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Population control of coypu *Myocastor coypus* in Italy compared to eradication in UK: a cost-benefit analysis

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Invasive alien species rank among the world's greatest threats to biodiversity and cause huge economic losses. Eradication is a key management strategy for newly introduced pests, but it is frequently discarded due to the high costs. When populations become established and conflicts increase, policy-makers often resort to permanent population control. However, no cost-benefit analyses have been carried out so far to compare the two alternatives. We present the first cost-benefit analysis by comparing the permanent control campaign of coypu *Myocastor coypus* in Italy with the successful eradication carried out in UK in the 1980s. Data regarding the eradication came from literature, while costs and benefits of control were quantified through a national survey. In Italy, during 1995-2000, the damage amounted to € 11,631,721, control activities cost € 2,614,408, and 220,688 coypu were removed. Control campaigns did not stop the population expansion nor the increase in damage and economic losses at a national scale. However, the efficacy of local campaigns varied among different ecosystems. According to our predictions, the Italian coypu range may expand 2.5-3.3 times, and economic losses may reach € 9-12 millions/year. A comparison between the costs of the successful eradication carried out in East Anglia (€ five million over 11 years) and the permanent control campaign in Italy (€ 14 million over only six years) shows that even very costly eradications, if successful, may have a very positive cost-benefit ratio in the long term.

Key words: biologic invasions, damage, economic losses, impact, invasive alien species, pest

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Invasive alien species rank among the world's greatest threats to biodiversity and cause huge economic losses to human activities (Wilcove et al. 1998, Mack et al. 2000). While the study of the impact of alien species on ecosystems and biodiversity traces back to the 1950s with the classic book by Elton (1958), quantification of the economic losses has been undertaken only recently (Pimentel et al. 2001, Zavaleta 2000, Perrings et al. 2001, Reinardt et al. 2003). In the Unites States alone, invasive alien species annually cost billions of dollars (Pimentel et al. 2000). It is now internationally acknowledged that the best strategy against biologic invasions is based on the following hierarchical approach: 1) prevention of alien species introduction; 2) in case prevention fails, prompt eradication; 3) when eradication is not feasible, consider the suitability of spatial containment and population control (Wittenberg & Cock 2001, Convention on Biological Diversity 2002, Genovesi & Shine 2004). Regarding the two latter recommendations, possible side effects of removal methods and public acceptance should be carefully considered.

Eradication is a key management option for preventing the impact of biological invasions, and in the last century several invasive alien species (e.g. vertebrates, terrestrial invertebrates, plants and marine organisms) have been successfully eradicated throughout the world (Simberloff 2002, Genovesi 2005). Eradication is preferred to control because it is definitive, and it does not require permanent removal efforts and standing costs, but this option is often discarded for political reasons due to the high immediate costs of the operations (Bomford & O'Brien 1995). Policy-makers often do not take action until the populations are already widely established in the wild, and damage becomes unbearable. At this stage, eradication is usually too expensive and technically complex (Bomford & O'Brien 1995, Genovesi 2000), and the viability of a permanent control campaign may be considered. By comparing the present situation with forecasts of future developments, several authors have indirectly suggested that prevention (Leung et al. 2002), eradication (Zavaleta 2000) and control (Anderson et al. 2004) of invasive alien species are cost efficient in the long term compared to no-action. However, no study ever calculated using actual data the trade-off between different management options in terms of biodiversity or long-term economic gain.

We have carried out the first cost-benefit analysis comparison of two different management approaches to pest species, eradication *versus* permanent control campaign, using coypu *Myocastor coypus* as our test case.

The coypu is an aquatic rodent native to South America which was imported for fur farming into Europe, Asia, Africa and North America (Lever 1985, Carter & Leonard 2002). The rodent repeatedly escaped from the farms and/or was released into the wild, and several populations have been established along river banks and in wetlands. In the areas of introduction, the coypu is considered a pest species because of its negative impact on biological diversity, ecosystems, crops and irrigation systems. Coypu can alter natural habitats by feeding on aquatic vegetation (Boorman & Fuller 1981, Reggiani et al. 1993) by destroying nests and by preying on eggs of several aquatic birds, including some endangered species (Scaravelli 2002, Tinarelli 2002). Moreover, the rodent can feed on a variety of crops and weaken riverbanks through its burrowing activity (Foote & Johnson 1993, Carter et al. 1999). For these reasons coypu is on the list of the 100 World's Worst Invasive Alien Species (Invasive Species Specialist Group 2000). Several countries are carrying out permanent population control campaigns (Lever 1985), and the rodent has been successfully eradicated from two small areas in the United States (Carter & Leonard 2002) and from a large area in East Anglia, England (Gosling 1989). The coypu has been imported into Italy since 1928 for fur farming. Since the 1960s, it has been both accidentally and intentionally released into the wild. In the last few decades, the population density and distribution of coypus has increased dramatically (Cocchi & Riga 2001, Bertolino et al. 2005), and its ecological plasticity has facilitated the expansion in both optimal and suboptimal habitats (Scaravelli 2002). The coypu is a mammal with self-sustaining populations, and thus it is automatically protected under the Italian legal framework. Coypu can be harvested year-round for damage prevention, but control operations require the authorisation by provincial authorities or status as protected areas based on a technical opinion of the Italian Wildlife Institute (IWI), and can only be undertaken by authorised operators. The only two control techniques allowed in Italy are live-trapping by means of cage-traps, and direct shooting which should preferably be limited to periods of persistent frosts (Cocchi & Riga 2001). Trapped coypus are either shot or, according to Directive 93/119/CE on animal welfare, euthanised with chloroform at the capture site. In Italy, wildlife is a State property and thus the State, regions or provinces must compensate damage caused by pest species. Carcasses are considered as high risk waste to be burned in incinerators, buried in the ground or used to produce animal feed (before the restrictions introduced following the Foot-and-Mouth outbreak), depending on the decision by the local health authority.

At present, coypu cannot be eradicated in Italy because the population is widespread and well established and thus, the most common management policies are permanent control campaigns carried out locally in response to social pressures. In the attempt of supporting and coordinating local population containment operations, in 2001 the IWI produced general guidelines for the control of the species (Cocchi & Riga 2001). A sound application of these guidelines would require a clear understanding of the efficacy, costs and benefits of each management option, but the available literature does not provide such data. Our purpose is to provide a cost-benefit analysis of permanent population control and eradication. For this purpose, at first we assess the total economic losses caused by coypu (cost of control, damage to agriculture and to the irrigation systems) in Italy during 1995-2000, and we evaluate the positive effect of control in terms of population decrease and damage containment. Then, we compare these data with costs and benefits of the successful eradication campaign carried out in East Anglia in the 1980s (Gosling 1989). In order to provide a more general overview of the results of the ongoing permanent control campaign, we also forecast a future scenario in terms of both population range and economic losses. Finally, we discuss the possible variations in the cost-efficiency of eradication and permanent control campaigns in different ecological settings.

Material and methods

Our study is based on a national survey conducted in the following different steps: 1) identification of all administrations compensating damage due to coypu and/or carrying out control operations during 1995-2000; 2) posting of questionnaires to all departments responsible for damage compensation and/or pest control; 3) telephonic reminders to the administrations that did not respond to the questionnaires. We contacted by telephone all the public administrations within the national coypu range as defined by Cocchi & Riga (1999; Fig. 1) and updated data to the present situation by using information provided by the relevant authorities. These were 15 regional game departments, 74 provincial game departments, 15 regional park departments, 47 parks and protected areas, 2 water magistracy offices, 3 super-regional hydraulic offices, 2 civil engineers, 15 regional basin offices, 16 provincial hydraulic offices and 78 land reclamation authorities. To maximise the details of our survey, we additionally contacted several minor authorities (18 local hunting units, 10 municipalities and 2 mountain communities) delegated by the above-mentioned administrations for local management operations. In total, we contacted 297 institutions.

Figure 1. Coypu distribution (■) in Italy according to Cocchi & Riga (1999).

Two different types of questionnaires (Q.I and Q.II) were used. Q.I, containing 60 questions regarding damage caused by coypu to agriculture and information about control operations, was sent to all departments responsible for wildlife management (e.g. the regional and provincial wildlife departments and park departments). Q.II, focusing on the economic losses caused by damage to the irrigation systems, was sent to all departments re-

Table 1. Survey of economic losses caused by coypu in Italy synthesising the questions included in Questionnaires I (A) and II (B). Each question required a separate answer for each year during 1995-2000.

A) Questions included in questionnaire I - damage to agriculture, prevention and management operations. The questions are divided by subject (first row), and for each topic data were required as follows: Area (^{A}), Cost (^{C}), Number (^{N}) and Type (^{T}).

Damage to agriculture and Prevention	Control operations	Long-lasting materials	Other materials	Employed/Unemployed operators
Damage estimated by experts ^{C}	Coypus trapped ^{N}	Traps $^{C, N, T}$	Anaesthetic $^{C, T}$	Veterinary services ^{C}
Damage compensated ^{C}	Coypus shot ^{N}	Night/traps ^{N}	Ammunition ^{C}	Employed operators ^{N}
Damage due to wildlife ^{C}	Control operations ^{A}	Traps used by operators ^{N}	Plastic bags for cadavers ^{C}	Hours of paid work $^{C, N}$
Prevention $^{A, C, T}$		Traps used by volunteers ^{N}	Mono-use gloves ^{C}	Unemployed operators ^{N}
		Euthanasia-kit $^{C, N}$	Bait for traps $^{C, N, T}$	Hours of non paid work $^{C, N}$
		Freezers $^{C, N}$	Carcasses disposal $^{C, T}$	Compensation for unemployed ^{C}
		Electricity for freezers ^{C}	Rent of utility rooms ^{C}	Training courses ^{C}
		Cages for transport $^{C, N}$		
		Cars used *$^{C, N, T}$		
		Km covered *^{N}		
		Boats used *^{N}		
		Boats maintenance ^{C}		
		Rafts used *$^{C, N}$		

* Specifically used for coypu control activities.

B) Questions included in questionnaire II - damage to irrigation systems.

Total cost of routine management of pensile embankments (not only for damage due to coypu).
Length of pensile embankments (km of right and left side) interested by the above-mentioned routine management.
Estimated incidence (%) of the damage caused by coypus on the cost for the above-mentioned routine management.
Cost of specific operations on riverbanks due to emergency situations caused by coypus.
Length of riverbanks (km) interested by the above-mentioned emergency operation.
Economic losses due to flooding specifically caused by coypus digging activity (e.g. collapse of riverbanks, blow-outs and infiltration).

sponsible for water management (e.g. drainage authorities). Table 1 synthesises the questions included in the two questionnaires. In total, 130 questionnaires (52 Q.I and 78 Q.II) were mailed. The use of questionnaires as a means of collecting data in ecology has been recently criticised by White et al. (2005). However, our survey followed most of the recommendations listed by these authors. Moreover, unlike other studies which indirectly attempted to estimate the presumptive costs caused by alien species (Pimentel et al. 2000), our survey only considers the expenses actually incurred by the local authorities.

Data analyses

The cost of trapping was calculated by summing up the costs of traps, cages for transport, kits for euthanasia ($\bar{x}$ = € 66/kit), anaesthetics, ammunition (when used for killing trapped animals), plastic gloves and bags, use of cars and boats, rafts, baits, staff salary, volunteer reimbursement and training courses for volunteers. Cost of shooting was calculated by summing up the cost of weapons, ammunition, gasoline for cars, boat maintenance, staff salary, reimbursements and training courses for volunteers. When an administration used both control techniques and was unable to distinguish between the respective costs, we divided the total costs by the proportions of coypu trapped and shot. The cost of carcass disposal was calculated by summing up the costs of freezer purchase and functioning, rental of rooms for storing carcasses, cost of plastic bags and gloves, and transport in connection with disposal of carcasses.

In some cases, the missing costs for a few specific items were extrapolated by using the average corresponding values provided by the other institutions. In these cases we always re-contacted the concerned administrations in order to validate the extrapolated values. We thus calculated missing annual average costs of cage-traps, kits for euthanasia, freezers, gasoline, boats, rafts, personnel salary, and the missing average costs per coypu of anaesthetics, bullets, gloves, plastic bags or incineration of carcasses. We applied the IWI administration procedures to estimate the cost of gasoline and electricity and to calculate amortisation periods. We used a reimbursement value of 1/5 of the annual price per litre of gasoline per km (Agip Petrol), and a cost of € 0.20/KW for the electricity for freezers. We considered a 12-years amortisation period for freezer purchase and an 8-years period for cage-traps, kits for euthanasia, rafts and metal nets.

Finally, we updated to year 2000 currency values all the Italian costs by using the Italian Retail Price Index (ISTAT 2004), and all the costs of the eradication in East Anglia by using the British Retail Price Index (Office for National Statistics 2004). The British Index is comparable with the Italian Index calculated from the variation of retail prices to families (P. Garoglio, pers. comm.).

All statistical analyses were performed by using the SPSS statistical software (12.0). We used the GLM procedure to test for the effect of control operations on the damage rate of increase by treating this parameter as the dependent variable and the management approach (control or no control) as a factor. Assumptions on data distribution and equality of variance used were tested whenever required.

Effect of control and climate on population trends

Control operations aim at containing the population rate of increase and the amount of damage. Direct density estimates were not available in Italy and thus, in order to assess the effect of control on coypu population, we calculated indexes of population trends. In accordance with Gosling et al. (1988), in most cases the number of coypu removed approximately reflects the population density. Hence, we calculated an index of population trend as the average annual number of coypu removed per unit area (coypu removed/km^2/year), and an index of removal effort as the average annual cost of control (trapping and shooting) per unit area (€/km^2/year).

Gosling (1981) showed that cold weather influences coypu body condition, reproductive parameters and consequently population size. We tested for the effect of winter frosts on coypu population trends in a sample of the Italian provinces, located in the northernmost portion of the coypu range, for which data on both coypu management and daily temperatures were available. We used the annual number of days with temperature $\leq 0°C$ as an index of winter harshness.

Potential range expansion

In order to predict the potential future range expansion, we considered the suitable areas not yet colonised by coypu by using the habitat suitability model developed by Ottaviani (2004) for the National Ecological Network (Boitani et al. 2002). The model was produced by integrating into a GIS the principal environmental variables associated with coypu presence. Environmental parameters were selected from the Faunal Database REN and included possible and optimal altitude intervals, the species' environmental preferences with respect to the 44 land-use classes of Corine land cover III and the influence of the road network on the habitat suitability model. Information was processed by overlapping a digital terrain model (DTM) in raster format (1 pixel = 75 m), a land-use map (1:100,000), a road network map (1:250,000) and a hydro graphic map (1:250,000). The final model partitioned the entire Italian territory into high, medium, low and unsuitable habitats for coypu.

Results

Virtually all administrations paying for damage to agriculture and/or conducting population control replied to the questionnaires (Q.I response rate = 97%). For some key information, e.g. the annual number of coypu removed, the response rate reached 100%. Some administrations suffering damage to the irrigation systems might not have been covered by the survey since the response rate for Q.II was 71%, and several offices did not respond to further solicitations.

Total economic losses

About 80% of the contacted institutions, distributed in 15 of the 20 Italian regions, reported the presence of coypu. During 1995-2000, the number of provinces reporting coypu presence increased from 57 to 61. The number of institutions paying for damage to riverbanks, running control operations and compensating damage to agriculture increased by 38, 429 and 650%, respectively. In Table 2 (A), we present the annual, average and total losses caused by coypu in Italy. These values shall be considered as conservative because not all administrations fully compensated the damage to agriculture or provided the required data on damage to riverbanks, and management operations was partly conducted by landowners and volunteers at their own expenses.

Table 2. Coypu management in Italy from 1995 to 2000 expressed as economic losses (in €), number of coypu removed and details about management operations. A) includes compensated damage to agriculture ([1]), expenses for riverbank readjustment ([2]) and cost of control operations (i.e. trapping, shooting and carcass disposal ([3]). B) gives number of coypu removed through trapping and direct shooting, and C) the number of traps purchased and operators involved in control.

	Year							
	1995	1996	1997	1998	1999	2000	Average	Total
A) Costs (€)								
Agriculture [1]	48,962	138,061	140,221	131,914	205,773	288,206	158,856	935,138
Riverbanks [2]	673,526	781,588	1,641,168	2,141,616	2,676,694	2,781,992	1,782,764	10,696,583
Management [3]	248,136	369,596	294,140	467,733	531,216	703,588	435,735	2,614,408
Total costs	970,624	1,289,245	2,075,529	2,741,263	3,413,683	3,773,786	2,377,355	14,246,129
B) Coypus removed								
No. trapped	8,700	24,654	7,435	19,870	25,293	32,717	19,778	118,669
No. shot	840	5,156	16,305	22,518	25,579	31,621	17,003	102,019
Total removed	9,540	29,810	23,740	42,388	50,872	64,338	36,781	220,688
C) Traps and staff								
No. of purchased traps *	1,260	1,827	2,134	3,628	4,426	7,155	3,405	20,430
No. of authorised operators	241	237	464	1,139	1,176	1,479	789	

* The number of traps actually in use was higher than the number of traps purchased from 1995 to 2000.

Damage to agriculture

During 1995-2000, an average of € 158,856 ± 80,624 (mean ± SD) was spent every year on compensating damage to agriculture. The most affected crops were rice *Oryza sativa*, sugar beets *Beta vulgaris*, carrots *Daucus carota* and chicory *Cichorium intybus*. The damage caused by coypu made up only a small proportion of the total amount compensated for wildlife damage ($\bar{x}$ = € 3,197,895 ± 961,551/ year). However, the proportion of coypu damage in respect to the total wildlife damage increased from 3 to 8% over six years.

Damage to riverbanks

The damage to the drainage systems was > 10 times higher than the losses to agriculture, and accounted for 75% of the total expenses recorded in the six years (see Table 2A). Several types of damage were reported: the drilling of pensile embankments caused infiltration, blow-outs, landslides, collapses of docks, sudden drainage of wet protected areas, obstruction of irrigation canals and collapse of rice-field banks. In addition, we have received reports of cases of agricultural machinery sinking into burrows, drainage of lakes in public parks in order to remove the coypu, control operations carried out in sewerage systems and several car accidents. However, these events were not economically quantified and were not included in our estimates. Moreover, in two cases river banks, weakened by intensive coypu digging, collapsed and caused floods that devastated villages and croplands. These floods caused exceptional losses that have been quantified at € 22,724,103. This amount was also not included in our analyses because inadequate bank maintenance and intense rainfall were concomitant causes of the floods.

Prevention

Very few administrations applied prevention methods to agriculture. Electrical and/or mechanical fences are seldom used to prevent recurrent and economically relevant losses to particularly important crops. By contrast, the use of mechanical systems (wire mesh) for protection of embankments is slowly increasing (Cocchi & Properzi 2003).

Management

A total of 220,688 coypus were removed during 1995-2000; 54% through trapping and 46% through direct shooting (see Table 2B and C). The total annual number of coypus removed increased (average increase rate: $\bar{x}$ = 0.54 ± 1.47/ year, N = 75) linearly (linear regression: R^2 = 0.93, $F_{5,6}$ = 51.17, P = 0.002), as did the total costs of management ($\bar{x}$ = 0.79 ± 6.60/year, N = 77; R^2 = 0.87, $F_{5,6}$ = 26.80, P = 0.007). The largest part (60%) of the overall cost of control was related to trapping activities, while direct shooting and carcass disposal accounted for 32 and 8%, respectively. In some cases, the competent sanitary authority granted the permission to bury carcasses directly in the ground, thus avoiding the high costs of incineration ($\bar{x}$ = € 3.21/ coypu plus $\bar{x}$ = € 101.00/call for transport) or producing animal feed (€ 21.00/coypu).

Efficacy of control

Changes in population trends

In the provinces (N = 11) that carried out control operations for five to six years, the index of population trend was not limited by the increase in control effort (Table 3). Indeed, removal effort was positively correlated with the index of population trend, and this relationship was still significant in five cases when considering each province separately. The index of population trend was not affected by the index of winter harshness ($\bar{x}$ = 40.11 ± 16.04) in the three sample provinces (Pearson correlation: Ferrara: R = -0.01, N = 5, P = 0.99; Ravenna: R = 0.47, N = 5, P = 0.425 and Venice: R = 0.83, N = 5, P = 0.086).

Reduction of damage

During the survey years, two provinces suffering severe losses to agriculture due to coypu (Rovigo: $\bar{x}$ = € 39,675/year and Padova: $\bar{x}$ = € 32,041/year) had to revise their management strategies solely for bureaucratic reasons, and they drastically reduced their compensation for damage. These provinces were excluded from our correlation analyses between damage and population trends. During 1995-2000, the compensation paid for damage to agriculture per km^2 constantly increased (linear regression: R^2 = 0.15, $F_{82,83}$ = 13.69, P = < 0.001; average increase € 1.74/ year ± 5.52, N = 62). We expected a reduction in damage in response to control operations but, on the contrary, we found that damage increased both for provinces running control operations (R = 0.24, N = 52, P = 0.043) and for provinces that did not (R = 0.36, N = 31, P = 0.024). Furthermore, provinces carrying out control operations suffered greater economic losses than provinces that did not (Mann Whitney U test: Z = -2.06, N = 83, P = 0.039). Three years after the start of control operations the same provinces paid for damage compensation on average 81% more than the year before control started (Wilcoxon W test: Z = -2.20, N = 6, P = 0.028).

As control intensity varied greatly among provinces, we tested for correlation between this parameter and the amount of damage. In general, the number of coypus killed per km^2 was positively correlated with estimated damage (Spearman correlation: r = 0.30, N = 52, P = 0.017). Provinces conducting non-intensive control (≤ 2 coypus removed/km^2) did not exhibit a similar trend (r = 0.03, N = 32, P = 0.430), whereas the correlation was significant when > 2 coypu per km^2 were removed (r = 0.54, N = 20, P = 0.007; Fig. 2). Accordingly, provinces running intensive control suffered greater damage (Z = -2.00, P = 0.045). The number of years that the province had carried out control operations did not affect the damage to agriculture (r = -0.01, N = 52, P = 0.965).

Damage to drainage systems increased during the survey period (increase rate: 0 = 0.34 ± 1.49/year; linear regression: R^2 = 0.02, $F_{216, 217}$ = 5.16, P = 0.024). The increment was still highly significant when considering only the institutions that compen-

Table 3. Efficacy of control operations on coypu population trends in Italy. The results of correlation tests between the index of removal effort and the index of population trend for the 11 provinces that conducted control operations for five to six years. Significant P values are evidenced in italics, and * indicates Spearman correlation coefficient, and **Pearson correlation coefficient.

Province	Correlation coefficient	P	No. of years
Bologna	0.54*	0.266	6
Cremona	0.93*	*0.008*	6
Ferrara	1*	*0.000*	5
Padova	1*	*0.000*	5
Mantova	0.43*	0.397	6
Modena	0.60*	0.285	5
Perugia	0.71*	0.111	6
Ravenna	0.90*	*0.037*	5
Rovigo	0.20*	0.704	6
Venice	0.87*	0.058	5
Vicenza	1*	*0.000*	6
Total	0.94**	*0.002*	6

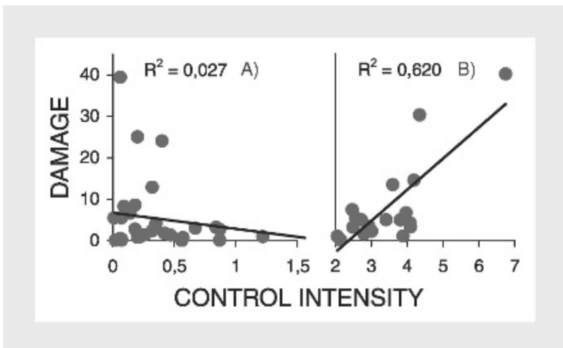

Figure 2. Effect of control intensity (i.e. number of coypus removed/km^2) on damage to agriculture (in €/km^2) in Italy during 1995-2000. If the control was non-intensive (i.e. ≤ 2 coypus removed/km^2), the number of coypus removed did not affect damage to agriculture (A), whereas if the control was intensive (i.e. > 2 coypus removed/km^2), the two variables were positively correlated (B). Note that in A) the highest value reported for damage belongs to a province which did not start the control operation until the damage became great.

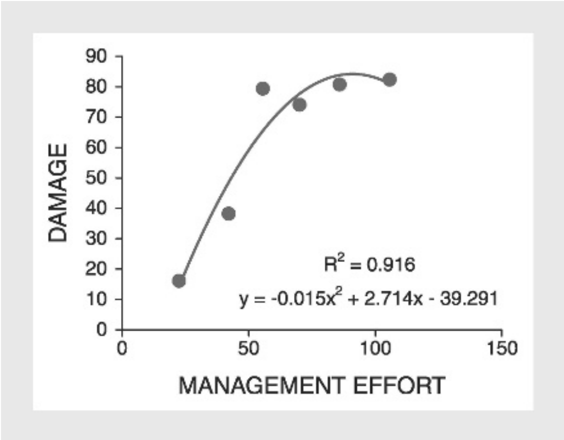

Figure 3. Efficacy of management efforts (in €/km²/year) on the reduction of damage (in €/km²/year) caused by coypus in Italy during 1995-2000. Management effort was calculated as the average annual cumulative costs of management (including trapping, shooting and carcass disposal). Damage was calculated as the average annual economic losses caused by coypus (including damage to agriculture and irrigation systems/km²).

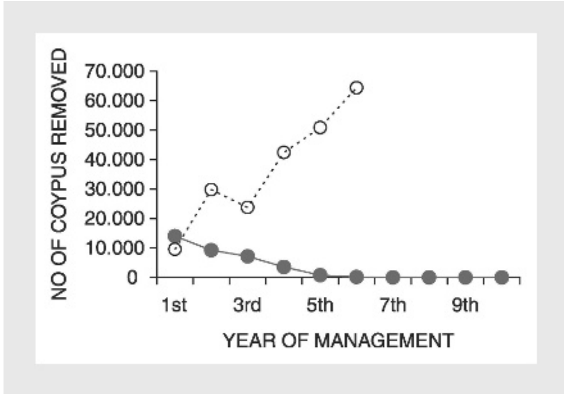

Figure 4. Comparison between total number of coypus removed (per year) in the successful eradication campaign in East Anglia during 1981-1992 (●, —), and in the control operations in Italy during 1995-2000 (○, - - - -).

sated the damage for six consecutive years (Kendall's W: $W_{5,85} = 0.06$, $P < 0.001$). In no case did we find a significant negative correlation between damage and number of removed coypu.

Damage trend

During the years covered by the survey, the damage to agriculture increased faster for provinces conducting control operations than for provinces that did not (GLM: $F_{2,83} = 5.54$, $P = 0.006$). The intensity of control did not affect the rate of increase of damage, which was similar during 1998-2000 for provinces removing > 2 and < 2 coypus per km², respectively (GLM: $F_{2,47} = 2.10$, $P = 0.134$).

Economic cost-benefit evaluation

During the surveyed period, management effort was positively correlated with the amount of damage ($r = 0.94$, $N = 6$, $P = 0.002$). However, this relationship was significantly better represented by a convex curve ($F = 16.39$, $P = 0.024$; Fig. 3). The cost of removing a single coypu was higher when adopting trapping techniques (€ 13.25/coypu; N = 118) than direct shooting (€ 8.21/coypu; N = 102).

Permanent control campaign in Italy compared to eradication in East Anglia

The number of coypus removed in the first year of the eradication campaign in the UK was lower than the number of animals killed in Italy in the first year of survey (9,540 and 14,007 respectively; Fig. 4). Thereafter, the number of coypus removed in Italy increased dramatically, and in year 2000 it had doubled the number of animals removed in the entire 11 years of eradication campaign in the UK (Table 4). In year 2000 alone, the amount paid in Italy covered 75% of the overall costs of the eradication in East Anglia. In relation to the ongoing expansion of the coypu range, we estimated the potential consequent increase in economic losses. For this purpose we used the habitat suitability model (Ottaviani 2004), and we compared the size of the

Table 4. Comparison between the total cost of the successful 11-year eradication campaign in East Anglia (Gosling & Baker 1989, S. Baker, pers. comm.) and the costs of the permanent control campaign in Italy during the last surveyed year (2000). In the two columns to the right future costs are predicted (damage to agriculture, irrigation systems and total costs of management) and the number of coypus removed, based on two scenarios: best case (minimum predicted expansion) and worst case (maximum predicted expansion).

	East Anglia (11 years: 1981-1992)	Italy (1 year-2000)	Predicted future costs and removal efforts	
			Minimum expansion	Maximum expansion
Area-km²	5,379*	41,515**	× 2.5	× 3.3
No. of removed coypus	34,822	64,338	160,845/year	212,315/year
Total costs	€ 5,000,000	€ 3,773,786	€ 9,434,465/year	€ 12,453,494/year

* Total area covered by the Coypu Control Organization (Morton et al. 1978)
** Total area interested by coypu control operations in Italy in year 1999-2000; note that the Italian coypu range was 68,599 km².

present range with the size of the suitable habitat not yet colonised by coypu. We considered two different scenarios for the future range expansion: the best-case scenario (coypu will colonise only optimal habitats) and the worst-case scenario (coypu will colonise optimal and suboptimal habitats). According to the best-case scenario, the present range will increase 2.5 times, whereas in the worst-case scenario, it will increase 3.3 times. We multiplied the cost of management in year 2000 for each of the two indices of range expansion, and similarly we calculated the potential increase in the number of coypus removed (see Table 4). Given the high level of uncertainty of these predictions, we stress that these numbers provide only an order-of-magnitude estimate of future economic losses and population expansion in Italy.

Discussion

Our survey clearly shows that the permanent coypu control campaign that goes on in Italy is not cost efficient. Indeed, at national level the applied control effort neither effectively contains the ongoing rapid population expansion nor the dramatic increase in economic losses. During 1995-2000, despite that € 2,614,408 were spent on removing 220,688 coypus, the overall damage caused by the rodent reached a total of € 11,631,721, most of which (92%) inflicted on irrigation systems.

After several decades of passive acceptance of the coypu, during 1995-2000 an increasing number of institutions started control activities, compensated for losses to agriculture and claimed damage to the irrigation systems. The number of operators officially involved in control plans increased from 241 to 1,479, and the number of traps purchased annually rose from 1,260 to 7,155. However, control operations were planned according to the availability of funds and rarely according to a scientific evaluation of the achievable results. In some cases control was interrupted for bureaucratic reasons, although Micol (1990) clearly showed that a suspension of the operations can seriously undermine the effects of management. In addition, the efficacy of control operations was evaluated only rarely.

At national scale, the coypu removal rate did not exceed the population rate of increase. However, the average control intensity in Italy was low (1.2 coypu removed/year/km^2) compared to the control applied in East Anglia ($\bar{x}$ = 2.6 coypu removed/km^2 in 1981), where trapping intensity was the most important factor in explaining variation in population reduction rate among years (Morton et al. 1978, Gosling & Baker 1989). It is important to note that non-intense management operations may have destructuring effects on coypu populations, which might in turn reduce the efficacy of the operation itself. In fact, the preferential capture of adult males may increase the proportion of juveniles and females in the population, favouring a higher recruitment rate and immigration, and creating optimal conditions for a subsequent population increase (Cocchi & Riga 2001, Gosling & Baker 1989, Velatta & Ragni 1991, Riga & Cocchi 1997).

As for reduction of damage, the applied control effort was unable to reduce significantly the economic losses caused by coypu to agriculture and to the irrigation systems, although our results suggested the possibility that damage may eventually stabilise (see Fig. 3). Unexpectedly, the damage to agriculture was higher and had a more rapid growth rate in provinces conducting control operations than in the provinces that did not. This simply reflects the fact that provinces started control plans only when the economic losses were too high to be ignored. Similarly, the intensity of control was positively correlated with damage to agriculture, but only above a certain threshold in control effort. This suggests that the control effort that Italian administrations were able to undertake reduced both population growth rates and damage when population density was low, but was not effective once coypu reached high densities.

The total cost incurred during the six surveyed years (> € 14 millions) already greatly exceeds the cost of the successful 11-year eradication campaign in East Anglia (~ € 5 millions), which was considered very expensive at the time. The success of the English eradication project was achieved through a careful planning based on a 2-year trial and by continuous programme re-evaluations (Gosling & Baker 1987, 1989). Twenty-four English trappers alone managed to reduce the number of coypus trapped from 14,000 to zero in only nine years (see Fig. 4). Conversely, an average of 789 operators/year and > 3 million trap nights did not succeed in containing the coypu population rate of increase nor the damage in Italy. In addition, as the habitat in Italy suitable for coypu is 2.5-3.3 times larger than the present range, the species is likely to continue to expand in the mid-term, and the national economic losses may increase up to € 9-12 million/year. Considering also that in many areas the population density is far from saturation, the cost of management may increase far beyond our predictions.

The results we present refer to the national scale, but it is important to emphasise that some local well-planned control programmes actually succeeded in achieving significant results in terms of population containment (Bertolino et al. 2005), reduction of economic losses (Velatta & Ragni 1991, F. Velatta, pers. comm.) and preservation of biodiversity (Bertolino et al. 2005). However, the success of these local management operations is dependent on a careful planning which takes into account the particular ecological settings of the area.

For instance, two similar removal efforts addressed, respectively, to an isolated population confined to a lake and to a population inhabiting a wetland interconnected to the Po River delta, led to opposite results. While the control programme carried out in Lake Trasimeno (Velatta & Ragni 1991) triggered a significant population collapse which eventually ended with the complete eradication of the coypu, the one carried out in the area with a high immigration rate had no effect on population dynamic or size (Cocchi & Riga 2001). Since coypu in Italy occupy a continuous range interconnected by an entangled network of water courses, this example stresses the importance of organising management operations at the appropriate spatial scale in order to limit the counteracting effects of immigration (Reeves & Usher 1989, Tongiorgi et al. 1998).

In addition, the timing of management operations may influence their success. Indeed, the eradication in East Anglia was strongly facilitated by a sequence of harsh winters that reduced breeding success and juvenile survival (Gosling & Baker 1987). Our survey did not consider seasonal variations in the number of coypu trapped and thus, failed to detect an influence of the weather on coypu population trends. However, Reggiani et al. (1995) detected a short-term limiting effect of harsh weather on demographic parameters in central Italy, suggesting that control operations might be more cost efficient during cold winters even in the mild climate of the Mediterranean basin.

Finally, the success of management operations in terms of preservation of biodiversity might be more easily achieved when the operations are focused on particularly vulnerable areas. Tinarelli (2002) proved that the great-crested grebe *Podiceps cristatus*, the little-grebe *Tachybaptus ruficollis* and the small hybrid-tern *Chlidonias hybridus* preferably breed in areas where coypu are controlled. Bertolino et al. (2005) showed that coypu control allowed the recovery of the yellow water-lily *Nuphar lutea* which was removed by coypu feeding activities. D'Antoni et al. (2002) found higher richness in natural vegetation species where coypu were absent. However, the assessment of coypu damage in different ecosystems is complex, empirical evidence is scarce and scientific data are urgently needed (Boorman & Fuller 1981).

Through the comparison between the successful eradication in East Anglia and the high costs of permanent control in Italy, this case study shows that a huge investment in an eradication campaign, when feasible, may turn into a profitable saving in the long term. The great economic and ecological consequences of the Italian approach to coypu management compared to the successful East Anglian eradication campaign may be used as a persuasive example for policy-makers whenever pest species invasions occur. In this regard, the case of Spain is worth mentioning. The Spanish coypu population is limited to a few hundred individuals distributed in a small number of colonies in the northern part of the country (Herrero & Couto 2002, Echegaray & Hernando 2003). Even though the total removal of the species does not appear particularly complex at this stage, no eradication plan has been considered so far by the competent authorities. However, in light of the suitability of the habitat and of the climatic conditions, the coypu is expected to increase its range with consequences similar to those we are experiencing in Italy.

Recommendations

Based on the alarming outcomes of our study, we recommend researchers and managers dealing with recent introductions of invasive alien species to select the best management alternative through a careful literature review of the long-term costs and benefits of different approaches in different ecological and economical settings. Thereafter, we recommend researchers to rapidly publish their results in the form of cost-benefit analyses, including both economical and ecological issues, in order to assist policy-makers in identifying the most appropriate response to biological invasions in other contexts.

In addition, we provide the following general recommendations for a better management of invasive alien species: 1) promptly eradicate in isolated and newly colonised areas whenever it is technically feasible; 2) plan control policies at an adequate, biologically sound spatial scale taking into account the potential counteracting effects of immigration; 3) intensify control efforts in the most vulnerable areas in terms of biodiversity and human activities; 4) identify the limiting factors for the species and focus management efforts accordingly; 5) always evaluate the efficacy of management operations and adjust future plans accordingly; 6) support research on effective control and prevention methods in different ecosystems.

At last, we suggest exploring the possibility to use pest species coming from permanent control campaigns as a source of income. For instance, in areas with intense population control activities, the carcasses of wild coypus might be utilised in the leather tanning industry in addition to the farmed conspecifics, to reduce the high costs due to invasive alien species.

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