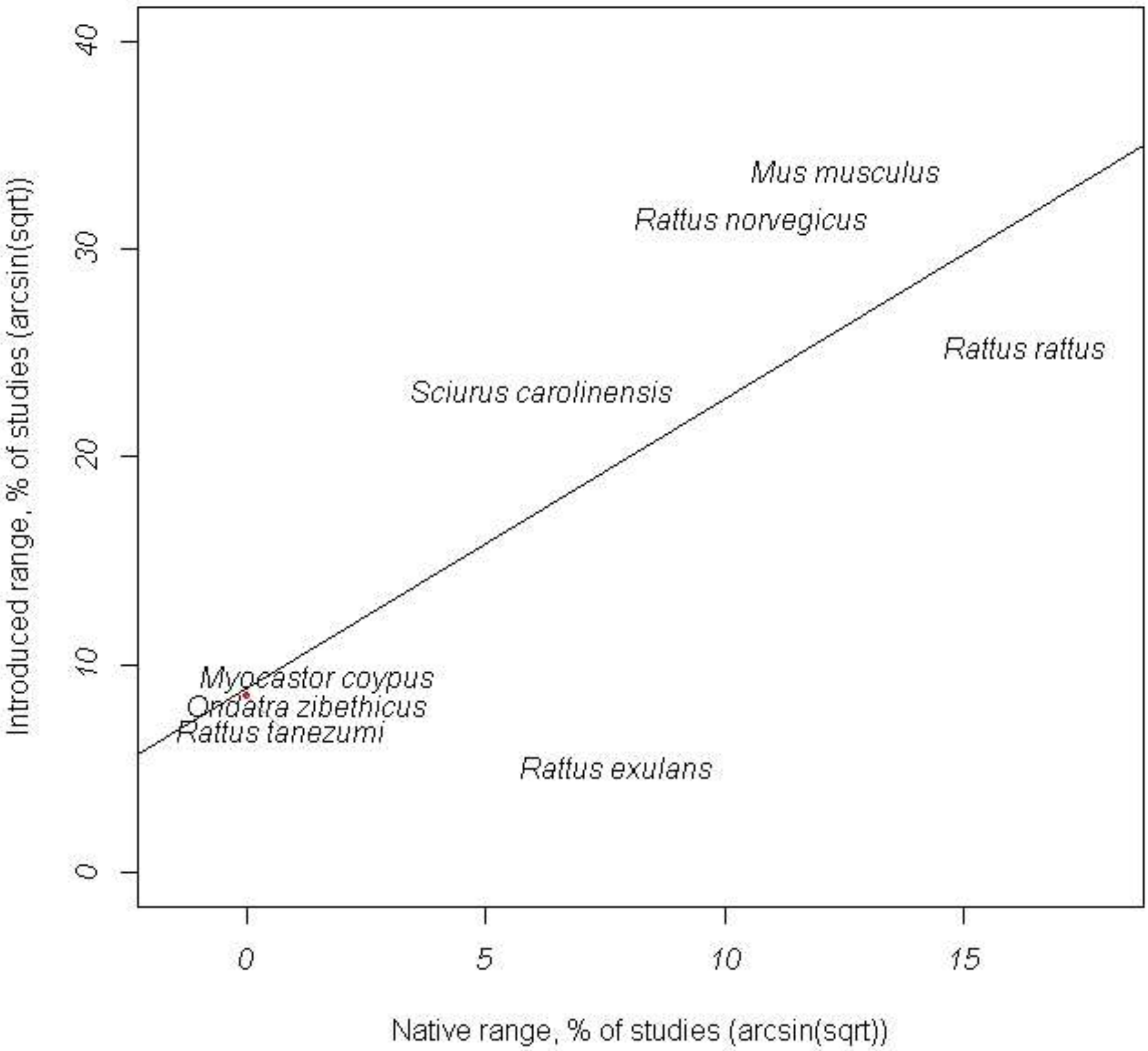

Fig. 2. Correlation between the percentage of studies focusing on the eight alien species in their original distribution range (x axis) and where they have been introduced (y axis) (r=0.76. P=0.03). Percentages were arcsine square root transformed before analysis.

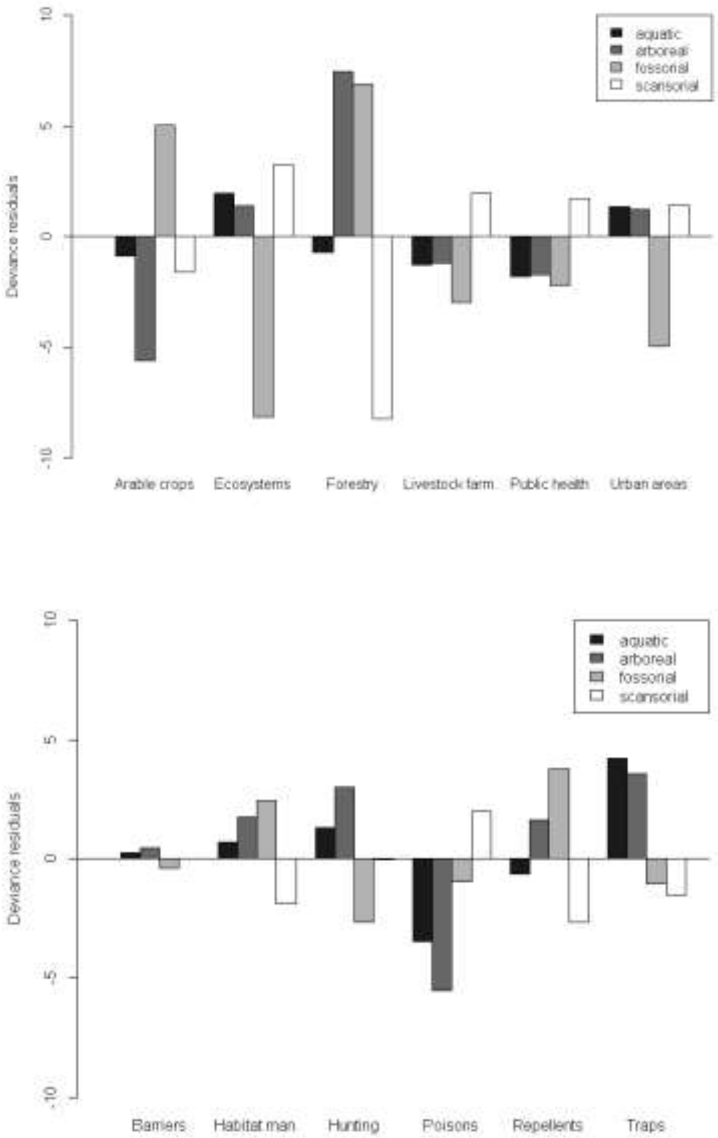

Fig. 3. Deviance residuals obtained from two Poisson log-linear analyses comparing the contingency table of rodent pests' lifestyle (arboreal, scansorial, fossorial, aquatic) vs. impact (3a) and vs. control methods (3b).

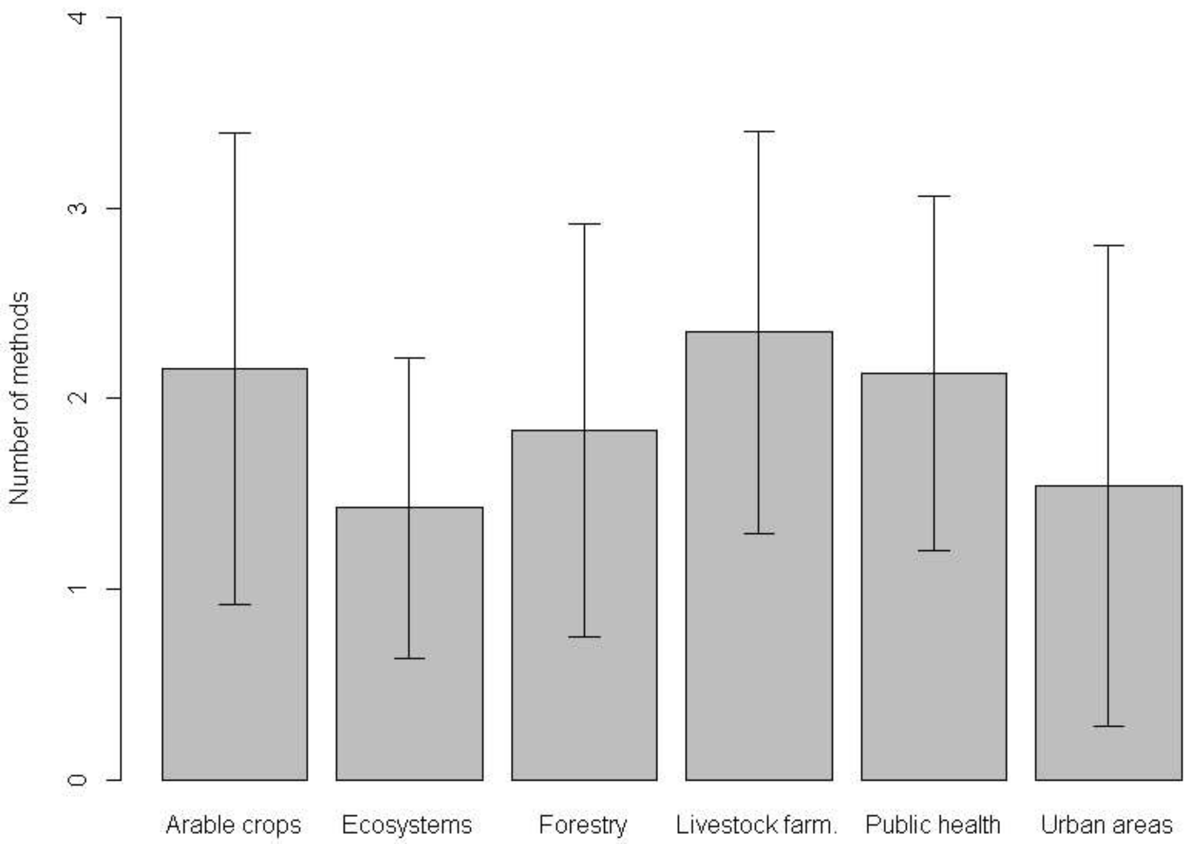

Fig. 4. The mean and standard deviation of the number of methods adopted for controlling rodents for the six main impacts.

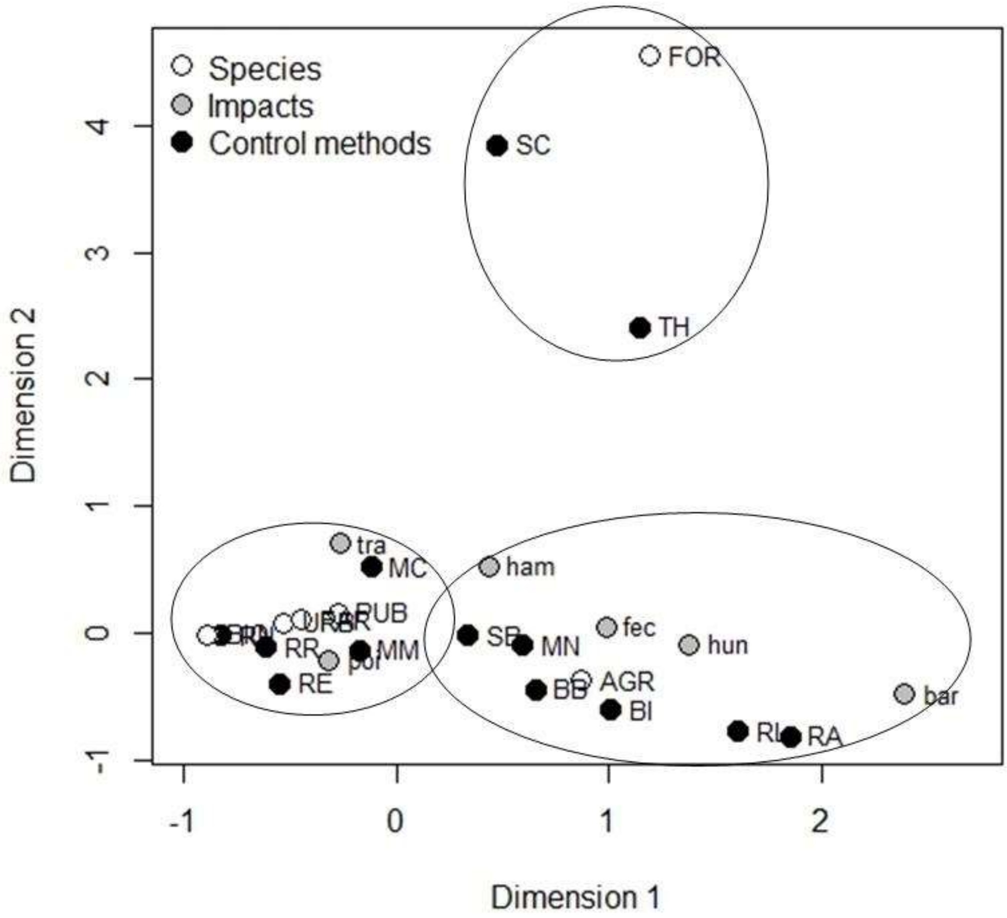

Fig. 5. Pattern of association among categories of three variables (species, impacts and control methods) as resulting from Multiple Correspondence Analysis. Forestry = FOR, arable crops = ARA, ecosystems = ECO, public health = PUB, livestock farming = LIV, urban areas = URB, poisons = poi, traps = tra, habitat management = ham, hunting = hun, barriers = bar, fertility control = fec, *Thomomys* spp. = Th, *Sciurus carolinensis* = Sc, *Spermophilus beecheyi* = Sb, *Mastomys natalensis* = Mn, *Bandicota bengalensis* = Bb, *Bandicota indica* = Bi, *Rattus losea* = Rl, *Rattus argentiventer* = Ra, *Rattus rattus* = Rr, *Rattus norvegicus* = Rn, *Mus musculus* = Mm, *Rattus exulans* = Re, *Myocastor coypus* = Mc

Table 1. Criteria adopted to assess the importance of taxa (mostly species), impacts and control techniques. The aspects they were used for are listed in the second column, while in the third column a description of each criterion is given. As shown, we used all criteria for ranking species (including species divided by lifestyle: arboreal, scansorial, fossorial, aquatic) and control methods, but only the first three for ranking impacts.

	Criterion	Aspects	Description
1	average importance between continents	species, control methods, impacts	the mean of the percentages of studies focusing on the considered species/impact/control method between the six continents
2	maximum importance within a continent	species, control methods, impacts	the maximum value of the percentage of studies focusing on a given species/impact/control method within a continent
3	number of continents	species, control methods, impacts	the number of continents for which there is at least one study focusing on a given species/impact/control method
4	average importance between impacts	species, control methods	the mean of the percentages of studies focusing on the considered species/control method between the six impacts
5	maximum importance within an impact	species, control methods	the maximum value of the percentage of studies focusing on a given species/control method within an impact
6	number of impacts	species, control methods	the number of impacts for which there is at least one study focusing on a given species/control method

Table 2. Ranking of top 15 rodent pest taxa of the world, obtained by adopting the 6 criteria shown in Table 1.

	Continents						Impacts						**Total**	
	Average		Maximum		Number		Average		Maximum		Number			
Pest taxon	%	rank	%	rank	n	rank	%	rank	%	rank	n	rank	**sum of ranks**	**rank**
Rattus rattus	17	1	27	3	6	1	16	2	36	1	5	2	**10**	**1**
Rattus norvegicus	16	2	29	2	6	1	17	1	30	3	5	2	**11**	**2**
Mus musculus	12	3	30	1	6	1	14	3	33	2	6	1	**11**	**2**
Rattus exulans	4	4	17	6	4	4	3	6	13	6	3	6	**32**	**4**
Sciurus carolinensis	2	7	13	7	2	6	3	5	15	4	4	5	**34**	**5**
Spermophilus beecheyi	2	8	10	8	1	16	4	4	9	9	5	4	**49**	**6**
Mastomys natalensis	4	5	25	4	1	16	2	11	5	15	3	6	**57**	**7**
Rattus argentiventer	3	6	17	5	1	16	2	9	10	7	2	17	**60**	**8**
Bandicota bengalensis	1	9	9	9	1	16	2	10	5	14	3	6	**64**	**9**
Thomomys spp.	1	14	7	13	1	16	2	8	10	8	2	17	**76**	**10**
Myocastor coypus	1	12	5	17	3	5	1	18	4	20	3	6	**78**	**11**
Calomys laucha	1	13	8	12	1	16	1	12	9	10	2	17	**80**	**12**
Aplodontia rufa	1	22	4	22	1	16	2	7	14	5	2	17	**89**	**13**
Bandicota indica	1	17	6	15	1	16	1	14	5	16	2	17	**95**	**14**
Cynomys ludovicianus	1	21	4	19	1	16	1	17	2	26	3	6	**105**	**15**

Table 3. Ranking of the most-studied impacts and other topics related to rodent management.

	Continents						Total	
	Average		Maximum		Number			
Impacts	%	rank	%	rank	n	rank	sum of ranks	rank
Arable crops	45	1	86	1	6	1	3	1
Ecosystems	30	2	75	2	6	1	5	2
Urban areas	8	4	15	4	6	1	9	3
Livestock farming	8	3	24	3	4	6	12	4
Public health	7	5	13	6	5	4	15	5
Forestry	6	6	14	5	5	4	15	5
Other topics								
Impact on non-target species	39	1	100	1	4	2	4	1
Resistance	28	2	100	1	5	1	4	1
Test of efficacy	22	3	74	3	4	2	8	3
Behavioural aspects	6	4	17	4	4	2	10	4
Animal welfare	3	5	17	5	1	5	15	5
Impact on humans	2	6	10	6	1	5	17	6

Table 4. Ranking of the control methods used to manage rodent populations at the global level.

	Continents						Impacts						Total	
	Average (%)		Maximum (%)		Number		Average (%)		Maximum (%)		Number			
Methods	%	rank	%	rank	n	rank	%	rank	%	rank	n	rank	sum of ranks	rank
Poisons	44	1	77	1	6	1	50	1	79	1	6	1	6	1
Traps	16	2	20	3	6	1	15	2	29	2	6	1	11	2
Habitat management	16	3	33	2	6	1	12	3	22	3	6	1	13	3
Damage prevention/forecasting	3	7	5	7	5	4	3	4	8	6	6	1	29	4
Barriers	4	5	14	5	4	7	3	5	10	4	4	9	35	5
Repellents (chemical and acoustic)	4	4	12	6	3	9	2	8	9	5	5	6	38	6
Hunting	2	8	5	8	5	4	3	6	7	7	5	6	39	7
Predators and parasites	2	9	4	10	5	4	3	7	4	10	6	1	41	8
Fertility control	1	10	3	11	4	7	2	9	5	8	5	6	51	9
Intervention on ectoparasites/pathogens	3	6	15	4	1	12	1	11	3	11	2	11	55	10
Fumigants and explosives	1	11	3	12	3	9	1	10	4	9	3	10	61	11
Behavioural mechanisms	1	12	4	9	3	9	0	12	1	12	2	11	65	12

Table 5. Analysis of the best fit (linear, quadratic and cubic models) for temporal trends in the impacts studied in the last twenty years

	best fit	*d.f.*	*r square*	*F*	*P level*	*b1*
Arable crops	linear	1,19	0.179	4.14	0.05	-0.88
Ecosystems	linear	1,19	0.282	7.47	0.01	1.30
Forestry	linear	1,19	0.382	11.73	0.003	-0.99
Public health	linear	1,19	0.246	6.19	0.02	0.65

Table 6. Analysis of the best fit (linear, quadratic and cubic models) for relationships between socio-economic indicators (predictor variables, as given by the World Bank; Anonymous 2010b) and the frequency of the impacts studied in the various countries. Abbreviations: GNI: gross net income; PPP: purchasing power parity; R&D: research and development.

Predictor	Dependent	Best fit	R Square	F	df	P level	Constant	b1	b2	b3
Health expenditure per capita (current US$)	Ecosystems	Cubic	0.20	4.50	3, 54	0.007	85.4	-161.2	90.0	-14.0
Health expenditure per capita (current US$)	Forestry	Linear	0.14	8.86	1, 56	0.004	-9.1	6.7		
Health expenditure per capita (current US$)	Arable crops	Cubic	0.27	6.64	3, 54	0.001	-149.2	357.6	-179.0	26.2
Researchers in R&D (per million people)	Forestry	Cubic	0.30	5.53	3, 38	0.003	-179.2	267.0	-121.2	17.4
Population growth (annual %)	Forestry	Linear	0.11	7.07	1, 58	0.010	18.0	-31.7		
Population growth (annual %)	Ecosystems	Quadratic	0.11	3.46	2, 57	0.038	3.1	175.3	-307.5	
Population growth (annual %)	Arable crops	Quadratic	0.14	4.76	2, 57	0.012	39.4	-97.1	265.0	
GNI per capita, PPP (current international $)	Arable crops	Linear	0.15	9.20	1, 54	0.004	133.9	-22.7		
GNI per capita, PPP (current international $)	Ecosystems	Linear	0.11	6.90	1, 54	0.011	-45.4	16.0		
Economically active population in agriculture (number)	Ecosystems	Linear	0.32	27.40	1, 57	0.000	129.9	-18.2		
Economically active population in agriculture (number)	Arable crops	Linear	0.20	14.18	1, 57	0.000	-53.7	16.0		