

Invasive mammals

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Summary

Every region of the world is concerned by potential mammal invasions, as humans are already present on all the world's land masses. All these invasions are a result of species introductions by humans for one reason or another. The authors briefly review the known movements and observed consequences of mammal-related invasions. They take examples from all five continents, as well as from a few island systems. The ancient introduction of game species, and later of domestic species, has been followed more recently by movements of commercial species. We are now seeing the emergence of what are known as entertainment species. In a number of cases, such introductions have led to the establishment of new epidemiological cycles that previously might never have been thought possible. According to current indicators, this phenomenon is not on the wane.

Keywords

Continents – Invasive species – Islands – Island ecology – Mammals.

Introduction

The history of the human species is probably difficult to separate from that of the species that have accompanied it since humans evolved in Africa in the distant past. There is a long list of species that can be classified in numerous ways, including prey species, dangerous species, companion animals, animals endowed with spiritual or symbolic meaning, parasites and micro-organisms. Mammals are doubtless a special group among this varied collection of animals, as they include humans. It is becoming increasingly clear that humans have been modifying the ranges of many species for a very long time. This article therefore provides a brief overview of the known movements and observed consequences of mammal-related invasions. As the authors do not set out to be exhaustive, only a few examples are discussed in detail, not without a modicum of subjectivity. They have chosen to subdivide them geographically, by continent, starting with the one inhabited for the longest time, continuing with those occupied more recently and finishing with islands. The quality of the available information varies. Some ancient movements are still hypothetical for lack of

in-depth studies. Much additional research would be needed to refine the data and interpretations.

Lever (15) and Long (16) provide a general overview of the subject. Numerous other studies concentrate either on a smaller geographical area or on a species group. References are cited as the article unfolds.

Africa

Biogeographers divide the African continent – the continent of origin of the human species and the starting point of human expansion – into two sections separated by the Sahara desert. In zoogeographical terms, the area north of the Sahara corresponds to the Palearctic Region and the area south of the Sahara, to the Ethiopian Region. Kingdon (14) has written one of the latest compendiums of African mammals, pending the forthcoming publication of his atlas of African mammals. Existing data seem to indicate that, apart from domestic species, few mammal species exotic to the African continent became established during ancient times. The case of domestic species is not discussed in

depth in this article. The invasion of the African continent by the bovine species, both non-humped cattle and zebu, is described in another article in this volume (22). The non-domestic species that did become established are found in the extreme north and south of the African continent, that is to say, the shores of the Mediterranean Sea and the Cape of Good Hope region. There are red deer (*Cervus elaphus*) and Asian buffalo (*Bubalus bubalis*) in the north, and fallow deer (*Dama dama*), Himalayan tahr (*Hemitragus jemlahicus*) and Eastern grey squirrels (*Sciurus carolinensis*) in the south. The history of the introduction of each species is different (10). Around the Cape, animals were either introduced or escaped from captivity in recent times, roughly since the early 20th Century. In the north, the history is more complex and goes further back in time. The deer of the oak forests along the border between Algeria and Tunisia are the only African cervids to have lived in the wild for several millennia. Recent data from molecular phylogenetic analyses suggest, or at least do not preclude, a possible ancient introduction via the Tyrrhenian Islands (Corsica and Sardinia), into which the red deer had itself been introduced (25). The Asian buffalo (or water buffalo), with a single herd living in the Ichkeul National Park in northern Tunisia, is a remnant of age-old trading between Africa and Asia at a time when the Middle East was not so arid.

The coypu or swamp beaver (*Myocastor coypus*) (Fig. 1), a large South American amphibious rodent, was introduced into East Africa more recently, and the anthropophilic Asian musk shrew or Asian house shrew (*Suncus murinus*) is an ancient introduction via the African coast ports of the Indian Ocean (11).

On the whole, these species do not seem to pose any particular problems, even though the tahr population is



Fig. 1
Coypu (*Myocastor coypus*) in captivity

The coypu is a South American rodent that was introduced widely around the world for fur farming and escaped from captivity
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kept under control in the Cape region and the musk shrew potentially contributes to the epidemiological cycles of various micro-organisms (15, 16). However, no contemporary summary is available on the subject as it relates to the African continent as a whole.

Europe

A recent review summarises knowledge of mammal introductions into Europe (7). It lists all the introductions that have taken place since the year 1500 in the 43 countries and nine island systems that make up the Europe region. It includes no fewer than 88 introduced species, 64 exotic to Europe and 20 specific to one subregion of the continent but introduced into another. In a further four cases it is unclear whether or not they are indigenous populations. Not all have founded a line. Only 33 of the exotic species appear to have become established.

However, as practically all domestic mammal species in Europe were introduced (their original areas of domestication being outside Europe, very often in the Near East), we should perhaps also look at events in the invasion process that took place long before 1500. When we do this, the history of introduction becomes very long and rather complex. The Mediterranean islands provide evidence of past stages in this invasion process, with the mountain sheep, the mouflon (*Ovis gmelini*), still present in Cyprus, Sardinia and Corsica, or the wild goat (*Capra aegagrus*) present in Crete and on a few other eastern Mediterranean islands (2, 18). Both are cases of animals undergoing domestication that escaped several thousand years ago and returned to the wild, so providing evidence of a stage in the process. Moreover, the history of the establishment of mammal populations in the Mediterranean islands since the early Neolithic period until the present day provides an excellent model for studying the impact of human activities on isolated mammal populations that were established during the Tertiary era. These populations were confronted with the arrival of humans and their associated invasive species, whether commensal species, game species or species in the process of domestication (18).

The authors do not review all these species but cite a few significant examples of major past and contemporary stages in the invasion process. The most ancient introductions of wild species include the house mouse (*Mus musculus*) and the black rat (*Rattus rattus*) (Fig. 2), both originating from Asia. Two other species also have a very long history but, unlike the house mouse and black rat, they were introduced deliberately. They are the European rabbit (*Oryctolagus cuniculus*), which probably originated from the Iberian Peninsula, and the fallow deer (*Dama dama*), from Anatolia. Their current geographical



Fig. 2
Black rat (*Rattus rattus*) in Tenerife, Canary Islands

The black rat was unintentionally introduced by humans in ancient times

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range is the result of movements that began in ancient times. Closer to the present day, many game species and fur-bearing animals have been moved, introduced, or have even escaped from farms into the wild. This is the case of the sika deer (*Cervus nippon*), Reeve's muntjak deer (*Muntiacus reevesi*), the American mink (*Neovison vison*) and the raccoon dog (*Nyctereutes procyonoides*), for example. The most recent arrivals, some dating from only the late 20th Century or the very early 21st Century, were introduced as companion or ornamental animals. Examples include four species of squirrel, all of which have either become established in Europe or are in the process of doing so: the Eastern grey squirrel (*Sciurus carolinensis*), the first to arrive and three recent Asian species (*Tamias sibiricus*, *Callosciurus erythraceus* [Fig. 3] and



Fig. 3
Pallas's squirrel (*Callosciurus erythraceus*) in Antibes, France

A native of Southeast Asia, this squirrel was introduced into France in the latter half of the 20th Century

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C. fynlaisonii). The Egyptian fruit bat, *Rousettus aegyptiacus*, was also found recently in the Canary Islands (7, 20).

An analysis of available data reveals a number of trends. Invasion is continuing at an even faster pace. Prior to 1800, the rate of establishment was 0.03 species every year. Now it is one species every five years. The reasons for such introductions have also changed over time. After the introduction of game and domestic species, commercial species began to be introduced. We are now seeing what are known as entertainment species. The impacts remain the same. Examples of the impoverishment of Europe's natural biodiversity include the decline of the red squirrel (*Sciurus vulgaris*) after the grey squirrel (*S. carolinensis*) was introduced into Great Britain, or the retreat of the European mink (*Mustela lutreola*) before the advance of the American mink (*Neovison vison*) in France (20). The establishment of possible or confirmed reservoirs for micro-organisms that are potentially pathogenic to humans, domestic animals or indigenous wildlife has been confirmed with, for example, the role of the raccoon dog (*Nyctereutes procyonoides*) as a rabies virus reservoir in Eastern Europe. Lastly, as the pace of such establishments is not slowing down, ecologists have inferred that there is no apparent saturation effect (7).

Asia

Europe's direct neighbour, the Asian continent, has also been inhabited by humans for a long time and has given rise to numerous domestic plant and animal species. Human movements have led to the introduction of several mammal species. The current range of some of these mammals was modified a very long time ago, with some spectacular declines as well as a few introductions. The case of the boar (*Sus scrofa*) in the Sunda Islands, where it was introduced after being domesticated, is a case in point. Throughout the islands it interbred and was crossbred with several island populations of wild swine, including some endemic species such as *S. barbatus* in Borneo and *S. celebensis* in Sulawesi. These island populations were themselves moved eastwards onto islands well beyond the Wallace line (the imaginary line separating Asian and Australian fauna) that did not naturally host artiodactyl mammals. The current pattern is therefore rather complex (3, 9).

The progress of human populations throughout the Sunda Islands is not unlike that of the populations that settled the Mediterranean islands with, in both cases, radical upheavals in the composition of the fauna following their arrival. Several thousand years ago, these settlers were capable of travelling by sea with animals of a fair size, such as wild pigs of several species or cervids such as the rusa deer (*Cervus timorensis*). For many years, the Sumatran

elephant (*Elephas maximus sumatrensis*) was itself thought to be a result of an ancient human introduction. Nowadays the hypothesis that they occurred naturally seems more likely. In fact, a detailed history of the establishment of mammal populations on the islands of tropical Asia is yet to be written.

Further to the east and north, the Japanese archipelago hosts a multitude of introduced mammals, associated with often endemic island forms (1). They include two species of small carnivore originating from continental Asia, the Javan mongoose or small Indian mongoose (*Herpestes javanicus*) and the masked palm civet (*Paguma larvata*). The Javan mongoose is also found in the Antilles, where it contributes to the epidemiological cycle of rabies, and the masked palm civet was involved in the emergence of severe acute respiratory syndrome (SARS) in southern China in 2002 and 2003.

In the Asian territory of the former Soviet Union countries, numerous species movements took place during the course of the 20th Century, mainly for economic reasons associated with the fur trade. Some were local species, such as the bobak marmot (*Marmota bobak*), which was moved from one province to another, while others were exotic species such as the muskrat (*Ondatra zibethicus*), which originated from North America (15, 16).

The Americas

Most of what we know about the history of the Americas dates from the 16th Century onwards. Animal movements prior to that are still hypothetical. The first humans to arrive via north-east Asia had departed before the major stages of domestication were complete. Mammal invasions therefore post-dated the arrival of Europeans. Two original examples are worthy of note (26).

Like all armadillo species, the nine-banded armadillo (*Dasypos novemcinctus*) originates from South America. Its historic range nevertheless extended as far as the southern United States. Until the early 20th Century, it had not spread beyond latitude 33° north, and remained limited to a few arid regions of Texas. Nowadays it is found as far afield as Oklahoma, South Carolina and Florida, and is still spreading. This armadillo is a model for the study of reproduction, because its regular reproduction cycle results in identical quadruplets. It can also act as a natural host to the mycobacterium responsible for leprosy.

The Virginia opossum (*Didelphis virginiana*) has also made substantial inroads into the north-eastern United States, having crossed from the shores of the Chesapeake Bay to the Canadian border between the 16th and 21st Centuries (26).

It is hard to find a simple explanation for these natural invasions, which were perhaps facilitated by far-reaching, human-mediated changes to local landscapes. However, the opossum's presence all along the Pacific coast of the United States was the result of an intentional human introduction.

The first European settlers introduced numerous exotic mammal species into both North and South America. The classic examples are game species: the boar (*Sus scrofa*), red deer (*Cervus elaphus*), fallow deer (*Dama dama*) and brown hare (*Lepus europaeus*), which were released into a number of countries (15, 16). The North American beaver (*Castor canadensis*) and the reindeer (*Rangifer tarandus*) were introduced into Tierra del Fuego (24). Their impact on the local flora can be considerable and competition with indigenous rodent and cervid species can be fierce.

A special case is that of large private estates in the United States, often in the south, into which an astonishing and diversified range of ungulate animals was introduced. Some were crossed with the Barbary sheep (*Ammotragus lervia*) from the Sahara, the blackbuck (*Antilope cervicapra*) from northern India, or numerous species of African antelope and Asian deer. Several of these species have established a line in the wild and in some cases their populations are more numerous than the same species in their country of origin (16, 26). These introductions preceded modern-day biosecurity rules regarding animals. Could these bovids and cervids also have introduced micro-organisms?

Another noteworthy case is that of feral pigs, large populations of which are found in the United States where they are intensively hunted. They are descendants of the first pigs brought by Europeans after the 16th Century, which later returned to the wild. Feral pigs are to be distinguished from the boars (*Sus scrofa*) imported from Europe more recently, not always to the same areas (26). During the same period, that is to say, when Europeans first started to arrive, long-horned cattle breeds were introduced, but have now been virtually wiped out, together with horses and donkeys, which have since returned to the wild and are still present in some American states. Although the impact of these herds on the fragile vegetation of the semi-desert areas where they live is still disputed, it may exceed the capacity of these environments to support them. These wild herds also compete with indigenous wild ungulates and are potential reservoirs for micro-organisms.

Australia

Australia provides an almost textbook example of the introduction of mammals on the scale of an island



Fig. 4
Red-necked wallaby (*Macropus rufogriseus*) in Queensland, Australia

The red-necked wallaby escaped from captivity in Great Britain and France and founded a line

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continent. The original mammalian fauna did not comprise solely monotremes and marsupials (Fig. 4). There were also rodents, chiroptera and marine mammals that were, and still are, highly endemic (19). The main introduction by the first human settlers was the dingo, which, either alone or in association with hunters of ancient times, was sufficient to completely wipe out a number of local species, including the largest modern-day carnivorous marsupial, the Tasmanian wolf or thylacine (*Thylacinus cynocephalus*). In the early 20th Century, it could still be found in Tasmania, where the dingo had not been introduced. The Europeans brought with them an impressive array of domestic and wild mammals, and a whole host of Australia's unique mammals have become extinct or exist only on isolated coastal islets. While predators like the red fox (*Vulpes vulpes*) or the domestic cat have certainly played a role in these extinctions, the development of sheep farming and competition from rabbits have weakened further the habitats of species already under threat. Six cervid species were introduced but in most cases are limited to small areas of Australia. In fact, the most abundant species are domestic species returned to the wild, which sometimes have a very wide range, such as donkeys, horses, dromedaries (*Camelus dromedarius*), pigs (Fig. 5) and Asian buffaloes (*Bubalus bubalis*). There are an estimated 250,000 dromedaries at large in Australia, which is the largest feral population known today. Buffaloes are a special case. Introduced into Darwin Region in the north of the Northern Territory during the early 19th Century, these feral buffaloes have posed a dual ecological and animal health problem, as they are infected with bovine tuberculosis. For this reason they have been subjected to a rigorous control programme. Donkeys, horses and pigs also pose environmental problems in places where they



Fig. 5
Feral pigs in Kakadu National Park, Northern Territory, Australia

These pigs are a fairly recent introduction and are now considered a nuisance

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exist in large numbers. In some areas where local fauna and flora are protected, residents are not permitted to keep cats.

Oceanic islands

The most spectacular situations, where invasive species have had the most dramatic impact on local fauna, have occurred in the oceanic islands scattered around the world's oceans, on which sailors landed, invariably accompanied by one or more of the following species: the black rat (*Rattus rattus*), the Norway rat (*R. norvegicus*) (Fig. 6), the Pacific rat (*R. exulans*), the house mouse



Fig. 6
Norway rat (*Rattus norvegicus*), Saint-Barthélemy, Lesser Antilles

This rat is practically cosmopolitan nowadays

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(*Mus musculus*), and the domestic cat, dog, pig and goat. Past extinctions on oceanic islands can be traced back more or less to the arrival date of the first sailors, whether thousands or hundreds of years ago. The case of the Mediterranean and Sunda Islands and the Japanese Archipelago are described above. Some islands are referred to as continental islands, which in former times were attached to larger land masses, depending on the sea level, which rose and fell, especially during alternating glaciations and interglacial periods in the early Quaternary period. Conversely, New Zealand, New Caledonia, the central Pacific islands, the Mascarene Islands in the western Indian Ocean and certain islands in the Antilles chain in the Atlantic Ocean are oceanic islands, i.e. those that have been isolated from land for a very long time and have a sparse but often highly original flora and fauna. The species brought by the various human settlers of these islands had a heavy impact on this flora and fauna.

Réunion Island, one of the Mascarene Islands, can be taken as a model case (4, 21). The estimated number of species that have become extinct since Europeans first settled this uninhabited island following its official discovery in 1500 is increasing all the time as researchers learn more about it. Some small bird and reptile species became extinct even before they could be observed alive. In the case of Réunion Island, while there are possibly just as many species of fauna and flora as prior to 1500, the current species are unfortunately increasingly cosmopolitan, whereas the extinct species were unique to the archipelago, or even to Réunion Island itself. The causes of extinction are well known: rapid over-farming by settlers of a small surface area, competition with introduced and favoured exotic species and also, perhaps, the introduction of pathogenic micro-organisms. Even though the latter explanation has not always been proved, it is strongly suspected, because so many species appear to have become extinct abruptly. Two recent publications report two cases where there is a proven connection with pathogenic micro-organisms: apparently the rat endemic to Christmas Island (*Rattus macleari*) became extinct after the black rat (*R. rattus*) was introduced along with its murine trypanosomiasis (30), and large numbers of subantarctic fur seal (*Arctocephalus tropicalis*) died as a result of a pathogen carried by house mice (*Mus musculus*) unloaded onto Marion Island (6).

New Zealand has also been the subject of studies, such as King's on the impact on indigenous birds of introduced small carnivorous mammals (12). The book's title is unambiguous (*Immigrant Killers*). Curiously enough, some species that appear fragile in their native regions can be highly resilient in areas where they have been introduced (13).

All the results point in the same direction. Indeed, some introductions have allowed new micro-organisms to

become established in hitherto protected areas. The bovine tuberculosis mycobacterium was introduced into New Zealand along with cattle. The brushtail possum (*Trichosurus vulpecula*) was introduced into New Zealand from Australia at the same time and has become the reservoir for the bacterium. Further examples can be found on other islands. The small Indian mongoose (*Herpestes javanicus*), which was introduced into the Antilles, contributes to the rabies cycle (23). The tailless tenrec (*Tenrec ecaudatus*) from Madagascar harbours leptospira in Réunion Island where it was introduced. It is still fairly common there and is hunted (27). As its name would suggest, the Asian musk shrew (*Suncus murinus*), which was mentioned earlier in relation to Africa (11), is of Asian origin. It is widespread along the shores of the Indian Ocean, as well as in the islands and archipelagos of the Indian Ocean, having become established in the Maldives, the Seychelles, Madagascar and the Mascarene Islands, for example. On the island of Île aux Aigrettes (Seychelles) this shrew has become the subject of an eradication programme, as well as of a theoretical study based on a Bayesian method for determining the probability of eradicating it entirely (28). The model should doubtless be reproduced in other contexts and for other species.

It is paradoxical to see naturally isolated, and hence relatively protected islands, become testing grounds where micro-organisms and reservoir species that had never before encountered one another are brought into contact. Sometimes they seem capable of joining forces. It is no coincidence that islands have provided biogeographers with a theoretical instrument and a place for experimentation (8, 17, 29). Many of the resulting developments have potential applications in epidemiology.

Conclusion

Can general conclusions be drawn from these examples taken from very different lands? Do human movements spearhead the overall direction of species movements? Is this the explanation for the relatively small number of invasions of Africa, compared with the flood observed on some islands? Or is the answer that tropical environments, with their richer biodiversity, are more resistant than temperate environments? Are intact or largely unmodified ecosystems more resilient than agro-systems or severely degraded ecosystems? All these are questions that would merit more thorough and detailed analysis (5).

A fact that will no doubt emerge from the other articles in this thematic issue is that the most invasive species known to date is a mammal called the human. All studies of invasions associated with other species in the same zoological class have revealed that the initial movements of these species were instigated by human movements.

Should we therefore act on the cause (human movements) or the consequences (the introduction of non-human mammals)? This is a reasonable question given the impact on natural or modified environments of certain human actions, for example, action taken to limit the density of brushtail possums in New Zealand or to control coypus in France, in both cases using chemical methods. However, it is much more difficult to calculate the cost of the presence of these species than the cost of control. The presumed, estimated or proven damage caused by these species should be weighed against the environmental

consequences of the substances used to control them, something which is rarely done. As introductions are continuing at an ever-faster rate, there are doubtless few causes for optimism, either for the indigenous species, which are commonly under threat, or for the introduced species, which are hunted down, or for their respective environments, which they often share. Introductions of micro-organisms will inevitably continue in parallel.



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