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The small Indian mongoose (Herpestes auropunctatus) on Adriatic Islands: impact, evolution, and control

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To the Graduate Council:

I am submitting herewith a dissertation written by Arijana Barun entitled "The small Indian mongoose (Herpestes auropunctatus) on Adriatic Islands: impact, evolution, and control." I have examined the final electronic copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Ecology and Evolutionary Biology.

Daniel Simberloff, Major Professor

We have read this dissertation and recommend its acceptance:

Nathan Sanders, Gary McCracken, James Fordyce, Benjamin Fitzpatrick, Frank VanManen

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

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A Thesis Presented for the
Doctor of Philosophy
Degree
The University of Tennessee, Knoxville

Arijana Barun
May 2011

Dedication

To my husband Vlado, daughter Maria, and son Lucas:
For their unwavering support, love and patience.

To my family and my in-laws:
For help during the field work, but most importantly for never ceasing support
and encouragement.

To my advisor:
For believing in me, for challenging me and for supporting me.

To my friends and colleagues:
For field and editorial work, but most importantly for their persistent
encouragement.

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ABSTRACT

One cause of declines and extinctions of island species is carnivore introduction. Four carnivores, including the small Indian mongoose (*Herpestes auropunctatus)*, are on the IUCN's list of 100 of the World's Worst Invasive Alien Species. My thesis summarizes global patterns of carnivore introductions and examines ecological, evolutionary, and management impacts of this mongoose. I study abundances of reptiles and amphibians on mongoose-infested and mongoose-free islands in the Adriatic Sea to determine if factors other than mongoose presence can account for abundance differences. For several reptiles and amphibians, the mongoose is implicated as causing differences. Additionally, I assess species abundance in the small mammal community and activity times of introduced ship rats (*Rattus rattus*) on the same islands. The mongoose is implicated in a shift in rat activity times, but it is difficult to separate mongoose impacts on small mammal abundance from rat impacts.

To manage introduced carnivores, we can exclude, control, or eradicate them. I review literature data on mongoose eradication and control campaigns. I compiled a list of all islands with known mongoose populations and focused on assessing successes, failures, and challenges. The mongoose has been eradicated only on six very small islands. Management at low levels by various techniques has been attempted on many islands, with variable success.

On almost all islands of introduction, the mongoose has no potential competitors of similar size. However, on three Adriatic islands where the

mongoose was introduced, a similar-sized native carnivore, the stone marten (*Martes foina*), is present, while on one Adriatic island the small Indian mongoose is the sole carnivore. To see if character displacement occurs in the mongoose when the marten is present, and vice-versa, I examined size variation in the diameter of the upper canine tooth (the prey-killing organ) and skull length in these two species on these islands. Character displacement in both traits was evident for the mongoose but not the marten.

Lastly, I developed a simulation model to examine genetic consequences of serial introductions of the small Indian mongoose and found that the potential for population genetic data to determine introduction pathways and sequences is limited.

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GENERAL INTRODUCTION.

Declines and extinctions of island species as a result of anthropogenic impacts are well documented (Vitousek, 1988; Whittaker & Fernández-Palacios, 2007). One of the most important causes of these declines and extinctions is introduction of carnivores by humans (Barun and Simberloff 2010). Many carnivores were introduced accidentally, some escaped from captivity such as from fur farms, but most carnivores were deliberately released for economic gain, recreational hunting, or biological control of introduced pests such as rats and rabbits. Globally a minimum of 29 carnivore species have been introduced. Some populations have dwindled and disappeared without apparent reason, but many species have become serious threats. As a result, four carnivore species are listed among the IUCN's list of 100 of the World's Worst Invasive Alien Species. In chapter 1, I summarize global patterns of carnivore introductions and their negative ecological impacts on native species, examine a few notable examples of introduced carnivores, and review the importance of their control, management, and eradication on islands as well as mainland.

The small Indian mongoose (*Herpestes auropunctatus)* is one of the world's 100 worst invasive species (IUCN, 2000). Native to Asia, it was introduced to many islands in the Pacific and Indian Oceans and the Caribbean Sea, mostly in the late 19th and early 20th centuries, primarily in order to control rats in sugar cane fields. The other reason the mongoose was introduced was to control native

poisonous snakes: a pit viper, habu *Trimeresurus flavoviridis* on several islands in Japan, the fer-de-lance (*Bothrops lanceolatus* and *Bothrops caribbaeus*) on the West Indian islands of Martinique and St. Lucia, and the horned viper *Vipera ammodytes* on several islands in the Adriatic Sea. The mongoose is a generalist predator; it preys on native species and is blamed for the decline and extirpations of many native island species (see review by Hays & Conant, 2007).

There are many reports of population reductions of reptiles and amphibians caused by the mongoose, but there is usually controversy over whether the mongoose is truly the main culprit (Corke, 1992; Hays & Conant, 2007). The impact of a particular introduced predator is hard to isolate when others, such as rats and feral cats, are present. However, in the southern part of the Adriatic Sea, Dalmatia, the mongoose has been introduced to some but not all islands. In chapter 2, I examine the abundance of native reptiles and amphibians on three mongoose-infested and three mongoose-free islands to attempt to determine if factors other than mongoose presence can account for how native amphibian and reptile abundance differs between these two classes of islands.

In addition to impact on reptiles and amphibians, the small Indian mongoose is known to have negative impacts on small mammal communities on islands where it was introduced (see review by Hays and Conant 2007). In chapter 3, I assess the abundance of small mammal populations and the activity time of introduced ship rats (*Rattus rattus*) on three mongoose-infested and three mongoose-free islands in the Adriatic Sea, Croatia. I set up a trapping

system of INRA and ratière live traps on each island consisting of 30 traps of each type at 30m interval along the narrow dirt roads used as transects.

To alleviate problems caused by established introduced carnivores, we can exclude, control or eradicate them. Exclusion is done in a localized area where the target species is being removed, but outside the exclusion area the invader probably thrives. Control usually means reducing the size of the pest population to acceptable levels. The ultimate goal of many efforts to control introduced carnivores is eradication, but this is in many cases an impossible task, so the control must be done constantly or only during periods when the native species are at most risk. In chapter 4, I review data from the published and gray literatures on eradication and control campaigns targeting the small Indian mongoose. I focus on assessing successes, failures, and challenges and have compiled a list of all islands with known mongoose populations. My aim is to facilitate mongoose eradication efforts and direct researchers to areas of applied research that would aid this goal.

On most islands of introduction, except in the Adriatic Sea, the small Indian mongoose has no competitors of similar size. However, on three islands where the mongoose was introduced, a similar-sized native carnivore, the stone marten (*Martes foina*), is present and on only one Adriatic island is the small Indian mongoose the sole carnivore. Previous studies have shown that in the absence of competitors this mongoose has increased in male size in only 100–200 generations compared to its native populations in Asia, where it co-occurs with two larger mongoose species (Simberloff *et al.* 2000). This morphological change

is consistent with ecological release from competition with its congeners (Grant 1972). In chapter 5, I examined size variation in the maximum diameter of the upper canine tooth (the prey-killing organ) and skull length in the small Indian mongoose and stone marten on Adriatic islands to test for character displacement and release.

Recently, several studies have attempted to infer the chronological order of introduction from variation in genetic diversity among populations within an introduced species' range (Estoup *et al.* 2001; Kolbe *et al.* 2004; Dlugosch & Parker 2008; Simberloff 2009). Such attempts need careful interpretation, because genetic variation can also reflect differences in the number of founders, variation in genetic diversity between groups of founders, or simply the standing variation in the native population. In this context, in chapter 6, I have examined the serial introduction of the small Indian mongoose, *Herpestes auropunctatus*, and have developed a simple simulation model to evaluate more broadly the potential for population genetic data to confirm or refute the completeness of other historical introduction records. I used already published microsatellite data to parameterize simulations and test the credibility of historical introduction records of *H. auropunctatus* to five islands (Fiji, Okinawa, Amami-Oshima, Jamaica and Mauritius).

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CHAPTER I.

CARNIVORES

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Barun A, Simberloff D (2010) Carnivores. In: Simberloff D, Rejmanek M (eds).

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95-100.

The Carnivora are a diverse order of placental mammals: almost all Carnivora are primarily meat-eaters, though some species (such as the small Indian mongoose and the brown-nosed coati) are often omnivorous. Many predatory species other than mammals are colloquially termed "carnivores," but in this entry the word refers to a member of the Carnivora. Carnivores range in size from the least weasel through the southern elephant seal and include dogs, bears, raccoons, weasels, mongooses, hyenas, and cats. Many global declines and extinctions can be wholly or partially attributed to introduced carnivores. Carnivores were most often deliberately introduced to prey on pest animals, but many were also either escapes or intentional releases from fur farms. Predation by introduced carnivores is a major current threat to several species, but they have other impacts as well, affecting human health and economies and hybridizing with native species. Long-term carnivore control is required to prevent the declines and possible extinctions of some endemic species. Successful eradication campaigns are increasingly being undertaken, though these have largely been restricted to islands to date.

Global Patterns

The earliest introduced carnivore was probably the dog, brought to the Americas by Paleoindians and to Australia by Aboriginal explorers as early as 3000-5000 years BC. Most carnivore introductions were for the fur industry and occurred between 1850 and the early twentieth century, while accidental

introductions of cats and dogs peaked during the World War II as a result of military activities.

Carnivores were introduced for many different reasons. Some escaped from captivity such as from fur farms, but many were deliberately released for economic gain, recreational hunting, or biological control of introduced pests such as rats and rabbits. During the early stages of colonization of many parts of the world, many domestic animals have turned feral after arriving with humans, including cats and dogs among the carnivores. Cats were often on ships as companions or for rodent control, and many were introduced unintentionally during stopovers. Arctic and red foxes, sable, and American mink were introduced to Europe, Asia and many islands in the Pacific by the fur industry. They were kept either in enclosures or cages, but free-living populations soon arose. Some introductions in mainland Europe and Great Britain resulted from "animal liberation" activities. Hunters and trappers introduced large numbers of carnivores, such as 19,000 mink, 10,000 raccoon-dogs and 1,200 raccoons that were released on hunting grounds throughout the former USSR. Most species of *Mustela* and the Viverridae (mongoose and civet) family were introduced as biological control agents in attempts to reduce rabbit or rat populations, but in many cases the introduced carnivore became a more consequential pest itself.

Details on the majority of individual introductions are lacking, but because almost all introduced carnivore species are conspicuous we have relatively good accounts of their presence. Globally a minimum of 29 carnivore species have been introduced. Some populations have dwindled and disappeared without

apparent reason, but many species have become serious threats. Four carnivores are listed among the IUCN's list of 100 of the World's Worst Invasive Alien Species: feral cat (*Felis catus*), small Indian mongoose (*Herpestes auropunctatus*) (q.v.), stoat (*Mustela erminea*), and red fox (*Vulpes vulpes*). Many others vie for positions on this list: raccoon (*Procyon lotor*), raccoon-dog (*Nyctereutes procyonoides*), feral dog (*Canis familiaris*), and brown-nosed coati (*Nasua nasua*). Several mustelids introduced as a result of fur farms are also notorious: weasel (*Mustela nivalis*), ferret or polecat (*Mustela putorius*), and American mink (*Mustela vison*).

The rapid expansion of some native species beyond their usual range is sometimes viewed as an invasion. A good example is that of the coyote (*Canis latrans*), which until 1900 was present only west of the Mississippi River in the United States and west of Ontario's Lake Nipigon in Canada. Coyote populations have expanded eastward, helped by the disappearance of wolves and habitat modification. In Europe, a similar expansion of the golden jackal (*Canis aureus*) is occurring into the Balkans.

Notable examples

Cats (*Felis catus)* were domesticated from the Eurasian wildcat (*Felis silvestris*) in the eastern Mediterranean ca. 3000 years ago. Because cats were good at controlling rats, they travelled around the world on ships. During stopovers some escaped, but many were also intentionally introduced to control

rodents near newly established colonies. Domestic cats are very adaptable and have survived in inhospitable conditions on many remote oceanic islands. Wherever cats are present they have immense impacts on wildlife, preying on small mammals, birds, reptiles, and amphibians. Cats are touted as by far the most dangerous introduced carnivore for native prey because they were introduced to many islands worldwide. They are responsible for 26% of all predator-related island bird extinctions. Possibly the most famous example of extinction was of the Stephen Island wren (*Xenicus lyalli*), the only flightless songbird in the world, which was caused by one lighthouse keeper's cat in 1894. In subsequent years cats caused 12 more extirpations of native birds from this island. Stomach contents of a single feral cat caught in New Zealand contained at least 34 native skinks (*Leiolopisma spp*.).Unlike some predators, a cat's desire to hunt is not suppressed by adequate supplemental food. Even when fed regularly by people, a cat's motivation to hunt remains strong, so it continues hunting. In addition, hybridization and disease transmission between domestic cats and wildcats is by far the greatest threat to the existence of wildcat subspecies all over their range of distribution. Feral cats act as reservoirs in the transmission of many diseases, creating a health hazard affecting both wildlife and human populations. In the US in 2000, 249 of the 509 cases of rabies detected in domestic animals were found in cats.

The **stoat** or **ermine** or **short-tailed weasel** (*Mustela erminea*) is native almost everywhere throughout the northern temperate, subarctic and Arctic regions of Europe, Asia, and North America. The stoat is an intelligent,

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versatile predator specializing in small mammals and birds. It is fearless in attacking animals larger than itself and adapted to surviving periodic shortages by storage of surplus kills. Stoats have been introduced for small mammal control to several Scandinavian islands, mainland Shetland Island, and the north of Scotland. In an unsuccessful attempt to control introduced rabbit populations, hundreds of stoats were introduced to New Zealand in the 1880s despite objections by ornithologists (Fig. I-1A). The success of stoats in New Zealand is likely at least partly related to their capacity to survive in any habitat, from sea level to elevations well above tree line. In New Zealand they are responsible for significant damage to populations of native species such as two threatened endemic birds, the yellowhead (*Mohoua ochrocephala*) and takahe (*Porphyrio hochstetteri)*, which still exist on the New Zealand main islands but only in protected areas where stoats are controlled or eradicated (Fig. I-1B). Two other native bird species, the kakapo (*Strigops habroptila)* and saddleback (*Philesturnus carunculatus)*, are found only on offshore islands as a result of predation by the stoat and also several other introduced predators. The stoat contributed with the ship rat (*Rattus rattus*) to the extinction of at least five endemic bird subspecies. Although stoat populations in New Zealand have declined from a peak in the 1940s, stoats are still abundant on the two main islands and several of the nearer small fringing islands, which they reached by swimming.

The **red fox** (*Vulpes vulpes*; Fig. I-2) is native to Europe, Asia, North Africa and boreal regions of North America. It has been introduced to Australia

and many regions of North America (multiple times to many eastern US states, lowlands of California and Aleutian Islands, Alaska). It is now the most widely distributed carnivore in the world mostly because it can colonize very rapidly when prey are abundant. The rate of spread in Australia was 160 km/year and can be closely linked with the spread of the introduced rabbit. Foxes were often imported by hunt clubs (Alaska) and even more frequently escaped from fur farms (California, Canada). From 1650 to 1750 European foxes were introduced many times to eastern states and have possibly hybridized with local populations. Red foxes negatively affect many native species. The spread of the fox in Western Australia appears to coincide with the disappearance or population decline of several small and medium-sized rodent and marsupial species, but their true impact is masked by agricultural development and other introduced species (cats, dogs, sheep, and cattle). The Aleutian Canada goose (*Branta canadensis leucopareia*) and other ground-nesting birds have been severely reduced in numbers as a result of red fox translocations. For example, on Shaiak Island, two red foxes devastated a colony of 156 000 nesting seabirds when all eggs and nestlings were killed and cached all over the island. The red fox is an important wildlife vector of rabies in Europe, the US, and Canada. Millions of dollars are spent each year on bounties to reduce numbers and to vaccinate foxes. On the other hand, introduced sterilized red foxes were used successfully as biological control agents to eliminate introduced Arctic foxes (*Alopex lagopus*) from two arctic islands.

The **raccoon** (*Procyon lotor*; Fig. I- 3) is native to North America, but as a result of fur farm industries it was introduced to islands off Alaska, Canada and the continental US. In the mid-20th century raccoons were deliberately introduced by hunters or fur industries to France, Germany, the Netherlands, and Russia. In Japan, up to 1,500 raccoons were imported as pets each year after the success in the 1960s of the anime series "Rascal the Raccoon." They are now widely distributed across the European mainland, the Caucasus region, and Japan. For many years it was believed that an indigenous species of raccoon inhabited the Bahamas but recent morphological and genetic analyses show that Bahamas raccoons are recent descendants of raccoons from North America. Owing to their adaptability and increased habitat availability raccoons have extended in their native range from deciduous and mixed forests to mountainous areas, coastal marshes, and even urban areas, where some homeowners consider them pests. They are one of the major wildlife vector of rabies in the US, and restocking of raccoon populations by hunting clubs in the 1970s led to the spread of rabies from the southeastern to the mid-Atlantic US. Raccoons plague game management by preying on waterfowl, quail and many other ground-nesting birds. On the Queen Charlotte Islands and other islands off the coast of British Columbia, introduced raccoons are responsible for the destruction of 95% of seabird colonies. The raccoon is the most economically important furbearer in the United States. Over five million raccoons were harvested per year in the early 1980s in the United States alone.

Negative impacts

Impacts of introduced carnivores have ranged from almost none to major economic, health, ecological and cultural loss.

Human and veterinary health problems caused by wild carnivore populations have been a major concern for public health departments and international organizations. Several introduced carnivores are important reservoirs of rabies, such as the small Indian mongoose in the West Indies and feral dogs and cats in many parts of the world. Salmonella may be transmitted from dogs to humans via flies feeding on feces. Dogs, through their urine, have been implicated in spreading leptospirosis to people. Feral cats serve as a reservoir for many wildlife and human diseases, including toxoplasmosis, mumps, cat scratch fever, leptospirosis, distemper, histoplasmosis, plague, rabies, ringworm, salmonellosis, tularemia, and many endo- and ectoparasites.

Many economic costs are generated by introduced carnivores, particularly feral dogs and cats. The direct costs of managing populations of introduced carnivores to acceptable levels can be huge. Millions of dollars in the United States were paid out in bounties in the last 30 years to reduce red fox populations but with little success. Many other indirect costs accrue over time. For example, the small Indian mongoose will kill every chicken in a coop in broad daylight, so small-scale chicken farming is completely absent in areas where the mongoose is present, or chickens have to stay in well-built enclosures.

The ecological impacts of introduced carnivores are varied, including their roles as predator, as competitor of biologically similar species, and as threat to

hybridize with native congeners. The best-known impact of introduced carnivores is predation of native animals. The population-level impact of this predation can be either none, co-existence in an equilibrium, or extinction of the prey species or population. Empirical evidence of the first two impacts is scant because a stable relationship between an introduced predator and native prey is probably uncommon but also because of the difficulty in demonstrating prey regulation. One notable example might be the reported inability of the small Indian mongoose to reduce populations of introduced rat species on some islands where it was introduced. There are many examples of major declines, local extirpations, and island extinctions of native prey owing to the introduction of carnivores. Many introduced carnivores have become notorious solely because of this impact. For instance, the small Indian mongoose has been responsible for many extinctions, extirpations, population reductions and range restrictions of birds, amphibians and reptiles on islands. It is not uncommon for many species to exist on mongoose-free islands but to be absent or in low numbers on nearby islands where the mongoose is present. The extinction of the Stephen Island wren by a housecat, mentioned above, is another example. Introduced American mink are implicated in the decline of many seabirds and inland waterfowl in Great Britain, as well as the water vole (*Arvicola terrestris)*.

Competition with native species occurs when individuals of native species suffer reduced abundance, fecundity, survivorship or growth as a result of resource exploitation or interference with introduced species. On the Kerguelen Islands where cats are present, there are not enough petrels for the native skuas

to eat to reproduce and the skua population has plummeted. The presence of an introduced congener might prevent the establishment of a subsequently introduced species. For example, introductions of Arctic foxes (*Alopex lagopus*) to islands where red foxes were absent were successful, but where red foxes occurred the Arctic species disappeared.

Hybridization involving introgression of introduced species with natives is an even subtler impact, because it leads gradually to the loss of genetic integrity of native species and extinction as a separate species. If interbreeding has occurred for a long time there may be no reliable methods for phenotypic or genetic comparison, and the precise history and impact of this process cannot be described. This is the case with dingoes and wild domestic dogs in Australia, and feral cats and wildcats in Scotland. Hybridization with dogs has also led to the introduction of dog genes into gray wolves (*Canis lupus*) and the endangered Ethiopian wolf (*Canis simensis*). There may even be impacts when interspecific matings do not lead to genetic introgression. For example, the larger American mink males mate with European mink (*Mustela lutreola*) females, which then do not permit other males to approach them. The embryos resorb and the female leaves no offspring for that year, while the American mink females reproduce. This removal of females from the breeding population must exacerbate the imperilment of the European mink.

In addition to direct effects on prey populations, introduced carnivores can generate a trophic cascade strong enough to alter the abundance and composition of entire plant communities. The introduction of arctic foxes to the

Aleutian archipelago induced strong shifts in plant productivity and community structure. Foxes reduced nutrient transport from ocean to land by preying on seabirds, affecting soil fertility and transforming grasslands to dwarf shrub/forb-dominated ecosystems.

In some locations, many different species of carnivores have been introduced, and they may interact with one another and with other species (e.g., rats) to modify food web structure, making it difficult to characterize the impact of a single introduced predator on native species. For example, the Hawaiian Islands have no native mammals, but several introduced carnivores (cats, dogs, mongooses) have devastated populations of native birds. Rats can also prey on some of the same species that introduced carnivores consume. In addition, introduced prey species (rats, mice, and rabbits) are probably supplementing the diet so predators can increase their numbers and maintain pressure on even low numbers of native prey, eventually leading to extirpations of native fauna. The Macquarie Island parakeet (*Cyanoramphus novaezelandiae erythrotis*) was unaffected by cat predation until rabbits were introduced. Rabbits provided the cats with a food supply year round, allowing cat numbers to multiply and drive the parakeet to extinction. Often interactions between introduced species have a synergistic effect on local species. For example, the construction of a tourist hotel on Caicos Island led within three years to the near extirpation of the 5500 endemic West Indian rock iguanas (*Cyclura carinata*) that were hunted by introduced cats and dogs. Most likely, the cats prayed on the young and the dogs

on larger adults of iguanas, but it is difficult to disentangle the different effects of many carnivore species combinations.

Many introduced carnivores have more severe impacts on prey than native predators do, because in communities where predators and prey have coexisted for long periods prey species evolve behaviors and morphologies that reduce the chance of encounters with predators or increase the likelihood of escape once predators are detected. In contrast, naïve prey in communities with novel introduced carnivores lack those avoidance behaviors. For example, Australia never had placental carnivores until they were introduced by humans, and these new predators (cats and red foxes) have different hunting and tracking tactics then native predators. The best-known impact of alien carnivores, elimination of native birds and other vertebrates on oceanic islands, occurs mostly because of native avifaunal and herpetofaunal naiveté.

Management and eradication

To alleviate problems caused by established introduced carnivores, we can exclude, control or eradicate them. Exclusion is done in a localized area where the target species is being removed, but outside the exclusion area the invader probably thrives. In New Zealand several predator-proof fences have successfully excluded many introduced carnivores (cats, stoats, ferrets) and other introduced species. Once introduced predators have been removed, it is possible to restore areas to nearly the condition that obtained prior to human habitation of New

Zealand. In Australia, fewer kangaroos and emus are found on the northwestern side of the dingo proof-fence where dingos are present, suggesting that the dingoes' presence depresses their populations. However, fencing had a limited effect, so other forms of control (trapping, poisoning) are necessary.

Control usually means reducing the size of the pest population to acceptable levels. Because control is not complete removal of the invasive species, a constant and/or repeated effort is needed to keep the population at the desired level. The ultimate goal of many efforts to control introduced carnivores is eradication, but this is in many cases an impossible task, so the control must be done constantly or only during periods when the native species are at most risk. The small Indian mongoose is trapped on beaches on several islands in the West Indies during the peak of sea turtle reproduction. Such control temporarily reduces predation pressure on young turtles until they move to the sea. The drawback is that this procedure must be repeated every year. Many such control efforts are undertaken for other species of introduced carnivores in Hawaii, New Zealand, Australia, and many other islands.

Unlike control, eradication should have to be performed only once. Eradication is the complete removal of all individuals of the target. This is difficult to achieve because it is usually very challenging to remove the last individual of a population, and eradication, even where technically feasible, is often limited by prohibitively high costs. Nevertheless, introduced carnivores have been eradicated from many islands, some of which are quite large. For example, the Arctic fox was eradicated from Attu island, Alaska (905.8 km^2), cats

from Marion island, South Africa (190 km²), and the red fox from Dolphin island, Australia (32.8 km²). Overall, at least 75 feral cat, 42 fox, 5 feral dog, 35 mustelid, and 4 raccoon populations have been eradicated from islands worldwide. Three main eradication techniques are chemical (poisoning), physical (fencing, shooting, and trapping), and biological (introduction of a competitor or pathogen, or immuno-contraception). The most difficult part of any method is removing individuals when low densities are reached, because even a single pregnant female can initiate a population resurgence. For example, the attempt to eradicate the small Indian mongoose from Amami-Oshima, Japan, has been unsuccesful particularly because of the difficulties of removing the mongoose at low densities.

The upshot of carnivore eradications has often been an improvement in the status of the species under threat. But it is not always enough simply to eradicate the top predator. Eradication of cats from Little Barrier Island, off the coast of New Zealand's North Island, led to a decrease in breeding success of a resident seabird, Cook's petrel. The reason for this decline was an explosion in numbers of rats, which prey on the seabirds. Rat eradication was followed by a rise in petrel productivity. In addition, recolonization by local native species is not always possible following removal of an introduced carnivore, because some extirpated species were endemic to islands and lack neighboring populations that can act as recolonization sources, and also because introduced species may have irreversibly damaged the environment.

Long-term carnivore control will be required to stop the declines and possible extinctions of some endemic species. Widespread control of carnivores (such as immuno-contraception) is needed to aid eradication over large areas. There are also ethical considerations; biological control (particularly of cats) may prove unacceptable to the general public, so extensive public outreach campaigns must be conducted prior to control efforts.

See Also the Following Articles

Eradication; Hybridization and Introgression; New Zealand; Predators; Rats; Small Indian Mongoose

Glossary

biological control Introduction of a natural enemy of an introduced species, such as a predator or pathogen.

carnivore Member of the order Carnivora – dogs, bears, raccoons, weasels, mongooses, hyenas, and cats.

eradication Complete elimination of a species from a site.

extirpation Local extinction of a species.

feral: Wild, in reference to an animal population descended from domesticated individuals but now living independently of humans.

introgression: Backcrossing of hybrid individuals to individuals of one or both parental species.

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Appendix I

Figures

Figure I-1. (A) Stoat (*Mustela erminea*, also known as short-tailed weasel), Kanuti National Wildlife Refuge, Alaska. (Photograph by Steve Hillebrand, courtesy of U.S. Fish and Wildlife Service.)

Figure I -1. (B) Takahe (*Porphyrio hochstetteri*) killed by a stoat while on the nest. (Photograph courtesy of Department of Conservation, New Zealand.)

Figure I-2. Red fox (*Vulpes vulpes*), Cape Newenham State Game Refuge, Alaska.

(Photograph by Lisa Haggblom, courtesy of U.S. Fish and Wildlife Service.)

Figure I-3. Raccoon (*Procyon lotor*), Lower Klamath National Wildlife Refuge, California. (Photograph by Dave Menke, courtesy of U.S. Fish and Wildlife Service.)

CHAPTER II.

IMPACT OF THE SMALL INDIAN MONGOOSE (*HERPESTES AUROPUNCTATUS*) ON NATIVE AMPHIBIANS AND REPTILES OF THE ADRIATIC ISLANDS, CROATIA

Published in Animal Conservation and Co-authored by Daniel Simberloff and Ivan Budinski

Abstract

We studied impacts of the introduced small Indian mongoose *Herpestes auropunctatus* on the herpetofauna on six islands in the Adriatic Sea, Croatia, comparing abundances of reptiles and amphibians on three islands with the mongoose to those on three islands without the mongoose. We used four types of sampling surveys: distance-constrained surveys, visual encounter surveys, special searches and accidental trapping. The horned viper *Vipera ammodytes* and Balkan green lizard *Lacerta trilineata* were absent from two mongoose-infested islands (Korčula and Mljet) and rare on the third (Hvar); they were common only on the mongoosefree island where they had historically been present (Brač). The European green toad was absent from one mongoose-infested island, where it had historically been present and rare on the other two. It was common on two of the three mongoose free islands. Other herpetofaunal species were either very scarce or completely absent on the three mongoose-infested islands. Most of these species also occur on the mainland but are already scarce there; some are strictly protected under Appendix II of the Berne Convention. The recent spread of the mongoose to the European mainland suggests the need for urgent control to protect vulnerable herpetofauna.

Introduction

Extinctions of island species as a result of anthropogenic impacts are well documented (Vitousek, 1988; Whittaker & Fernández-Palacios, 2007). Island

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species generally have small populations, restricted genetic diversity and narrow ranges (Blondel, 1995), so even small changes can considerably affect their survival (Vitousek, 1988). Two major causes of the decline of island species are habitat degradation caused by human development and introduction of nonnative predators. In a review of amphibian and reptile extinctions that have occurred since 1600, Honegger (1981) found that most were island taxa. Henderson (1992) attributed most extinctions/extirpations of West Indies amphibians and snakes on large islands to the loss of habitat but those on small islands to introduced predators, especially the small Indian mongoose *Herpestes auropunctatus*.

The small Indian mongoose has been touted as one of the world's 100 worst invasive species (IUCN, 2000). Native to Asia, it was introduced to many islands in the Pacific and Indian Oceans and the Caribbean Sea, mostly in the late 19th and early 20th centuries, primarily in order to control rats in sugar cane fields. However, the success of the mongoose in this endeavor is questionable as rat numbers continue to be high (Hinton & Dunn, 1967). The other reason the mongoose was introduced was to control native poisonous snakes: a pit viper, habu *Trimeresurus flavoviridis* on several islands in Japan, the fer-de-lance on the West Indian islands of Martinique (*Bothrops lanceolatus*) and St Lucia (*Bothrops caribbaeus*) and the horned viper *Vipera ammodytes* on several islands in the Adriatic Sea. However, because the mongoose is a generalist predator, it also preys on other native species and is blamed for the decline and extirpations of many native species on islands. There are many reports of

population reductions of reptiles and amphibians caused by the mongoose, but there is usually controversy over whether the mongoose is truly the main culprit (Corke, 1992; Hays & Conant, 2007).

In the Adriatic Sea, the mongoose was introduced in 1910 to Mljet Island and subsequently to several other islands (Korčula, Hvar, Čiovo, Škrda) and the mainland Pelješac Peninsula. It is currently spreading along the Dalmatian coast and has reached the Neretva River in the north (Barun, Budinski & Simberloff, 2008) and Albania in the south. Other introduced mammalian predators on the islands are black rats *Rattus rattus* and feral cats, but their effects on the Croatian fauna are not documented. In addition to introduced predators, nearly all larger islands in Croatia have a native predator, the stone marten *Martes foina*. Therefore, native Croatian species have evolved in the presence of the stone marten, and they have confronted introduced predators, but the population impacts of these predators are unknown.

The impact of a particular introduced predator is hard to isolate when others, such as rats, are present. Fortunately, in the southern part of the Adriatic, Dalmatia, the mongoose has been introduced to some but not all islands. It is therefore possible to compare mongoose-free and mongoose- infested islands to attempt to determine if factors other than mongoose presence can account for how native amphibian and reptile abundance differs between these two classes of islands. That was the purpose of this study.

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Methods

Study area. Field work was conducted on six islands in the southern part of Adriatic Sea: Mljet, Korčula, Hvar, Lastovo, Brač and Dugi Otok; the first three have the mongoose and the last three do not. These islands are relatively similar in surface area (Mljet: 100km², Korč ula: 270km², Hvar: 299km², Lastovo: 53km², Brač: 394km², Dugi Otok: 114km²), elevation, geology, climate and vegetation. All these islands have a similar history of human occupation, similar agricultural practices and similar timing of introduction of most exotic species. Their landscape is a fine-grained mosaic of shrublands, scrublands, forests and small agricultural fields. Shrublands (maquis) are dense thickets of evergreen sclerophyll shrubs and small trees dominated by *Quercus ilex, Fraxinus ornus, Phillyrea latifolia, Pistacia terebinthus, Myrtus communis, Arbutus unedo, Laurus nobilis, Erica arborea, Lonicera implexa, Lonicera etrusca, Tamus communis, Smilax aspera, Rubia peregrina, Olea europaea oleaster* and *Asparagus acutifolius*. Scrublands (garrigue) are dominated by *Cistus incanus, Cistus creticus, Cistus salviifolius, Cistus monspeliensis, Er. arborea, Erica multiflora, Spartium junceum, Calicotome villosa* and *Rosmarinus officinalis*. Forests are dominated mostly by *Pinus halepensis*. Most local agriculture consists of olive groves and vineyards, with a few small vegetable fields with rich soil. All transects reported below run through all four vegetation types, but the proportion of each type may vary among transects.

Methods. We conducted sampling surveys on each island to assess the relative abundance of snake, lizard and frog species. Because the species ranged

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from active foragers to sit-and-wait (ambush) predators, from diurnal to nocturnal and from fully terrestrial to semi-aquatic and occurred over a wide range of abundances, we used four different sampling surveys: distance-constrained surveys, visual encounter surveys, special searches and incidental trapping. Active sampling plays an important role in herpetofauna studies, especially for agile and larger species. Using diverse types of sampling surveys was essential in order to survey different species, several of which were very scarce (Guyer & Donnelly, in press).

For distance-constrained surveys (transects), we used narrow, 2.5 km dirt roads as our main transects. On each island we selected three transects each running through all four vegetation types described above. A single researcher (I. B.) walked the transect at a constant pace, once a day at midmorning, and recorded all reptiles sighted within 1m on either side. We surveyed each transect once in April 2008 and once in May 2008.We recorded wind speed, cloud cover and air temperature at the beginning and end of each survey using a Kestrel 3000 Pocket Weather Meter (Nielsen-Kellerman Co., Boothwyn, PA, USA). We did not conduct surveys if there was excessive cloud cover, high wind or high or low air temperature. We surveyed one transect per morning, starting about 2 h after sunrise. We ran multiple regressions in JMP, version 8 (SAS Institute Inc., Cary, NC,USA) to test if weather conditions affected abundance of two species of lizards that were counted only on transects: the Dalmatian wall lizard *Podarcis melisellensis* and the sharp-snouted rock lizard *Dalmactolacerta oxycephala*.

Only April or May counts are shown, whichever was highest, and abundance data were summed for all three transects.

We recorded visual encounter surveys during walking and driving. We recorded mileage upon arrival on each island to ensure that we did not drive more on some islands than on others. We conducted additional walking surveys while checking traps. All islands had the same number of transects and traps, so we did not walk more on certain islands. We did not conduct visual surveys for reptiles at night.

Because we had observed many adult European green toads *Bufo viridis* and common tree frogs *Hyla arborea* around ponds on Brač and Lastovo, we conducted targeted searches for these species during day and night around ponds on the other four islands.

We sampled the European glass lizard *Pseudopus apodus* in traps that were part of a small mammal survey. We set up a trapping system of INRA and ratière live traps (Guédon, Bélair & Pascal, 1990) on each island consisting of 30 traps at 30m interval along the narrow dirt roads used as transects, as described above. To cover each side of the road, we placed every other trap on the opposite side of the road. We ran the trapping system for three days and three nights in April and again in May 2008. We marked locations so that in May traps were located exactly as in April. We baited all traps with a mixture of oat-flakes, peanut butter and sardine oil, changing baits once during the 3-day period

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or just after rain. We checked each trap early in the morning and late in the evening before sunset to catch mostly nocturnal small mammals but also the diurnal mongoose.

We also identified the gut contents of all 57 mongooses trapped in May and April on Mljet, Korčula and Hvar. Prey items were categorized into the following major taxonomic groups: mammals, birds, snakes, lizards, invertebrates and plants. Mammals were classified to species based on comparison with reference hair samples; birds could not be identified (only small or finely chewed feathers were found); lizards were classified to species when possible and invertebrates to order.

Results

We recorded 15 species of Reptilia and two species of Amphibia (Table II-1). Two additional reptile species (grass snake *Natrix natrix* and Anatolian worm lizard *Blanus strauchi*) and one amphibian species (marsh frog *Pelophylax ridibundus*) have been reported on some islands, but we did not find them. We also trapped 57 small Indian mongooses on three islands. Mongooses were most abundant on Mljet, and abundance was five times less on Hvar (Table II-1). Weather conditions (cloud cover, wind speed and air temperature) were not significant determinants of the numbers of the two lizard species encountered only on transects, the Dalmatian wall lizard ($F_{3,33}=1.17$, $P=0.3371$) and the sharp-snouted rock lizard ($F_{3,33}=1.6287$, $P=0.2035$).

Snakes. The total number of snake species among the islands is 10, but not all species are present on all islands (Table II-1). If we look just at the total number of snakes on each island, Mljet and Korčula (each with six snakes), stand out as having three times fewer individuals recorded than Hvar, Brač, Lastovo and Dugi Otok, which have 19, 18, 26 and 18, respectively (Fig. II-1). We found no snakes on transects except for two large whip snakes *Dolichopis caspius* on Lastovo, where this species is very numerous (26 individuals). We found all other snakes either during road surveys or in traps. In our surveys, we found no horned vipers on Mljet and Korčula, but we found two individuals on Hvar and two on Brač. We also did not find the four-lined snake *Elaphe quatuorlineata* on Mljet and Korčula, but on mongoose-free Brač we found four individuals, three road kills and one incidental encounter. We found no individuals of the Balkan whip snake *Hierophis gemonensis* on Mljet, but we found one individual on Korčula, 14 on Hvar, three on Brač and seven on Dugi Otok.

Lizards. We observed a total of seven lizard species on the six islands, but not all lizard species are present on all islands (Table II-1). In addition, we did not find the Turkish gecko *Hemidactylus turcicus*, which has been recorded on the islands. It is nocturnal, and we did not survey at night. The largest lacertid lizard on these islands is the Balkan green lizard *Lacerta trilineata*. We found no individuals on Korčula and only two on Hvar. On Brač , we frequently encountered it on transects (26) and found many during visual surveys (50). The sharp-snouted rock lizard was not recorded on Hvar, one was recorded on Brač, and on Mljet, Korčula and Lastovo it was numerous. We recorded 33 Moorish

geckos *Tarentola mauritanica* on Hvar. The European glass lizard has been recorded on all six islands. We did not find it on Mljet, and its abundance on Korčula was much lower than on the other four islands. The abundance of all species of lizards among transects within islands varied; some of this variation may be attributed to habitat differences.

Amphibians. Only four species of amphibians inhabit these six islands (Table II-1). The European green toad was historically present on all six; we found a few specimens on Korčula and Hvar but only after extensive targeted search around ponds and inside man-made water containers. Similar searches produced none on Mljet (and the local biologist has seen none). On Brač and Lastovo, we found many specimens of this species on transects, conducting road surveys, or while checking traps. On Dugi Otok, we found just one individual of this species, but this is the only island where it did not rain while we were sampling. On all islands but Dugi Otok, it rained either in April or May when we were present. Frogs are more active when it rains, and our data are consistent with this pattern. On the two islands where the European green toad is numerous we recorded higher numbers when it rained (Brač 12, Lastovo 53) than when it was dry (Brač 5, Lastovo 12).

Stomach contents. We examined contents of 57 mongoose stomachs. Nineteen stomachs were empty. The rest usually had combinations of vegetation (four), unidentifiable hair (five; one identified to *Apodemus sylvaticus*), bones (three) or bird feathers (three), snake skin (one) and invertebrates (24, mostly beetles in Cetonidae and the Egyptian grasshopper *Anacridium aegyptium*).

Many stomachs had reptile remains that were easily identified to species:

Dalmatian wall lizard (12), Moorish gecko (three) and Balkan whip snake (one).

In a single mongoose stomach from Hvar we found one Balkan whip snake, one

Dalmatian wall lizard and one Moorish gecko. In another stomach of a mongoose

from Korčula we found three Dalmatian wall lizard individuals and many

invertebrates. Overall, three mongooses from Mljet had reptiles in their

stomachs, as did six from Korčula and four from Hvar. Only mongooses from

Hvar had snakes in their stomachs, and we caught by far the fewest mongooses

on this island (five compared with 31 and 21 for Mljet and Korčula, respectively).

This is a very small sample size, but it does reflect the higher abundance of

snakes on Hvar compared with Mljet and Korčula.

Discussion

Snakes. Historical records show the horned viper was very frequently

encountered on Mljet, which was known as the 'island of snakes' (Tvrtković &

Kryštufek, 1990). We do not know the initial abundance of other species present

on islands before the mongoose introduction but we are certain that the horned

viper's high abundance on Mljet in 1910 warranted such concern among

authorities that the mongoose was introduced to control this snake. In our

surveys we did not find a single viper on Mljet or Korčula, where the mongoose

has been present since 1910 and 1927, respectively (Tvrtković & Kryštufek, 1990),

but Budinski et al. (2008), after extensive search, found one on Mljet in 2007. On

Brač, the only mongoose-free island where it was historically present, we found it, but rarely. This species is listed as strictly protected under Appendix II of the Berne Convention, which sets out to conserve wild flora and fauna and their natural habitats by all member states of the Council of Europe, European Union and several other neighboring countries. Our result is not surprising, because extirpations or extinctions in the Caribbean of *Alsophis* and *Liophis* snake species have occurred primarily on those islands with mongoose populations (Sajdak & Henderson, 1991). We were surprised to find two individuals on Hvar, where the mongoose has been present since c. 1970 (Tvrtković & Kryštufek, 1990). However, extensive talks with local hunters revealed that they have been conducting island-wide yearly predator control for several years. The reduced number of mongooses trapped in our study (Table II-1) and the survival of the horned viper on this island may reflect this activity.

Island size may be critical in determining whether an extirpation occurs (Henderson, 1992). This factor could also explain why on Mljet (which is almost three times smaller than Korčula and Hvar), we found significantly fewer individual snakes, and not nearly as many species as historical records show (Tvrtković & Kryštufek, 1990). Henderson (1992) noted that there are no recorded post-Columbus extirpations of *Alsophis* or *Liophis* snakes on any island that has remained mongoose-free, whereas mongoose-infested islands have recorded a mean number of 0.78 extirpations (range 0–2). Our islands show a similar pattern. We found no extirpations of snakes on islands without the

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mongoose, suggesting that human land development is not the only or even main cause of the reduction in snake diversity on Mljet and Korčula.

In addition, the recorded high or low abundance of several snake species can be explained by their life histories. For example, the eastern Montpellier snake is known as the fastest European snake and when threatened hisses loudly and for long periods; it may also flatten and inflate the front of the body and spread the neck. We believe this behavior disrupts the predatory behavior of the mongoose, and it might be the reason this species is still present on islands with the mongoose.

Lizards. Elevated numbers of the Balkan green lizard in areas where the mongoose is controlled or absent are also evidence that the mongoose has a strong impact on at least some native reptiles and that trapping the mongoose does increase native reptile numbers. The Balkan green lizard is very abundant on other Adriatic islands where the mongoose is absent (A. Barun & I. Budinski, pers. obs.), but these (Cres, Lošinj, Krk) were not part of our study. The mongoose is present on the island of Čiovo where the Balkan green lizard was historically present. A. B and I. B. visited Čiovo several times from 2004 through 2009 during spring, summer and fall months and found no Balkan green lizards. This lizard is quite numerous on the mainland along the coast, but we do not know its status where the mongoose is present. The Balkan green lizard is morphologically and ecologically similar to the ground lizard *Ameiva polops*, which was eliminated from the main island of St Croix after the introduction of mongoose in 1884 but persists on neighboring smaller islands lacking mongooses

(Henderson & Powell, 2009). In Viti Levu, Fiji, the mongoose is believed to have extirpated two native skinks *Emoia nigra* and *Emoia trossula* (Brown & Gibbons, 1986; Zug, 1991).

Comparing small lizards on different islands is difficult because lizards are prey to many different predator species and their abundance might be inversely correlated with predator abundance (snakes, larger lizards, including the European glass lizard, and the mongoose). For example, the low abundance of the Dalmatian wall lizard on Brač might be due to high abundance of its native predators (several snake species and the European glass lizard) and/or competition with the much larger Balkan green lizard. On Mljet, the overall lower abundance of the Dalmatian wall lizard could be attributed to competition with the sharp-snouted rock lizard, which is also numerous on this island (Fig. II-2). It is difficult to draw overall conclusions about population impacts on small lizards, but we know that the mongoose preys on them because we found many in mongoose stomachs.

Henderson (1992) noted that in the West Indies *Anolis* lizards are regularly preyed upon, but he was unaware of any species of *Anolis* whose numbers seemed drastically reduced owing to predation by native or introduced predators. While conducting similar walking transects to ours, Case & Bolger (1991) found that the abundance of a diurnal lizard was 100 times higher on seven Pacific islands without the mongoose than on 11 islands with the mongoose. We believe our failure to observe a similar pattern resulted from the uneven distribution of predator and competitor species on several of our islands,

and the small number of sampled islands (three) that had the mongoose. It would have been difficult to increase our sample size because there are only two other islands in the Adriatic with mongoose populations, and they are very small.

It is difficult to sample the European glass lizard on transects when numbers are very low. We have discovered that this species, when abundant, is readily attracted to bait, because we found it frequently in traps set for small mammals and the mongoose. This species is very rare on Korčula and was not recorded on Mljet, but it was numerous on all other islands (Table II-1). We are aware of no other studies that examine the impact of the mongoose on legless lizards.

Amphibians. Many authors have shown that amphibians are rare when the mongoose is present. On Amami-Oshima island, Japan, the Amami tip-nose frog *Rana amaminensis*, Otton frog *Rana babina subaspera* and Ishikawa frog *Rana ishikawae* were all scarce in areas that had been invaded by the mongoose long ago (Watari *et al.*, 2006). The edible frog *Leptodactylus pentadactylus* has been extirpated from three Caribbean islands with the mongoose but is still present on two mongoose-free islands (Barbour, 1930). The mongoose is implicated in the decline of the two native frogs (*Platymantis vitianus* and *Platymantis vitiensis*) in Fiji (Kuruyawa *et al.,* 2004). Therefore, it is not surprising that the three frogs (European green toad, common tree frog and marsh frog) were either very scarce or completely absent on three mongoose-infested islands in the Adriatic. A survey conducted in spring and fall of 2007 in the National Park of Mljet found the marsh frog only in a lake (Budinski *et al.*,

2008). This species is aquatic during the day, so it is unsurprising that it was found in the lake, but it is surprising that neither survey found it away from the lake. April 2008 had above average annual rainfall, so our recorded low abundance of this species was not because of a dry year.

Stomach contents. Even though we have no clear evidence that the mongoose preys on the species that are in low abundance, the gut content analyses show that the mongoose does prey on reptiles. On Amami-Oshima, the mongoose preys chiefly on insects and birds throughout the year, but on amphibians and reptiles more frequently in summer and on mammals in winter (Yamada & Sugimura, 2004). We have sampled during spring and early summer, so many reptiles in the mongoose guts might reflect the season.

Conservation implications

Assessment of responses to mongoose predation is often complicated by the presence of multiple native predator or competitor species, other management activities and/or human habitat alterations. In our study, several other predator species were present on all islands: feral cats, black rats and the stone marten. The decrease in abundance and extirpations of reptile and amphibian species are not due to predation by rats because there is no significant difference in rat abundance between mongoose-free and mongoose infested islands (A. Barun & D. Simberloff, in prep.), and we have no evidence to suggest that the feral cat populations are the same or different and/or being controlled on

any islands. The stone marten is mostly nocturnal, so it would have little to no impact on the diurnal snakes and lizards we studied. Also, abundances of the Balkan green lizard, the European glass lizard and most snake species are much higher on islands with just the stone marten, rats and cats, but not the mongoose (Lastovo, Dugi Otok, Brač , Cres, Krk, Lošinj) (A. Barun & I. Budinski, pers. obs.).

Long-term survival of amphibian and reptile species with low densities, such as several of those recorded on Adriatic islands, is questionable, and in the long run those species may be doomed to local extinction (Vitousek, 1988). Species that are historically present but unrecorded in our research are possibly already locally extinct or they might be restricted to areas or marginal habitats where we did not sample. It is important to note that most amphibian and reptile species we studied also occur on the mainland and are already in low numbers, and some are strictly protected under Appendix II of the Berne Convention. Amphibian populations along the Croatian coast are mostly isolated in small karstic ponds and threatened with local extinction because of the drying up or overgrowth of these ponds (Hutinec *et al.*, 2006). If the mongoose continues to spread along the coast it will threaten not only amphibians and reptiles but also many other conservation projects. The demonstrated impact of the mongoose on island herpetofaunal should be considered in light of the recent spread of this predator to the European mainland (Barun *et al.*, 2008). Once introduced elsewhere, the mongoose has spread very rapidly, and its presence on the Balkan Peninsula, which is a hotspot of European biodiversity, should raise alarms for

other faunas too (see Hays & Conant, 2007 for a review of the impact on other groups).

In sum, although interactions among multiple species confound interpretations of many of the patterns we have documented, our evidence is strong that the small Indian mongoose considerably affects several species, in particular several snake species, the Balkan green lizard, and the European green toad. Noteworthy is that the horned viper (a protected species) and the Balkan green lizard, though rare on Hvar, are apparently more common there than on the other two mongoose-infested islands (Korčula and Mljet). Alone among these islands, Hvar has been the site of an informal, private campaign to hunt and trap mongooses, and it is possible that this campaign has permitted larger populations of at least these two reptiles. If this is so, it suggests that an expanded, systematic effort to eradicate or at least suppress mongoose populations on these islands, under the auspices of the Croatian government, would substantially and rapidly benefit some reptile populations. Finally, the demonstrated impact of the mongoose on the herpetofaunal of these islands lends urgency to the need to confront the expanding population of this carnivore, which has recently spread south on the mainland to Montenegro and Albania and has established a toehold on a much smaller Croatian island far to the north of those we studied (Barun *et al.*, 2008).

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Appendix II

Tables and Figures

Table II-1. Species of Reptilia and Amphibia (rows) on islands (columns). X indicates species historically present on an island (Kryštufek & Kletečki, 2007), and in parentheses are the numbers of individuals found on an island. For snakes, amphibians, turtles and the Balkan green lizard *L. trilineata*, we report the total number found in April and May. For three species of small lizards, *P. melisellensis, D. oxycephala and T. mauritanica*, which were counted only on transects, we report the highest number recorded for the island for either April or May.

	Mongoose present			Mongoose absent		
	Mljet (31)	Korčula (21)	. . . . . (.)	. . . .	. . . . . .	. . . .
. . . .						
European Green Toad *(Bufo viridis)*	X	X (2)	X (4)	X (65)	X (18)	X (1)
Common Tree Frog *(Hyla arborea)*	-	X (16)	X	X	-	X (28)
Marsh Frog *(Pelophylax ridibundus)*	X	-	-	-	-	-
Turtles						
Hermann's Tortoise *(Testudo hermanni)*	X	X (1)	X	X	-	-
European Pond Terrapin *(Emys orbicularis)*	X	-	-	-	-	-
Marsh Frog *(Pelophylax ridibundus)*	X	-	-	-	-	-
Lizards						
Dalmatian Wall Lizard *(Podarcis melisellensis)*	X (155)	X (91)	X (30)	X (68)	X (352)	X (49)
Sharp-snouted Rock Lizard *(Dalmatolacerta oxycephala)*	X (53)	X (29)	X	X (1)	X (84)	-
Moorish Gecko *(Tarentola mauritanica)*	-	-	X (33)	-	-	-
Balkan Green Lizard *(Lacerta trilineata)*	-	X	X (2)	X (50)	-	-
Turkish Gecko *(Hemidactylus turcicus)*	X	X	X	X	X	X
Anatolian Worm Lizard *(Blanus strauchi)*	-	-	X	-	-	-
European Glass Lizard *(Pseudopus apodus)*	X	X (1)	X (19)	X (57)	X (12)	X (54)
Snakes						
European Cat Snake *(Telescopus fallax)*	X	X	X (1)	X	-	X
Balkan Whip Snake *(Hierophis gemonensis)*	X	X (1)	X (14)	X (3)	-	X (7)
Montpellier Snake *(Malpolon insignitus)*	X (3)	X (3)	X (1)	X (2)	-	X (8)
Four-lined Snake *(Elaphe quatuorlineata)*	X	X		X (4)	-	-
Aesculapian Snake *(Zamenis longissimus)*	X (1)	-	X (1)	X (7)	-	-
Leopard Snake *(Zamenis situla)*	-	X (2)	-	-	-	X (3)
Horned viper *(Vipera ammodytes)*	X	X	X (2)	X (2)	-	-
Smooth snake *(Coronella austriaca)*	X (2)	-	-	X	-	-
Large Whip Snake *(Dolichopis caspius)*	-	-	-	-	X (26)	-
Grass Snake *(Natrix natrix)*	-	X	X	X	-	X
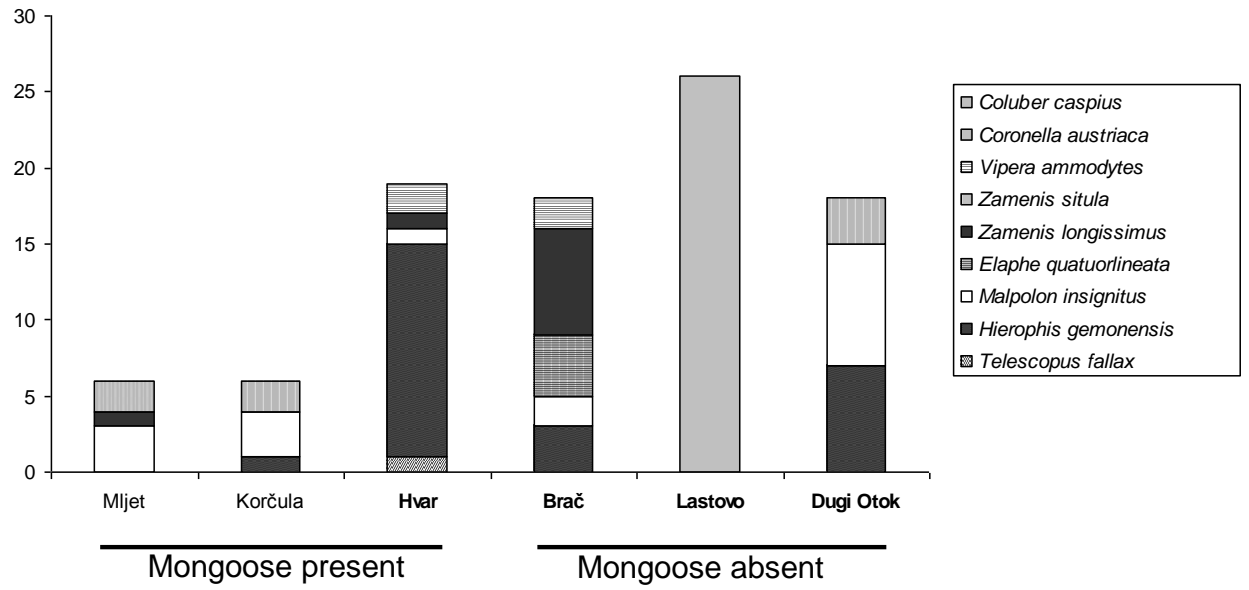
Figure II-1. Total number of snakes recorded for the surveyed islands.
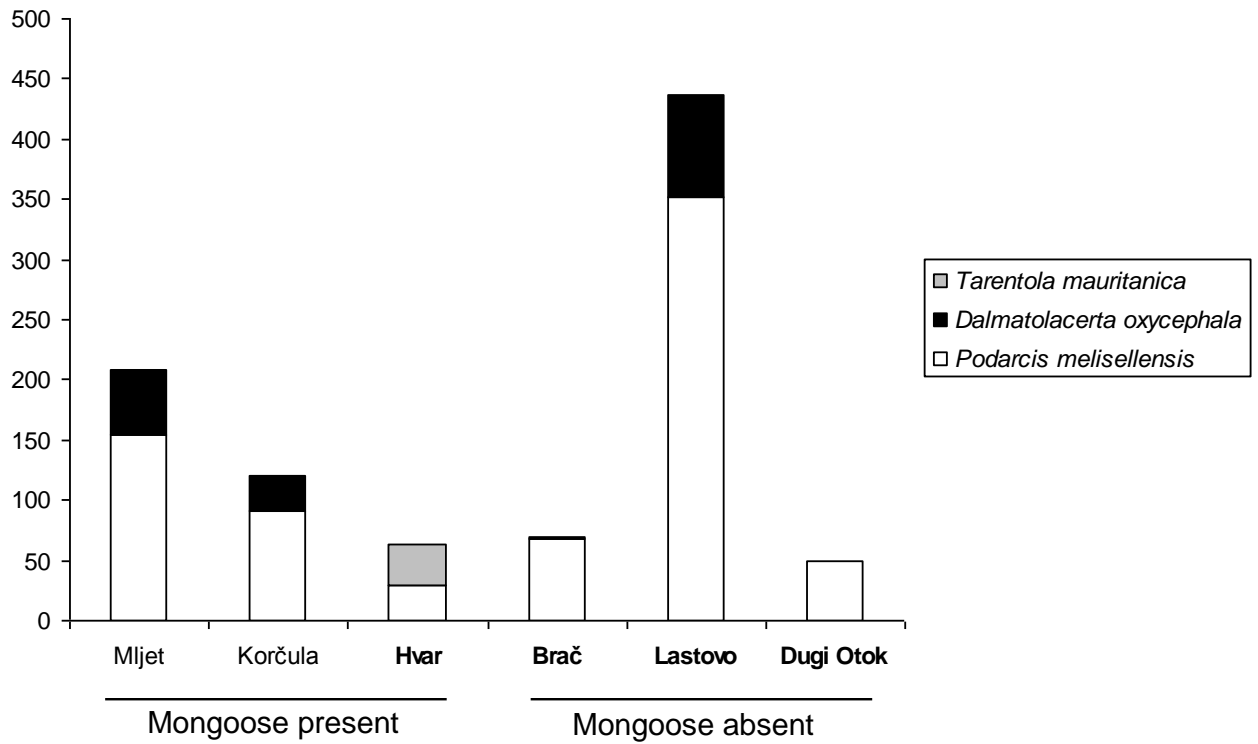
Figure II-2. Total number of small lizards (*Podarcis melisellensis,*

Dalmatolacerta oxycephal, Tarentola mauritanica) recorded for the surveyed

islands.

CHAPTER III.

IMPACT OF THE INTRODUCED SMALL INDIAN MONGOOSE (*HERPESTES AUROPUNCTATUS*) ON ABUNDANCE OF THE SMALL MAMMAL COMMUNITY AND ACTIVITY TIME OF THE INTRODUCED SHIP RAT (*RATTUS RATTUS*) ON ADRIATIC ISLANDS, CROATIA

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Abstract

The small Indian mongoose (*Herpestes auropunctatus)* is one of the world's 100 worst invasive species (IUCN, 2000). It has negative impacts on several small mammals on islands where it was introduced. We assess the abundance of small mammal populations and the activity time of introduced ship rats (*Rattus rattus*) on three mongoose-infested and three mongoose-free islands in the Adriatic Sea, Croatia. We set up a trapping system of INRA and ratière live traps on each island consisting of 30 traps of each type at 30m interval along the narrow dirt roads used as transects. Our results support an already large but mostly speculative literature that suggests inability of the small Indian mongoose to reduce high abundances of introduced *R. rattus*. Further, we suggest that the low abundance of native small mammals is probably not solely caused by the mongoose but also by high *R. rattus* populations on all six islands. In addition, we provide evidence that *R. rattus* has changed its activity time to become more nocturnal on mongoose-infested islands, possibly to avoid predation by the mongoose. As *R. rattus* became more nocturnal, the diurnal mongoose may have become the main predator on amphibians, reptiles, and poultry.

Introduction

The small Indian mongoose (*Herpestes auropunctatus*) has been listed by the IUCN (2000) as one of the world's 100 worst invasive species. Native to

southern Asia, it was introduced to many islands in the Pacific, the Indian Ocean and the Caribbean Sea (Simberloff *et al.* 2000, Thulin *et al.* 2006).

Most introductions were in the late 19th and early 20th century to control rats in sugar cane fields, but the success of the mongoose in this regard is questionable as rat numbers remain high (Hays and Conant 2007). Stone *et al.* (1994) have attributed this failure to the diurnal activity of the mongoose whereas rats are primarily nocturnal. Earlier authors have disputed this theory, claiming that the small Indian mongoose is an excellent ratter (Pemberton 1925, Barnum 1930, Doty 1945). Sharing this opinion, Doty (1945) nevertheless said that the mongoose has excellent ratter capacity but was made obsolete by the development of improved techniques of rat poisoning. However, Urich (1914) pointed out that rats became rare after introduction of the mongoose in the 1870s in Trinidad, and Espeut (1882) claimed mongoose introduction yielded huge monetary benefits in Jamaica.   Seaman (1952) found that ship rat populations were as high on St. Croix as 50 per hectare despite the presence of the mongoose. He believed that rats were as much a problem as before the introduction. In short, the literature on the mongoose as a ratter is conflicting. At best the mongoose only partially reduced populations of rats (Hinton and Dunn 1967). Moreover, data are mostly anecdotal, and there are no controlled studies looking at the mongoose's ability to control rats.

Aside from the ship rat specific case, no comprehensive study has been devoted to the impact of the mongoose on the abundance of native small mammal populations, although several studies have proposed the mongoose as a

major cause for the decline of species. For example, Woods and Ottenwalder (1992) suggested that introduction of the mongoose has contributed to extinction of four species of Haitian island shrews (*Nesophontes spp.*). Borroto-Paéz (2011) believed that the mongoose has been largely responsible for the endangered status of Cuban solenodon (*Solenodon cubanus*) and is suspected in the likely extinction of the dwarf hutia (*Mesocapromys nanus*). Yamada and Sugimura, (2004) linked the decline in the abundance of the threatened native rabbit (*Pentalagus furnessi*) on the Japanese island of Amami-Oshima to the spread of the mongoose across the island.

On Adriatic Islands, the mongoose was introduced in 1910 to Mljet Island to control a poisonous viper (*Vipera ammodytes*) and subsequently spread to several other islands (Korčula, Hvar, Čiovo, Škrda) (Tvrtković and Kryštufek 1990, Barun *et al.* 2008). Recently introduced to the Pelješac Peninsula, it is spreading along the southernmost part of the Dalmatian coast and has reached the Neretva River in the north (Barun *et al.* 2008) and Albania in the south (Ćirović *et al.* 2010). Nearly all Croatian large islands host a native carnivore, the stone marten (*Martes foina*), plus feral cats (*Felis sylvestris*) and the ship rat (*Rattus rattus*). The latter was introduced to the western Mediterranean region over 2000 years ago (Audouin-Rouzeau and Vigne 1994, 1997, Martin *et al.* 2000). The impact of the mongoose on rat and native small mammal abundance is unknown, but assessing the impact of one particular species among a predator community is not easy. Fortunately, the mongoose has been introduced to some but not all islands of Dalmatia. It is therefore possible to compare mongoose-

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infested and mongoose-free islands to attempt to determine the impact of the mongoose on the abundance of rats and native small mammals.

If introduced predators are capable of changing the abundance of their prey, conversely, prey may be able to assess predation risk and may behave accordingly, shifting their feeding, social, or escape behavior (Lima and Dill 1990, Kronfeld and Dayan 2003). For example, *R. rattus*, generally nocturnal, will be active and forage during the day if benefits outweigh risks. Berdoy and Macdonald (1991) have shown that socially subordinate individuals were forced to be diurnal to escape competition from dominants, and Fenn and Macdonald (1995) have shown that nocturnal visits by predators made it more dangerous for rats to be active by night than by day, forcing rats to be diurnal. Nellis and Everard (1983) found that rats became primarily nocturnal and arboreal after the introduction of the mongoose. In sum, rats can become more active diurnally, but cases of such a reversion are scarce and possible mechanisms untested. To test the hypotheses that rat activity times may depend on whether a nocturnal or diurnal predator is present, we have examined our trapping data for rat activity on islands with only the predominantly nocturnal stone marten, and on islands with both the stone marten and the diurnal mongoose.

The goals of this study are: i) to assess the abundance of introduced rats and native small mammals on mongoose-infested and mongoose-free islands; ii) to compare rat activity times on mongoose-infested and mongoose-free islands, all with the marten.

Methods

Study area and field methods. We conducted this study in 2008 on six islands in the southern part of Adriatic Sea: Lastovo (5,300 ha), Brač (39,400 ha), Dugi Otok (11,400 ha), Mljet (10,000 ha), Korčula (27,000 ha) and Hvar (29,900 ha). The first three are mongoose-free and the others are mongoose-infested. These islands are relatively similar in elevation, karst geology, Mediterranean climate and vegetation, but vary in surface area. They have a similar history of agricultural practices, human occupation, and timing of introduction of most exotic species. Their landscape is a fine-grained mosaic of small agricultural fields, scrublands (garrigue), shrublands (maquis, mattoral), and forests. Agricultural production is mainly for local consumption and consists of olive groves and vineyards, with a few small vegetable fields with rich soil. Garrigue (scrubland) is mostly dominated by *Erica arborea*, *E. multiflora, Cistus incanus*, *C. creticus, C. salviifolius, C. monspeliensis, Spartium junceum, Calicotome villosa*, and *Rosmarinus officinalis*. Thickets of evergreen sclerophyll shrubs and small trees (maquis) are dominated by *Fraxinus ornus, Pistacia terebinthus, Quercus ilex, Phillyrea latifolia, Myrtus communis, Arbutus unedo, Laurus nobilis, Erica arborea, Lonicera implexa, L. etrusca, Tamus communis, Olea europaea oleaster, Smilax aspera, Rubia peregrina*, and *Asparagus acutifolius*. Forests are dominated mostly by *Pinus halepensis* and evergreen oak *(Quercus ilex)*.

To determine small mammal abundance on every island, we set up three transects of 30 trapping spots distributed at 30 meter intervals in 900m long

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transects along narrow dirt roads, each running through all four vegetation types described previously. Proportions of the various vegetation types may vary among transects, but all transects traversed all four vegetation types. Trap locations were placed sequentially on opposite sides of the road and each location received two live traps: one INRA trap to capture mammals weighing less than 30 g and one ratière trap (Guédon *et al.* 1990) to trap heavier mammals, particularly ship rats and mongooses. Traps were baited with a mixture of oat-flakes, peanut butter, and sardine oil, and bait was changed once during the three-day trapping period or just after rain. We ran the trapping system for three days and three nights in April and repeated the procedure in May at the same locations. We did not trap during rainy nights. We checked each trap early in the morning to collect nocturnal small mammals and before sunset to collect the diurnal mongoose. Trapped animals were either euthanized and preserved for museum deposition or released at least one kilometer away from the transect.

Local habitat structure and analysis. To describe vegetation structures, four sample locations were evenly spaced along each transect, and the following data were collected within a 50-meter radius: % cover of bare ground, dead wood, rock, detritus, grasses in three layers (0-0.25 m, 0.25-0.5 m, 0.5-1 m); % cover of vegetation layers (0-0.25 m, 0.25-0.5 m, 0.5-1 m, 1-2 m, 2-4 m, 4-8 m, 8-16 m, 16-32 m, >32 m), maximum height of vegetation, canopy height, and % cover of each woody plant species. Within each vegetation layer, the relative cover was defined as the projection of the foliage volume of the layer on a horizontal plane. This was estimated by comparison with a reference percent

cover chart (Prodon and Lebreton, 1981). At each point we also recorded percent cover of each woody plant species present and its average height.

We used PRIMER (Plymouth Marine Laboratory, UK) to conduct an analysis of similarity (ANOSIM) followed by pairwise comparisons to examine if two habitat variables (habitat characteristics and percent cover of each woody plant species) differed between islands with and without the mongoose. In the analysis, we nested six islands into two main grouping factors: mongoose present and mongoose absent. For each habitat variable, habitat characteristic, and percent cover of each woody plant species, we constructed a nonmetric multidimensional scaling (NMDS) plot, a nonparametric approach, using Bray–Curtis similarity coefficients from a triangular matrix (Bray and Curtis 1957) of euclidean distances of islands with versus islands without the mongoose. The NMDS plot can also illustrate similarity and/or dissimilarity in habitat characteristics between the two island groups.

Abundance analysis. To compare abundances of single species between islands with and without the mongoose, we calculated a Minimum Number Alive index (MNA) (Hilborn *et al.* 1976). This index is a ratio of the number of trapped animals belonging to one species to the number of trap-nights. However, several traps may be inoperative for one or all target species during parts of trapping sessions. Traps were inoperative for all species when they were found closed and empty. Traps were inoperative for a species when they contained an individual of any other species. The number of trap-nights used to compute the MNA index

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was the number of functional trap-nights for each target species (Pascal *et al.* 2009). The species one (*Sp1*) MNA index was computed as follows:

*Sp1*MNA = *Sp1*C/(NT-NTO – Sum AllSpp)

*Sp1*C is the number of captures for species one, NT is the total number of trap-nights, and NTO is the number of trap-nights the trap was inoperative for species one, whereas SumAllSpp is the total number of all other species captured in traps.

To compare *R. rattus* and wood mouse (*Apodemus sylvaticus*) abundances between islands with and without mongooses, we calculated mean MNA indexes for each species for the three transects for each island and compared those values for the three islands with mongooses vs. the three mongoose-free islands with a t-test. To compare *R. rattus* activity times on mongoose-infested and mongoose-free islands, we performed Fisher's exact test on the total number of captured rats for all three transects for each island, but we kept daytime captures separate from night captures. We performed all analyses in JMP, Version 8. (SAS Institute Inc., Cary, NC).

Results

ANOSIM indicated that composition of habitat characteristics did not differ between islands with the mongoose and islands without it (global R = -0.359, P = 0.1), nor did the percent cover of woody plant species differ (global R = -0.457, P = 0.1).

In Table III-1 we list the mammal species found on each island according to Kryštufek and Kletečki (2007) and the number of specimens trapped during our field operations. Apart from 23 reptiles (*Pseudopus apodus* and *Dalmatolacerta oxycephala*) and one amphibian (one *Bufo viridis*), the 699 other captures belonged to eight mammal species among the 14 species recorded as present on the studied islands. The largest samples came from three species, two aliens, *R. rattus* (499) and *H. auropunctatus* (57), and one presently considered native, *A. sylvaticus* (122). Specimen numbers of these three species constitute altogether 97 % of all mammalian captures and afforded the only opportunity to calculate MNA indices.

Mongooses were most abundant on Mljet and Korčula and much scarcer on Hvar (Fig. III-1). Dormice (*Glis glis*) were not caught because of the prolonged hibernation time of this species in trapping months. MNA of rats did not differ between islands with the mongoose and those without it (F = 0.291, df = 5, p = 0.619). Similarly, MNA of *A. sylvaticus* did not differ did not differ between mongoose-infested and mongoose-free islands (F = 3.523, df = 5, p = 0.134).

The frequency of rats trapped during the day on mongoose-free islands exceeded that on mongoose-infested islands, (P < 0.001, Fisher's exact test, Fig. III-1).

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Discussion

Our data are too scant to allow a precise sense of the impact of the mongoose on small mammals on these islands. However, combined with previous work on the mongoose diet on these islands (Barun et al. 2010), our results are suggestive. We have previously reported the following results from stomachs of 57 trapped mongooses: 19 were empty, 39 contained vegetation and/or animal remains, and only five produced hairs, one identified to *A. sylvaticus* (Barun *et al.* 2010).   The dietary results accord with those of several studies devoted to the mongoose diet in insular ecosystems, which concluded that the spectrum of items is very large and encompasses many plants and animals (i.e., Nellis and Everard 1983). It is likely that few of the small mammals we targeted were potential prey for the mongoose. Among the 14 mammalian species recorded on these islands, three are large and carnivorous, and two are arboricolous Myoxidae, all out of reach of the mongoose, which cannot confront the carnivorous species and is a poor climber. Among the nine remaining species, the hedgehog (*Erinaceus concolor)* and the hare (*Lepus europaeus)* both have natural defenses against mongoose predation (spines for the hedgehog and speed for the hare). Among the remaining species that may constitute prey for the mongoose are two shrews, *Suncus etruscus* and *Crocidura suaveolens*, and four rodents, of whic one is native (*Apodemus epimelas*), one is cryptogenic according to the definition of Carlton (1996) (*A. sylvaticus*), and two are alien and invasive (*Mus musculus* and *R. rattus*).

Although the INRA traps and the bait we used are effective for capturing

C. suaveolens (Pascal *et al.* 2009), and despite a significant trapping effort, the

number of trapped *C. suaveolens* was small (n=15). Nevertheless, despite the fact

that the species has been captured on the six islands under study, and despite the

fact that the total number of captures on mongoose-free islands is higher (11)

than on islands with mongooses (4), the sample sizes are not sufficient to allow

strong conclusions. Moreover, several *R. norvegicus* eradications on islands of

the English Channel and French Atlantic coast have shown a strong detrimental

effect of the rodent on two shrew species, *C. suaveolens* and *C. russula* (Pascal *et

al.* 2005). One cannot yet exclude a similar effect of *R. rattus* on *C. suaveolens*

for Croatian populations, and perhaps also on *S. etruscus*, recorded previously

only on Hvar, where we did not record it.

As stated previously, the small Indian mongoose has frequently been cited

as a species that could send already low island populations to the brink of

extinction. In addition to the examples cited above, on Amami-Ohshima Island,

the shrew *Crocidura orii* is considered endangered because of the mongoose

introduction (Yamada and Sugimura 2004). On Adriatic islands, the lesser white-

toothed shrew *C. suaveolens* is already thought to be very rare (Dulić 1969), but

which introduced predator is to blame cannot be determined.

As with *C. suaveolens*, INRA traps and the bait used are efficient for

capturing house mice on islands (Pascal *et al.* 2009). Despite this efficiency and

the trapping effort, we captured only one mouse, the species having been

recorded previously on these six islands. This result suggests that the species is

scarce. However, several rodent eradication attempts have shown that mouse outbreaks occur when rats are successfully eradicated (references in Caut *et al.* 2007), suggesting mouse suppression by rats. Thus, our result does not by itself strongly implicate an impact by the mongoose. Moreover, interaction among several Muridae species in insular ecosystems has been suspected elsewhere. For example, an inventory of the micro-mammalian fauna of the insular system located at the Atlantic mouth of the English Channel and composed of the large island of Ushant (1560 ha) and the 16 islands of the Moléne Archipelago (all less than 100 ha) was performed between 1992 and 2000. Four murid species were recorded, three introduced (*R. rattus*, *R. norvegicus* and *M. musculus*) and one native (*A. sylvaticus*). These four species are present on Ushant, but only one or none of the four on each island in the Moléne Archipelago (Pascal 2002). Preliminary results of archaeological research suggest that *A. sylvaticus* had been present on all these islands before invasion by the three other murids. These results suggest that strong interactions occur between these species, leading to replacement if island area is small.

Experimental conditions and our protocol do not allow us to address rigorously the question of the specific consequences of the introduction of the two major alien species, *H. auropunctatus* and *R. rattus*, on the native mammals. Nevertheless, the capture frequency of native species was more than three times greater on the islands without the mongoose (107) than on islands with the mongoose (33); the number of *R. rattus* captures was one-third higher in the first situation (303) than in the second (196). This general trend suggests that at least

one of the alien species has a detrimental effect on the native mammalian fauna, and probably both do.

In either case, our analyses show no statistical difference in *R. rattus* abundance on islands with and without the mongoose, and this result is in accordance with an already large but mostly speculative literature suggesting that the small Indian mongoose does not control introduced *R. rattus*. The traditional but false idea that mongooses are good ratters is similar to lore about the domestic cat. It has been demonstrated that domestic cats (May 1988) and feral cats (Nogales et al. 2004, Bonnaud et al. 2007, Matias and Catry 2008) have strong detrimental effects on native birds, small mammals, and herpetofauna, but their impact on rat populations is insignificant or non-existent in urban (Glass *et al.* 2009) and several island ecosystems.

Our analyses show that the percentages of rats trapped during the day on mongoose-free islands exceeded those on mongoose-infested islands. This result accords with the proposed mechanism explaining the poor performance of the mongoose in reducing rat populations (Nellis and Everard 1983) and the shift of rat activity under predation pressure (Fenn and Macdonald 1995). Additionally, as rats become less vulnerable to mongoose predation through modification of their activity time, the mongoose may increase predation pressure on amphibians, reptiles, and poultry (Barun *et al.* 2010). Our results expand on previous work and show that the mongoose may not only have detrimental effects on native species of conservation concern but may also affect behavior of another introduced species, *R. rattus*, that is a major target species of insular eradication

attempts (Howald *et al.* 2007). Consequences of such interspecific interactions must be taken into consideration in planning eradication operations (Courchamp *et al.* 2003).

Acknowledgments

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Appendix III

Tables and Figures

Table III-1: Mammalian species distributions on the islands under study after Kryštufek and Kletečki (2007). X : present; - : absent; numbers are numbers of trapped individuals during our experiment.

	Mongoose PRESENT			Mongoose ABSENT		
	Mljet	Korčula	Hvar	Brač	Lastovo	Dugi Otok
Herpestes auropunctatus	31	21	5	-	-	-
Martes foina	X	X	X	X	X	X
Canis aureus	-	X	-	-	-	-
Felis sylvestris (feral)	X	X	X	X	1	X
Rattus rattus	158	83	62	55	44	97
Mus musculus	1	X	X	X	X	X
Apodemus sylvaticus	-	22	4	54	29	13
Apodemus epimelas	1	X	-	-	-	-
Suncus etruscus	-	-	X	-	-	-
Crocidura suaveolens	2	1	1	6	1	4
Eliomys quercinus	-	3	X	X	X	-
Glis glis	X	X	X	X	-	-
Erinaceus concolor	X	X	X	X	X	-
Lepus europaeus	X	X	X	X	X	X
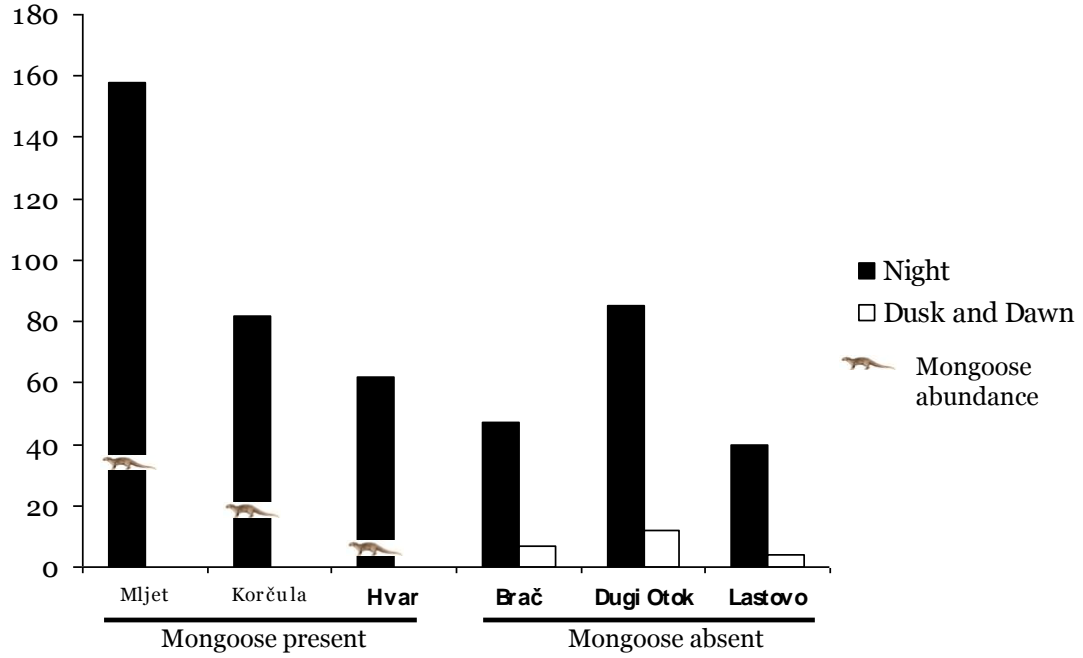
Figure III-1: Total number (April and May) of trapped rats during the day and night (dusk and dawn) on three islands with the mongoose and three islands without the mongoose. Mongoose abundance is illustrated with the picture of a mongoose for each island.

CHAPTER IV.

A REVIEW OF SMALL INDIAN MONGOOSE MANAGEMENT AND ERADICATIONS ON ISLANDS

In press in Island invasives: Eradication and management

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Abstract

The small Indian mongoose (*Herpestes auropunctatus*) is one of the world's 100 worst invasive species. It is a generalist feeder blamed for many declines and extirpations of vertebrates on islands. Native to Asia, it has been introduced to at least 64 islands (Pacific and Indian Oceans, Caribbean and Adriatic Seas) and the mainland (Europe, South America, Australia and North America). Most introductions were in the late 19th and early 20th centuries to control rats in sugar cane fields, but also to control snakes. Although recent mongoose introductions are few, the risk of intentional or accidental spread remains high, and many island taxa are susceptible to their effects. The mongoose has been eradicated from at least six islands (≤115 ha: Buck, Fajou, Leduck, Praslin, Codrington and Green) by trapping and secondary poisoning, but eradication has proven challenging. Two earlier island eradication campaigns against mongoose failed on Buck (182 ha) and Piñeros (390 ha) and campaigns are currently underway on the large islands of Amami-Oshima and northern Okinawa. Attempts to control the mongoose were numerous in the past, and several programmes are underway using trapping and/or poisoning. New techniques are being developed and show promise for eradication. The mongoose can be eradicated with current approaches on small islands with the aim of benefiting endemic species or preventing further introductions. More efficient methods and strategies are needed for successful eradication on larger islands and may facilitate containment of mongoose on the European and South

American mainlands.

Introduction

Native to the Middle East and much of southern Asia, the small Indian

mongoose (*Herpestes auropunctatus,* hereafter mongoose) (Hodgson 1836;

Veron *et al.* 2007; Patou *et al.* 2009) has been introduced successfully to islands

in the Pacific and Indian Oceans, the Caribbean and Adriatic Seas, and to

continental South America and Europe, but was unsuccessfully introduced to

North America and Australia (Nellis and Everard 1983; Nellis 1989; Nellis *et al.*

1978; Barun *et al.* 2008). Most introductions were in the late 19th and early 20th

centuries to control rats in sugar cane fields, but with questionable success as rat

population estimates remained high (Hinton and Dunn 1967). The mongoose was

also introduced to control native poisonous snakes including a pit viper, the habu

(*Trimeresurus flavoviridis*), on several islands in Japan, the fer-de-lance

(*Bothrops lanceolatus*) on Martinique and St. Lucia, *B. caribaeus* in the West

Indies, and the horned viper (*Vipera ammodytes*) on Adriatic islands.

The mongoose is a generalist predator that has been identified as one of

the world's 100 worst invasive species (IUCN 2000) because of its role in the

decline and extirpation of native mammals, birds, reptiles, and amphibians

(Baldwin *et al.* 1952; Pimentel 1955a; Seaman and Randall 1962; Nellis and

Everard 1983; Nellis and Small 1983; Coblentz and Coblentz 1985; Nellis 1989;

Case and Bolger 1991; Henderson 1992; Yamada 2002; Powell and Henderson

2005; Henderson and Berg 2006; Hays and Conant 2007, Barun *et al.* 2010). In their review of the effects of mongoose on native species, Hays and Conant (2007) found that greatest impacts were on native fauna with no past experience with predatory mammals. In addition, mongoose carries human and animal diseases, including rabies and human *Leptospira* bacterium (Pimentel 1955a; Nellis and Everard 1983).

Eradication of introduced mammals is a powerful conservation tool (Genovesi 2007), but mongoose eradication has been attempted on few occasions and with limited success. A known total of eight eradication campaigns and many control campaigns have been conducted to remove or reduce island mongoose populations. However, even with their limited scope, these attempts probably prevented further declines or even extirpations of native species, although definitive data are lacking. Very few teams have the technical expertise to remove mongoose successfully, even from small islands. Such lack of expertise is reflected by past failures and little progress beyond local control programmes. In addition, most control and eradication efforts are published in the grey literature, if at all, so information is often hard to find for conservation practitioners contemplating mongoose eradication.

We reviewed data from the published and grey literature on eradication and control campaigns, focusing on assessing successes, failures, and challenges. We compiled a list of all islands with known mongoose populations and communicated with researchers and managers who work either directly with the mongoose or with species it affects. Our aim was to facilitate mongoose

eradication efforts and direct researchers to areas of applied research that would aid this goal.

Biology of the mongoose

The mongoose is entirely diurnal (AB pers. obs.) and can swim and climb trees (Nellis and Everard 1983), but rarely does so. Mongooses avoid water when possible; they reduce their activity during rainy periods and will not voluntarily enter water deeper than about 5 cm (Nellis and Everard 1983). Such characteristics may account for the failure of mongoose to invade islands only 120 m from occupied sites (Nellis and Everard 1983). However, in Fiji, mongooses get fish out of nets in the water (Craig Morley pers. obs.). This may be a behavioural adaptation specific to that site.

Mongoose home ranges average 2.2 - 3.1 ha for females and 3.6 - 4.2 ha for males; home ranges often overlap and can be as small as 0.75 ha (Nellis and Everard 1983). Areas in the Caribbean may harbour 1-10+ mongoose/ha (Nellis 1989), but populations generally average 2.5 individuals/ha (Pimentel 1955a). On Oʻahu, Hawaiʻi, mean home ranges were 1.4 ha for females and five males shared a region of about 20 ha (Hays and Conant 2003).

Females are pregnant from February through August in Fiji (Gorman 1976b), the US Virgin Islands (Nellis and Everard 1983), and Hawaiʻi (Pearson and Baldwin 1953), but the mongoose on Grenada has a 10-month breeding season (Nellis and Everard 1983). Gestation takes 49 days, with litter size of 2.2

on average (range = 1 – 5) (Nellis and Everard 1983). The number of litters produced annually has not yet been determined. Pups begin accompanying their mother on hunting trips at six weeks of age (about 200 g body mass). The youngest wild-caught pregnant female was four months old (Nellis and Everard 1983).

Status of mongoose populations

Previous eradication attempts

Globally, at least 64 islands harbour introduced mongooses (Table IV-1), which are also on the northeastern coastal fringe of South America (Guyana and Surinam; Nellis 1989) and in Adriatic Europe (Croatia, Bosnia and Herzegovina, Montenegro; Barun *et al.* 2008).

Mongoose have been eradicated from six islands and were prevented from establishing on mainland North America when the first few immigrants were caught on Dodge Island, Florida. On Praslin Island, one mongoose was caught in a baited box trap (Dickinson et al. 2001, Quentin Bloxam pers. comm.). The Virgin Islands Division of Fish and Wildlife eradicated a breeding population of mongooses in the 1970s from Leduck Island using 19 x 19 x 48 cm Tomahawk box traps with meat bait (Nellis 1982) and another population from Buck Island in the 1980s also with box traps. This latter success followed an earlier failed attempt (see below). Buck Island has since remained free of the mongoose (McNair 2003; David Nellis pers. comm.).

A campaign on the French West Indian possession of Fajou Island used box-trapping for mongooses and possibly secondary poisoning from a simultaneous rat (*Rattus rattus*) and house mouse (*Mus musculus*) eradication effort using 50 ppm bromadiolone paraffin baits (Lorvelec *et al.* 2004). All trapped mongooses were dissected and none showed toxic bait in the stomach or haemorrhagic syndrome. During a one-month campaign in 2001, 18 people worked full-time to eradicate these three species.

The Antiguan Racer Conservation Project eradicated very small mongoose populations from two islands off Antigua in the West Indies. On Codrington Island, mongoose were eradicated using secondary poisoning from ingesting rats (*Rattus rattus*) poisoned with brodifacoum. The bodies of two poisoned mongooses were found (likely the total number that had been present on this very small island). There is also anecdotal evidence that mongooses were present on Green Island at least one year prior to the rat eradication but were absent afterwards. However, no mongoose carcasses were found during the rat eradication campaign (Jennifer Daltry pers. comm.).

In 1976, the US Fish and Wildlife Service received reports of a mongoose sighting at the Port of Miami on Dodge Island, Florida. Trapping conducted in the area yielded one young female. Interviews with people in the area revealed that two other mongooses had been killed by vehicles a month earlier (Nellis *et al.* 1978).

Failed mongoose eradications include Isla Piñeros, Puerto Rico, and an early attempt on Buck Island. The latter eradication campaign was initiated by

the US National Park Service in 1962 (Everard 1975; cited by Everard and

Everard 1992). After 10 years of trapping and poisoning, mongooses remained,

and eradication efforts were eventually stopped because the ranger conducting

the programme was transferred (Nellis *et al.* 1978, Nellis pers. comm.).

On Isla Piñeros fish baits with thallium sulfate may have killed all adult

mongooses, which ceased to appear in traps seven days after poisoning began.

However, four months later several juvenile mongooses were trapped, indicating

that either they had been present in dens, had been too small to spring the traps,

and/or bait density had been insufficient to put these juvenile mongooses at risk

possibly owing to a reduced home range (Pimentel 1955b).

Current eradication campaigns

We know of only two current island efforts to eradicate the mongoose.

Both attempts are in Japan where the mongoose is present on Okinawa and

Amami-Oshima in the Ryukyu Islands, and on the main island of Kyushu. The

Kyushu population is regarded by some as a recent discovery, but according to

locals, mongoose have been there for at least 30 years.

On Amami-Oshima, the Japanese Ministry of the Environment began

intensive mongoose control in 2000. Earlier control by local governments of

Naze city (1993-2003, 128 km²), Sumiyo Village (1998-2002, 118 km²), and

Yamato Village (1995-2003, 90 km²) captured 8,229 mongooses from 1993 until

1999. In an extensive alien eradication programme initiated by the Ministry of

the Environment, mongooses were livetrapped by local residents, mainly on a

bounty system from 2000 until 2004. Between 60,000 to 317,000 trap-nights

and 40 to 131 trappers captured 16,636 mongooses over the five years. The

trappers were paid about US$ 20 per mongoose the first year, about US$ 36 the

second and third years, and about US$ 45 the last year to try to increase

incentives at low abundance. In 2003, three full-time trappers were employed to

capture mongooses in low-density areas and began using kill traps. In 2009, 44-

48 people were working full-time as Amami Mongoose Busters. Over a five-year

period from 2005 until 2009, the Amami Mongoose Busters captured over 7,500

mongooses. From 2000 until 2004 about US$ 1,140,000 (122,000,000 JPY) was

spent on the Amami-Alien control programme and from 2005 to 2009 about US$

7,224,000 (695,000,000 JPY) on the Amami-Mongoose eradication programme

(Abe *et al.* 1991; Ishii 2003; Yamada 2002; Yamada and Sugimura 2004;

Shintaro Abe pers. comm.). A continuing eradication effort is planned until 2014.

On Okinawa, the Okinawa prefecture and the Japanese Ministry of the

Environment initiated an alien control programme (2000-2004) in the Yambaru

area of the northern part of the island, and in 2005 this became an eradication

campaign. By 2009, 30 people were employed as full-time Yambaru Mongoose

Busters. About four km of mongoose-proof fence was constructed in 2005 and

2006 by Okinawa prefecture to separate the trapped area (about 30,000 ha) from

the uncontrolled area. From 2000 until 2004, 1831 mongooses were captured

with 555,000 trap-nights, and from 2005 until 2009 the Yambaru Mongoose

Busters captured over 2680 mongooses with 2,431,000 trap-nights. The total

cost for the eradication programme from 2005 until 2009 in the Yambaru area by

Okinawa prefecture was about US$ 5,058,000 (486,000,000 JPY including fence construction) and for the mongoose eradication programme by the Ministry of the Environment was about US$ 2,352,000 (226,000,000 JPY) (Yamada and Sugimura 2004, Shintaro Abe pers. comm.).

Past and present "control"/management

Adriatic

In Europe, the mongoose is present on the Croatian islands of Mljet, Korčula, Hvar, Čiovo, Škrda, Kobrava, as well as the Pelješac Peninsula. The species has recently spread along the coast in Croatia, Bosnia and Herzegovina, and Montenegro at least as far as the Albanian border (Barun *et al.* 2008), but the full extent of the range is unknown. The coastal spread of mongoose may have resulted from several separate introductions. Two private mongoose control campaigns are being conducted by local hunters on Hvar and on Čiovo. On Hvar, under the guise of predator control, hunters are required annually either to pay a fee (equivalent to ca. $US100) or to submit three mongoose tails or one tail of a native stone marten (*Martes foina*). Most mongooses are trapped there in locally made cages or leg-hold traps. On Čiovo, the only Adriatic island with the mongoose and not the stone marten, the regional hunting organization distributes "rat" poison for mongoose control during the annual autumn meeting (this procedure is illegal in Croatia, so we could not determine which poison).

Caribbean

In the Caribbean, the mongoose is present on 33 islands, many of which have no control (Table IV-1). Of the occupied islands in the British Virgin Islands, only Jost Van Dyke (JVD) has ongoing mongoose control. The mongoose was introduced to JVD in the 1970s to get rid of the rear-fanged colubrid snake (*Borikenophis portoricensis*). In 2006, the JVD Preservation Society with the help of several volunteers started live-trapping mongooses (Susan Zaluski pers. comm.).

In Puerto Rico, the US Forest Service and USDA APHIS Wildlife Services livetrapped in El Yunque National Forest to protect the critically endangered Puerto Rican parrot (*Amazona vittata*). The US Forest Service annually spends about $10,000 a year with two personnel who trap periodically, so the cost for mongoose control alone is difficult to estimate. A scheduled control of rabies virus vectors was planned for 2010, and targets included the mongoose (Everard and Everard 1992; Pimentel 1955b; Felipe Cano pers. comm.).

In Jamaica, the Jamaican Iguana Recovery Group collaborated in 1997 with Fort Worth Zoo, Milwaukee County Zoo, Zoological Society of San Diego and the University of the West Indies, Mona, to initiate a mongoose control operation in the central Hellshire Hills to protect the critically endangered Jamaican iguana (*Cyclura collei*). Live traps are operational every day and >1000 mongooses have been trapped to date. The approximate cost is US$ 400/month for the salary for one person (Byron Wilson pers. comm.). Two islands near Jamaica, Goat Major

and Goat Minor, have been proposed for simultaneous eradication of mongooses and cats, in addition to goats.

On the US Virgin Island of St. Croix, USFWS conducts small-scale mongoose control near sea turtle nesting sites during the turtle breeding season at Sandy Point National Wildlife Refuge (Claudia Lombard, pers. comm.). Tomahawk traps are used along 200 to 500-m lines along the beach vegetation. A similar mongoose trapping programme by Virgin Islands National Park staff has been ongoing for five years on St. John. Mongooses are livetrapped on beaches at Hawksnest, Dennis, Jumbi, Trunk, Cinnamon, Maho, Francis, Leinster, Coccoloba, Western Reef Bay, Genti, Little Lameshur, Great Lameshur, and Salt Pond Bay; salt ponds; the National Park Service visitor center, and along some roadways on the north shore (Carrie Stengel, pers. comm.).

On St Lucia, the Durrell Wildlife Conservation Trust and St. Lucia Forestry Department (Ministry of Agriculture, Lands, Forestry and Fisheries) conducted two short removal experiments using live traps with chicken bait at an iguana nesting site (Matt Morton pers. comm.).

In 1902, the Agricultural Society on Trinidad started a bounty system of paying per carcass turned in; 30,895 mongooses were turned in from 1902 to 1908 and 142,324 from 1927 to 1930. We do not know when the bounty system stopped operating (Urich 1931).

In 1977, between July and December, a mongoose control operation performed by the Public Health Agency on Guadeloupe yielded 15,787 mongooses

(Botino 1977 in Pascal *et al.* 1996), but the capture technique details are unknown because all mongooses were submitted by local residents.

On Cuba, nation-wide mongoose rabies control was undertaken between 1981 and 1985. In the municipality of Arabos, Matanzas Province, in 1984, the mongoose control was carried out by injecting 1,161,682 eggs with strychnine sulfate. Eggs were placed in bamboo or tin pipes to protect them from other animals. Non-poisoned baits were used in mongoose traps that were spaced about 30 m apart over an unknown area. Five to ten people worked per team for a total of about 500 people during that entire operation (Everard and Everard 1992).

In the mid-1970s, mongoose rabies control was undertaken throughout Grenada using sodium fluoroacetate (1080) in 50g of glutinous boiled cowhide. Sixteen baiters/trappers and staff using two vehicles distributed about 300 baits per baiter every day for about nine months. Average mongoose densities dropped from 7.4 to 2.5, but within six months the population recovered (Everard and Everard 1992).

Pacific

In the Hawaiian islands, many sightings of mongooses and one road kill in the 1970s were reported on Kauai but none have been trapped recently despite an extensive effort over the entire island. Elsewhere, widespread control or eradication is not being attempted, but mongoose control is performed in many small (<100 ha) areas to protect birds in upland native bird sanctuaries,

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wetlands, and wet forests during the breeding season. Agencies involved include the US Fish and Wildlife Service, Hawaii Nature Conservancy, Hawaii State Department of Land and Natural Resources (Wildlife Division), US National Park Service, USDA Wildlife Services, (Department of Army) along with private landowners. Live-traps (Tomahawk) and registered (SLN-Hawaii) diphacinone (50 ppm) wax bait (in bait stations) are employed. The US Department of Agriculture on the island of Hawaii has recently completed field studies evaluating various lures, attractants, and bait types (Pitt and Sugihara 2009). Staff performing mongoose control work are also responsible for other duties, so it is difficult to estimate the total cost for the State of Hawaii (Robert Sugihara pers. comm.).

The small Indian mongoose occurs on 13 islands in Fiji, where a recent molecular study also identified some populations of the Indian brown mongoose, *Herpestes fuscus* (Morley 2004, 2007; Patou *et al.* 2009). Currently there are no attempts to eradicate either mongoose species from any of the Fijian islands (Craig Morley pers. comm.).

Recently, mongooses were seen in the Aleipata area of Upolu Island, Samoa and in New Caledonia. One male mongoose was captured during initial trapping on Upolo by the Samoan National Invasive Task Team (Mark Bonin and James Atherton pers. comm.). On New Caledonia, a mongoose infestation was recently reported in Nouméa, and two individuals were trapped (Patrick Barriere pers comm.).

South America

The mongoose is present in Suriname and Guyana but we are unaware of control efforts. Previous reports of the mongoose in French Guiana (Nellis 1989) are not supported by recent evidence (Michel Pascal pers. comm.; Soubeyran 2008).

Africa

On the main island of Mauritius, the Mauritian Wildlife Foundation started a control programme in the Black River Gorges National Park in 1988 as part of the Pink Pigeon Project of reintroduction and predator control (cats, rats, mongooses). Year-round control is conducted with 10-12 students, staff, and volunteers. Wooden box traps (live drop traps) baited with salted fish are primarily used, but for elusive individuals a mix of live/kill traps and change of bait is employed. Estimated total cost is ca. US$ 20,000 per year (Roy *et al.* 2002; Carl Jones and Vikash Tatayah pers. comm.).

The mongoose was introduced to Grand Comore during the colonial period (Louette 1987), but no control programme has been reported (Michel Louette pers. comm.). We have no information on mongoose control efforts on the Tanzanian island of Mafia, but the presence of mongoose was confirmed in a recent report (Walsh 2007).

Eradication methods

Traps and baits

Trapping and toxic baiting have been employed for mongoose control and eradication (Lorvelec *et al.* 2004; Nellis 1982; Nellis *et al.* 1978; Pimentel 1955b; Yamada and Sugimura 2004). Hunting is not known to be employed or expected to be effective.

Mongooses appear susceptible to live traps, particularly box traps, which have been the primary method used to control and eradicate the mongoose. However, anecdotal evidence suggests some animals may become trap-shy or are naturally wary and cannot be trapped with this method (Tomich 1969; AB pers. obs.). Padded leg-hold traps have been used successfully in Hawaii for adult mongooses, but juveniles often do not exert enough pressure to trigger traps unless the trigger is very sensitive (James Bruch pers. comm.). Live traps have the advantage that non-target captures can often be released unharmed, but ethical regulations require them to be checked frequently. Kill traps have been used on Okinawa and Amami-Oshima with great success. Recent trials of the Doc250 kill traps in Hawaii demonstrate that they may be more effective than box traps (Peters *et al.* this issue). Kill traps have the advantage that they do not require routine checks except to re-bait/scent or remove carcasses. Where housings around kill traps can eliminate (or reduce to acceptable levels) the risk to non-target species, kill traps would be the preferred trap type. For eradication campaigns, multiple trap and bait/scent types should be considered, as wariness or aversion to one combination may not be transferable to others.

Live traps have typically been deployed on grids. For eradications, at least one trap must be in each home range area, which is a minimum area of 0.75 ha (Nellis and Everard 1983). The successful campaign on Buck Island used box traps on a 50 x 50 m grid (National Park Service 1993), and that on Fajou used a 30 x 60 m grid (Lorvelec *et al.* 2004). As for other species, having key trap locations is more important than having traps spaced perfectly on a grid. GPS-marked trap locations can be reviewed later via GIS and any coverage gaps addressed. Eradication is possible in small-scale campaigns by trapping alone, but this requires significant manpower and resources.

To facilitate trapping, attractants such as varying types of food are often used. Nevertheless, using lures such as scent (glandular, etc), visual signs (feathers or fur), and auditory cues (prey distress/alarm call, or conspecific calls) may prove useful for mongoose removal or detection. Pitt and Sugihara (2009) found that perimeter baiting was effective, but artificial lures were not. Behavioural traits including home range marking, breeding behaviour, and continual hunting for prey (Gorman 1976b; Nellis 1989) suggest that including attractants might increase trapping and detection success.

Toxic baiting was advocated over 50 years ago as a means of increasing efficacy (Pimentel 1955b), yet few major advances have been made with this method. Because mongooses appear to have low selectivity and consume most bait types (Creekmore *et al.* 1994), baiting is likely to be highly effective. Key considerations include toxin type, bait type, baiting density, non-target species, and timing.

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For a chemical to be lethal it must have a pathway and be in a sufficient dosage. Different species have different tolerances to each chemical, and this trait is leveraged to minimise risks to non-target species while putting target species at risk (e.g., Murphy *et al.* this issue). Several toxins have been used historically for controlling mongooses, including thallium sulfate, sodium monofluoroacetate (1080), and strychnine sulfate (Pimentel 1955b; Everard and Everard 1992). Mongooses are highly susceptible to diphacinone (LD50 0.2mg/kg BW), a first generation anti-coagulant, and commercial diphacinone bait blocks have been used in Hawaii with mixed results (Stone *et al.* 1994). Diphacinone is currently the toxin of choice for targeting mongooses alone.

Baits used for delivering toxins to mongooses include chicken meat, boiled cowhide, eggs, salted fish, and commercial flavoured blocks (Pimentel 1955b; Everard and Everard 1992). The main problem with using toxic baits for carnivores is that baits typically used to deliver the toxin become unpalatable after a few hours. Baits have been developed for carnivores that remain palatable for >2 weeks for two large-scale programmes. In Texas, a rabies vaccination programme uses bait blocks effectively for multiple species, while in Western Australia a meat sausage bait was used to target cats and foxes (Skip Oertli pers. comm. 2009; http://www.dshs.state.tx.us/idcu/disease/rabies/orvp/; Algar and Burrows 2004). These baits may be effective for mongoose programmes.

An important aspect of any eradication attempt using toxic baits is that bait must be available to every individual. The baiting density to achieve this goal varies depending on many environmental factors. Baiting densities for mongoose

have already been investigated (Creekmore *et al.* 1994; Linhart *et al.* 1993; Linhart *et al.* 1997; Pimentel 1955b). A density of 24 non-toxic baits/ha has yielded a 96-97% efficacy rate on populations with 5.84 (±1.04 SE) and 5.75 (±1.04 SE) animals/ha (Creekmore *et al.* 1994). Bait consumption trials can be used to determine appropriate baiting densities required for mongooses in specific situations (Wegmann *et al.* this issue).

Maximising efficacy

Various methods with potential use against populations of mongoose may pose risks to non-target species of conservation, cultural, or social importance. In such cases, risk assessments should identify where mitigation methods may be needed or whether some methods should not be employed. Timing is a potential mitigation measure, as some non-target species may periodically be absent from islands. On some islands, native mammalian predators will complicate eradication. For example, Mafia has the Egyptian mongoose (*Herpestes ichneumon*), the Adriatic islands of Korčula, Hvar, and Mljet have the stone marten (*Martes foina*), and many islands have native rodents.

For other problem species of mammals, toxic baiting has been timed to maximise bait uptake by target species while avoiding times when young are being nursed or targets have restricted ranges. Bait uptake can be highest when the usual sources of naturally available food are constrained (Algar and Burrows 2004; Howald *et al.* 2007). Island-specific plans for mongoose should consider their breeding patterns following the increase in day length (Nellis and Everard

1983). Times when female mongoose are nursing young (and may have restricted

home ranges) should be avoided. The young in dens may not contact baits but be

sufficiently independent to survive, a likely reason for the failed eradication

attempt on Isla Piñeros, Puerto Rico (Pimentel 1955b). Mongooses can breed

year-round, so two pulses of baiting at an interval of 9 - 10 weeks are expected to

be required. The experience on Piñeros Island indicates that a single pulse of

baits can kill all adult mongooses, but independent young in dens survive

(Pimentel 1955b). Two pulses of baiting have yet to be tried for the mongoose but

have been effective on tropical rodents that also breed year-round. Until a single

method can demonstrably remove all animals (like poison operations for

rodents), eradication plans for mongoose should include other methods to detect

and remove survivors, a procedure currently used for cat eradications (Campbell

et al. this issue).

Aerial baiting may be the most cost-effective, efficient, scalable, and

replicable method, because mongooses forage almost exclusively on the ground,

where most bait will fall, and they readily take bait. Aerial baiting has successfully

delivered baits to eradicate rodents and cats, reducing costs and overcoming

issues with access caused by terrain and vegetation (Algar *et al.* 2001; Howald *et*

al. 2007). Hand-baiting could be used inexpensively on a small area to mimic an

aerial baiting programme and provide proof of concept.

Feral cats and mongooses are found together on many islands. Controlling

or eradicating one and not the other may yield little conservation benefit.

Targeting both species simultaneously may be an option. Although mongooses

are susceptible to diphacinone, cats are approximately 70 times more resistant (LD50 14.7mg/kg BW; Smith *et al.* 2000; Stone *et al.* 1994), and adult cats typically weigh at least 4 times more than adult mongooses. Diphacinone is thus suboptimal for targeting both species simultaneously. Para-aminopropiophenone (PAPP) is proposed as an alternative toxin for cats and other eutherian mammals such as canids and stoats in Australia and New Zealand as they are highly susceptible compared to most non-target species on islands (Fisher and O'Connor 2007; Marks *et al.* 2006; Murphy *et al.* 2007; Murphy *et al.* this issue; Savarie *et al.* 1983). Although no lethal dose (LD) data currently exists for mongooses, it is expected they would be highly susceptible to PAPP. Even if mongoose were four times more resistant than cats, the smaller body weight of mongooses would offset their relative resistance. Research is required to identify the lethal dose for mongooses, palatability, and the probability of emesis. Encapsulated PAPP, as is being developed for feral cats, would mask any flavor of the active ingredient and reduce the likelihood of emesis (Johnston *et al.* this issue).

Most islands with introduced mongooses are inhabited, so methods will need to be acceptable to the local populace while still being effective enough to ensure eradication. Live traps, and possibly kill traps and toxic bait stations, will be the key methods in urban areas where aerial baiting is typically not acceptable. Tamper-proof housings that eliminate access by children, pets, and non-targets must be developed before kill traps and toxic baits can be used in urban areas. Educating communities to the health risks mongooses pose to humans and

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livestock (Everard and Everard 1992) may facilitate acceptance of a campaign and the required methods by the community.

As for cats, mongoose eradications will require detection methods to confirm success. Methods for detecting cats can be applied to mongooses (see Campbell *et al*. this issue). Historically, box trapping has been the only detection method used in eradication campaigns. Larger and more complex campaigns will require additional methods and management tools to detect remnant individuals and confirm eradication. Tracking tunnels currently used in rodent eradication campaigns should be trialed for efficacy in mongoose detection. On Amami-Oshima dogs and camera traps are being used to detect mongooses (Shintaro Abe pers. comm.), but we were unable to find assessments of their efficacy.

Recommendations

Research funding for mongoose eradication trials is urgently needed. Baiting density, suitable toxins, lethal dosage and bait palatability vary depending on many environmental and behavioural factors. We encourage mongoose trials at smaller scales that can be replicated over larger areas by aerial baiting. Several islands that harbour the mongoose are small and uninhabited, and they can be used to test methods with limited liability.

The best opportunities for eradicating or containing an alien invasive species are often in sites were an invasion is in its early stages, when populations are small and localized and not yet well established. Priority for eradication

should also be given to islands that can serve as sources for introduction to other areas and those that harbour endemic fauna.

At present many islands inhabited by mongoose are too large for eradication. Intensive localized control could benefit species that are at risk until eradication methods are developed. If planned carefully, such control could be done during a period when the mongoose is at most risk.

As more mongoose eradications are attempted, it is important that lessons learned from each attempt (whether successful or unsuccessful) and the skills learned be shared to ensure success of future efforts.

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Appendix IV

Table

Table IV-1. World list of islands separated into geographic areas and mainland areas where the small Indian mongoose was introduced; islands marked + are interconnected; GID # is Global Island Database number for each island; if status column empty then no known control attempts.

Island	GID #	Country	Area (ha)	Humans	Status	Refs (presence)	Refs (control)
Adriatic							
Hvar	676	Croatia	29,737	Yes	Hunters trapping	53; 2	2
Korčula	730	Croatia	27,840	Yes		53; 2	
Mljet	1379	Croatia	9800	Yes		53; 2	
Škrda	----	Croatia	200	No		53	
Kobrava	24012	Croatia	52	No		25	
Čiovo	2855	Croatia	2900	Yes	Hunters poisoning, low pop, bridge to mainland	53; 2	2
Caribbean							
Jost Van Dyke	----	British Virgin Is	850	Yes	JVD Preservation Soc traps	40	52
Tortola +	1925	British Virgin Is	5570	Yes		40	
Beef Island	8867	British Virgin Is	372	Yes		40	
Praslin	----	St Lucia	1	No	Eradicated	15	15; 47
Trinidad	111	Trinidad & Tobago	476,800	Yes		59	54
Antigua	714	Antigua & Barbuda	28,100	Yes		40	
Codrington	84837	Antigua & Barbuda	0.5	No	Eradicated	26	26
Green	----	Antigua & Barbuda	43	No	Eradicated	26	26
Nevis	1462	St Kitts & Nevis	9300	Yes		40	
St Kitts	989	St Kitts & Nevis	16,800	Yes		40	
St Martin	1496	France/Netherl'ds[1]	8720	Yes		40	
Barbados	520	Barbados	43,100	Yes		40	
Piñeros	17066	US, Puerto Rico	390	No	Failed eradication attempt; no control	46	46
Vieques	1144	US, Puerto Rico	13,500	Yes		40	
Buck Island	----	US	72	No	Eradicated	38	38; 33; 44
St Croix	835	US	21,466	Yes	Localised control	40	11
St John	2018	US	5080	Yes	Localised control	40	12; 9
Leduck	75128	US	5.7	No	Eradicated	39	39
St Thomas	1697	US	8090	Yes	Low population	40	
Water Island	18293	US	199	Yes		40	
Hispaniola	21	Haiti/Dom.Rep.	7,648,000	Yes		40	
Carriacou	2661	Grenada	3770	Yes		20	
Grenada	651	Grenada	34,400	Yes	Rabies control	40	17
Puerto Rico	79	USA	910,400	Yes	Rabies control	40	17; 46; 18
St Lucia	409	St Lucia	63,980	Yes	Localised control	40	32
St Vincent	616	St Vincent	38,900	Yes		40	

Cuba	15	Cuba	11,086,100	Yes	Rabies control	40; 3; 4	17
Romano	403	Cuba	77,700	Yes		3; 4	
Sabinal	----	Cuba	33,500	Yes		3; 4	
Jamaica	66	Jamaica	1,118,960	Yes	Localised control	16	7
Goat Major +	107807	Jamaica	200	No		20	24
Goat Minor	17455	Jamaica	335	No		20	24
La Desirade	3574	France, DOM	2,064	Yes		40	
Fajou	18193	France, DOM	115	No	Eradicated	28	28; 34
Grande-Terre, Guadeloupe +	233	France, DOM	63,900	Yes		40	5
Basse-Terre, Guadeloupe	233	France, DOM	87,570	Yes		40	5
Marie Galante	1028	France, DOM	15,800	Yes		40	
Martinique	271	France, DOM	112,800	Yes		40	
Africa							
Mafia	513	Tanzania	39,400	Yes		59	
Grand Comoro	284	Comoros	114,800	Yes		29; 58	
Mauritius	197	Mauritius	204,000	Yes	Localised control	30	49; 8
Pacific							
Beqa	----	Fiji	3620	Yes		35; 13	
Kioa	3731	Fiji	1860	Yes		35; 13	
Macuata-i-wai	----	Fiji	306	fishermen		35; 13	
Malake	8463	Fiji	453	Yes		35; 13	
Nananu-i-ra	11141	Fiji	270	Yes		35; 13	
Nananu-i-cake	12726	Fiji	300	1 family		35; 13	
Nasoata	65589		74	1 family		13	
Vanua Levu	98	Fiji	553,500	Yes		35; 13	
Viti Levu	68	Fiji	1,038,700	Yes		36; 35; 13	
Yanuca	13448	Fiji	154	Yes		35; 13	
Druadrua	----	Fiji	390	Yes		35; 13	
Mavuva	49054	Fiji		Yes		35; 13	
Rabi (Rambi)	----	Fiji	6878	Yes		35; 13	
Hawaii	70	USA, Hawaii	1,043,200	Yes	Localised control	6	51; 48
Kauai	236	USA, Hawaii	162,400	Yes	Seen 1970s, not since	55; 10	48
Maui	195	USA, Hawaii	188,700	Yes		41; 19	
Molokai	370	USA, Hawaii	67,600	Yes		41; 19	48
Oahu	221	USA, Hawaii	157,400	Yes		42; 19	48
Amami-Oshima	361	Japan	71,200	Yes	Ongoing eradication	1	1; 56; 57; 23
Okinawa	263	Japan	227,130	Yes	Localised control	27	50
Kyusyu	33	Japan		Yes	Recent find, but present about 30 years	37	
Ambon	347	Indonesia	77,500	Yes		19	
Upolu	268	Samoa	111,500	Yes	Recent intro Aleipata area	31	
New Caledonia	49	New Caledonia		Yes	Recently introduced	45	
MAINLAND							
Guyana	----	South America	unknown	Yes		40; 21; 22	
Suriname	----	South America	unknown	Yes		40; 21; 22	

Croatia (incl Pelješac Pen.)	----	Europe	unknown	Yes	Coastal area, no known control	53; 2
Bosnia and Herzegovina	----	Europe	unknown	Yes	Coastal area, no known control	2
Montenegro	----	Europe	unknown	Yes	Coastal area, no known control	2, 14
Florida	----	USA		Yes	Eradicated	43

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CHAPTER V.

POSSIBLE CHARACTER DISPLACEMENT OF AN INTRODUCED MONGOOSE AND NATIVE MARTEN ON ADRIATIC ISLANDS, CROATIA

Co-authored by Daniel Simberloff, Shai Meiri, Nikola Tvrtković, and Zoran Tadić

Abstract

The small Indian mongoose (*Herpestes auropunctatus*) has been introduced to over 60 islands worldwide. On most of these islands the mongoose has no competitors of similar size. Previous studies have shown that male size has increased in only 100–200 generations compared to its native populations in Asia, where it co-occurs with two larger mongoose species. This morphological change is consistent with ecological character release. Here we examined the variation in the maximum diameter of the upper canine tooth (the prey-killing organ) and skull length in the small Indian mongoose and the larger stone marten (*Martes foina*) on seven Adriatic islands. The stone marten is present on three of the islands; on one island the mongoose is the sole carnivore. The small Indian mongoose has significantly smaller canines and skulls on three Adriatic islands compared to other islands of introduction. It is not larger on one Adriatic island, Čiovo, where it is the sole carnivore, than on other Adriatic islands. However, mongooses are scarce on Čiovo because of heavy poisoning by hunters, which might influence size as well. Introduced species not only evolve to respond to novel environments and competitors, they can also influence evolution of natives. The stone marten skulls are smaller on three islands with no mongooses than on one island and on the mainland, where the mongoose is present. Canine diameters of stone marten for both sexes are similar across Adriatic islands. We need more samples of the stone marten from mongoose-infested Croatian islands to be able to confirm these patterns for both traits.

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Introduction

The role of interspecific interactions and, in particular, of competition in structuring communities is controversial (Lewin 1983, Losos 2000, Schluter 2000, Hubell 2001). Brown and Wilson (1956) first suggested that two species with overlapping geographic ranges might evolve under the selective pressure of competition to avoid hybridization ("reproductive character displacement") or to avoid resource use overlap ("ecological character displacement"). The opposite phenomenon, termed "character release" by Grant (1972), is predicted to occur when either of the species occurs by itself and converges towards the second species. Many studies have sought morphological patterns of ecological character displacement and release in an array of extant and even extinct taxa for mammals, birds, reptiles, amphibians, insects, other invertebrates, and plants (reviewed by Dayan and Simberloff 2005). Among mammals, carnivores have played a major role because of their large morphological variation and easily seen advantages of different size in capturing prey of different size (Dayan *et al.* 1989, 1990, Dayan and Simberloff 1994, Davies *et al.* 2007).

Several studies have used introduced species to provide evidence that character displacement and release may occur as a response to novel environments and native communities in relatively short periods of time (reviewed by Dayan and Simberloff 2005, Strauss *et al.* 2006, see also Robinson and Parsons 2002 for a genetic basis for these responses). Introduced species are excellent "natural experiments" in which rates of change in size can be examined as community composition varies in natural settings. Introductions of murids to

Pacific and New Zealand islands (Yom-Tov *et al.* 1999) and studies of sticklebacks (Schluter 1994, Pritchard and Schluter 2001, Grey and Robinson 2002) are excellent examples, but fish studies have been criticized for using closely related species that have only recently diverged.

Not only do introduced species evolve in response to novel environments and competitors, but they can also affect the distribution, abundance, reproduction, behavior and morphology of native species. Strauss *et al.* (2006) provide examples of native species that have evolved in response to the addition of novel species to communities. Of thirty-three examples, twenty-one included morphological or physiological change, and character displacement is one of the possible evolutionary responses to introduced species. For example, decrease in benthic native brook char feeding morphs occurred with the introduction of benthic feeding competitors (Bourke *et al.* 1999). Within a short period after American mink (*Mustela vision*) were introduced to Belarus, native European mink (*M. lutreola*) increased in body size while the introduced *M. vison* decreased (Sidorovich *et al.* 1999).

Simberloff *et al.* (2000) examined size variation in three native mongoose (Herpestidae) species, including introduced island populations of the small Indian mongoose (*Herpestes auropunctatus*). In its native range in Asia, the small Indian mongoose is sympatric with one or two slightly larger congeners. Simberloff *et al.* (2000) showed that on many mongoose-free and previously carnivore-free islands to which it has been introduced, male small Indian

mongooses have increased in only 100–200 generations. This morphological change is consistent with ecological release from competition with its congeners.

Here, we expand on the study of Simberloff *et al.* (2000) by studying the morphology of the native stone marten (*Martes foina*) and the introduced small Indian mongoose (*Herpestes auropunctatus*) on Adriatic islands in Croatia. Adriatic islands are the only islands to which the small Indian mongoose was introduced that contain a native carnivore, the stone marten. The small Indian mongoose was introduced to several Adriatic islands to control the native venomous horned viper (*Vipera ammodytes*). Initially (in 1910), it was introduced to Mljet Island, and thereafter to several other islands (Korčula in 1927, Hvar in the 1950s, Čiovo in the 1970s, Škrda [date unknown]) and to the mainland Pelješac Peninsula (1927). It is currently spreading along the Dalmatian coast and has reached the Neretva River in the north and Albania in the south (Barun et al. 2008, Ćirovic *et al.* 2010). The introduction history, diet, and behavior of the small Indian mongoose are well known in its introduced range (Nellis and Everard 1983, Simberloff 2000, Hays and Conant 2007), but little has been published about its diet in its native range (Rana *et al.* 2005). On islands where it was introduced, the small Indian mongoose eats mainly small vertebrates, fruits, seeds, and insects: Hawaiian Islands (Baldwin *et al.* 1952, Hinton and Dunn 1967), Caribbean Islands (Williams 1918, Nellis and Everard 1983), Mauritius (Carié 1916), Croatia (Cavallini and Serafini 1995, AB pers. obs.). It can have a substantial impact on several native snakes, lizards, amphibians, small mammals, and birds (see review in Hays and Conant 2007,

but also Brown & Gibbons 1986, Sajdak & Henderson 1991, Zug 1991, Watari *et al.* 2006, Henderson & Powell 2009, Barun *et al.* 2010).

All large Croatian islands have a native carnivore, the stone marten, which arrived in Europe from the Middle East after the last glacial recession (Kurtén 1968, Anderson 1970). It is one of the most widespread carnivores, present from central and southern Europe to the Caucasus and western Russia, and from the Middle East to Afghanistan, Tibet, and Mongolia. In central Europe, the stone marten prefers urban areas and villages, but in Mediterranean areas it shifts its preferences towards rocky or forest habitats (Virgos and Casanovas 1989, 2000). Its diet consists of many wild animal and plant species (Baghlie 2002, Carvalho and Gomes 2004, Clevenger 1994, Lanszki 2003, Padial *et al.* 2002, Zhou et. al 2010). Diet varies seasonally, with mammals forming the bulk of the diet in the winter; birds are mainly consumed in spring; insects in the summer; and fruit during the summer, winter and autumn. Reptiles appeared in a very small percentage during the spring and summer (8 out of total 157 feces; Delibes 1978).

The ecological similarities of these two species and the presence of the mongoose on some but not all islands suggest the following questions:

1) On Adriatic islands where the slightly larger stone marten is present, is the small Indian mongoose smaller compared with other islands to which it has been introduced, and its size similar to that in its native range?

2) On the sole Adriatic island where only the small Indian mongoose is present, is it larger than on the islands where the marten is also present?

3) On Adriatic islands, in the presence of a slightly smaller introduced carnivore, the mongoose, has the stone marten increased in size?

4) How does size of the stone marten on Adriatic islands, where it is the only small carnivore except, in some cases, for the small Indian mongoose, compare to that in other mainland and island areas in Europe that have other carnivores?

Materials and methods

Island habitat characteristics. All islands are large and inhabited: Mljet 9,800 ha, Korčula 27,900 ha, Hvar 29,700 ha, Lastovo 4,600 ha, Brač 39,600 ha, Cres 40,500 ha, Čiovo 2,900 ha. The climate, typical of the Mediterranean region, is characterized by warm to hot, dry summers and mild, wet winters. Vegetation is a fine-grained mosaic of shrublands, scrublands, forests, and small scale agricultural fields. Shrublands (maquis) are dense thickets of evergreen sclerophyll shrubs and small trees dominated by *Quercus ilex*, but many other species are present as well. Forests are dominated mostly by *Pinus halepensis*. All islands reported above have all four vegetation types, but the proportions of the various types may vary among islands. The only exception is Cres, the most northerly of these islands, which has several continental plant species, including the dominant *Carpinus orientalis* and *Quercus pubescens*. Therefore, collection of the marten on Cres was limited to the southern part of island, where the vegetation is a mosaic of the four vegetation types mentioned

above. All of these islands have a similar history of human occupation and similar agricultural practices. Most local agriculture consists of olive groves and vineyards, with a few small vegetable fields where both the mongoose and the stone marten are frequently observed. In addition, all islands have a similar assortment of native mammalian species (Table V-1) and timing of introduction of most mammalian exotic species, all of which were present before the mongoose arrived.

Skull collecting and measurements. Small Indian mongoose skulls were collected on Mljet, Korčula, and Hvar by hunters from 2004 through 2008 and by AB during 2008 spring and summer surveys (AB, DS, NT in preparation). Small Indian mongoose skulls on Čiovo were collected either by local hunters, AB, or Ivan Budinski from 2005-2008. Hunters trapped live martens or collected road-killed individuals on Brač, Cres, Lastovo, Mljet, Korčula, and Hvar from 2005-2009. All skulls were cleaned by dermestid beetles in Z. Tadić's laboratory except for several stone marten skulls from Cres and Hvar collected in 1997/1998 that were part of the Croatian Natural History Museum mammal collection.

Measurements for the introduced island small Indian mongoose were previously reported in Simberloff *et al.* (2000) except for those of Fajou, Maui, Trinidad and Guyana, which were recently measured in private and museum collections. Stone marten specimens from European populations were measured in museum collections and were previously reported in Meiri *et al.* (2007).

We measured the maximum diameter of the upper canine teeth ($C^{sup}L$) and the condylobasal skull length (CBL) of these small Indian mongooses and

stone martens, as in Dayan et al. (1989), Dayan and Simberloff (1994), Simberloff *et al.* (2000), and Meiri *et al.* (2007) with digital calipers (precision 0.01 mm). We did not measure subadult individuals with unfused cranial sutures, and we omitted unsexed adults. Worn or cracked teeth were not measured. Sample sizes for the different traits differ because in a few instances, teeth were missing or the skull was broken (Table V-2 and V-5). We measured skull length because it is often taken as a measure of size in carnivores (Ralls and Harvey 1985, Gittleman and Van Valkenburgh 1997, Meiri *et al.* 2005b). For mustelids and herpestids, there is strong evidence that the upper canine tooth is used with great speed and accuracy to kill normal prey and that the diameter of this tooth may adapt each species to a particular array of prey sizes (Dayan *et al.* 1989, Dayan and Simberloff 1994, Simberloff *et al.* 2000).

To address whether presence vs. absence of the mongoose has influenced size of the stone marten on Adriatic islands, we ran an ANOVA with either skull length or tooth diameter as the response variable and location as the explanatory factor. We used Least Square Means independent comparison tests to compare one group of islands/mainland populations to other group. All analyses were done in JMP, version 8 (SAS Institute Inc., Cary, NC, USA).

Results

     Small Indian Mongoose. Upper canine diameter and condylobasal skull length are listed in Table V-2 for all mongoose specimens. Figures V-1A and V-1B depict skull length for each location for males and females, respectively, and Figures V-2A and V-2B depict canine diameters.

     One-way ANOVA shows the same pattern for male and female skull length (Figure V-1A and V-1B). For both sexes, the skull length of the small Indian mongoose on all three Adriatic islands with the marten is smaller than on all other islands of introduction and is similar to that in all three native regions in Asia. Male skull length differed geographically (ANOVA, $F_{16,393}$ = 26.02, P < 0.001, Table V-3A). A Least Square Means Independent Contrasts shows that males of three Adriatic islands with the marten are smaller than males of all other islands of introduction ($F_{1,395}$ = 264.32, P < 0.001), similar to males from all three Asian native regions ($F_{1,395}$ = 3.58, P=0.059), and similar to males from one Adriatic island lacking the marten ($F_{1,395}$ = 2.83, P=0.093). Similarly, female skull length also differs geographically (ANOVA, $F_{15,280}$ = 11.34, p < 0.001, Table V-3B). A Least Square Means Independent Contrasts shows that females of three Adriatic islands with the marten are smaller than females of all other islands of introduction ($F_{1,280}$ = 78.77, P < 0.001), smaller than those in three native Asian regions ($F_{1,280}$ = 65.19, P < 0.001), and larger then females from one Adriatic island lacking the marten ($F_{1,280}$ = 32.53, P=0.007).

     One-way ANOVA shows the same pattern for male and female canine diameter (Figure V-2 A and V-2B). For both sexes, the canine diameter of the

small Indian mongoose on all three Adriatic islands with the marten is smaller

than on all other islands of introduction and similar to that in all three native

Asian regions. Males differed geographically (ANOVA, $F_{15,354}$ = 11.68, p < 0.001,

Table V-3C). A Least Square Means Independent Contrasts shows that males of

three Adriatic islands with the marten are smaller than males of all other islands

of introduction ($F_{1,356}$ = 59.09, P < 0.001), even smaller than males from all three

native Asian regions ($F_{1,356}$ = 17.48, P < 0.001), and similar to males from one

Adriatic island lacking the marten ($F_{1,356}$ = 1.27, P=0.260). Similarly, female

canine diameter also differs geographically (ANOVA, $F_{15,262}$ = 5.01, p < 0.001,

Table V-3D). A Least Square Means Independent contrasts shows that females of

three Adriatic islands with the marten are smaller than females of all other

islands of introduction ($F_{1,262}$ = 22.96, P < 0.001), the same size as those in three

native Asian regions ($F_{1,262}$ = 1.14, P=0.286), and larger than females from one

Adriatic island lacking the marten ($F_{1,262}$ = 0.36, P=0.549).

Stone Marten. Upper canine diameter and condylobasal skull length are

listed in Table V-4 for all stone marten specimens. Figures V-3A and V-3B depict

skull lengths for each location for males and females, respectively, and Figures V-

4A and V-4B depict canine diameters. Crete, Korčula, and Mljet were excluded

from statistical analysis because of small sample sizes.

One-way ANOVA shows the same pattern for male and female skull length

of the stone marten (Figure V-3 A and V-3B). For both sexes, skull length of stone

martens on three Adriatic islands (Brač, Cres, Lastovo) are smaller than on Hvar,

where the small Indian mongoose was introduced. Skull length of male stone

martens from Hvar is similar to that of populations of mainland Europe and three Danish islands. Male skull length differed geographically (ANOVA, $F_{14,244}$ = 13.05, P < 0.001, Table V-5A). A Least Square Means Independent Contrasts shows that males of three Adriatic islands without the mongoose (Brač, Cres, Lastovo) are smaller than on mongoose-infested Hvar and Korčula ($F_{1,247}$ = 11.88, P < 0.001), and male stone marten skull length is smaller on Brač, Cres, and Lastovo than that of populations of mainland Europe ($F_{1,247}$ = 50.51, P < 0.001) and smaller than that of three Danish islands ($F_{1,247}$ = 48.83, P < 0.001). Similarly, female skull length also differs geographically (ANOVA, 0.001, $F_{1,185}$ = 12.15, Table V-5B). A Least Square Means Independent Contrasts shows that female skull length of three Adriatic islands (Brač, Cres, Lastovo) without the mongoose are smaller than on mongoose-infested Hvar and Korčula ($F_{1,186}$ = 17.20, P < 0.001), and female stone marten skull length is smaller on Brač, Cres, and Lastovo than in populations of mainland Europe ($F_{1,186}$ = 40.08, P < 0.001) and smaller than on three Danish islands ($F_{1,186}$ = 45.32, P < 0.001).

This pattern does not hold for canine diameter of male stone marten (Figure V-4A and V-4B). Male canine diameter shows no pattern (ANOVA, $F_{14,247}$ = 6.03, p < 0.001, Table V-5C). A Least Square Means Independent Contrasts shows that males of three mongoose-free Adriatic islands (Brač, Cres, Lastovo) do not differ from males on mongoose-ridden Hvar and Korčula ($F_{1,247}$ = 1.32, P=0.251), and male stone marten skull length on Brač, Cres, and Lastovo is not different from that of populations from mainland Europe ($F_{1,247}$ =0.65, P=0.419) and three Danish islands ($F_{1,247}$ = 0.083, P=0.773). Female canine diameter

differs geographically (ANOVA, $F_{14,181} = 6.43$, p < 0.001, Table V-5D). A Least Square Means Independent Contrasts shows that female canine diameter on three mongoose-free Adriatic islands (Brač, Cres, Lastovo) are smaller than on mongoose-infested Hvar ($F_{1,181} = 8.20$, P=0.005), and female stone marten canine diameter on Brač, Cres, and Lastovo does not differ from that of populations of mainland Europe ($F_{1,181} = 1.48$, P=0.225) and three Danish islands ($F_{1,181} = 0.01$, P=0.92).

Discussion

Small Indian Mongoose. Our observations are consistent with the hypothesis of Simberloff *et al.* (2000) that the small Indian mongoose has undergone character release in regions of introduction. We measured four additional populations of the small Indian mongoose: Fajou, Maui, Trinidad and Guyana. On the Hawaiian island of Maui and the Caribbean island of Trinidad, mongooses of both sexes are larger than those in its native area in Asia, in both traits. On Guyana, South American mainland, the mongoose appears to be smaller than on islands of introduction and similar in size to the mongoose in its native range; it is noteworthy that Guyana has native carnivores larger than the mongoose, including mustelids, the greater grison (*Galactis vittata*) and tayra (*Eira barbara*).   However, the small sample size prevents us from further analysis and conclusions.

The introduced population of Fajou is an exception to the ecological release pattern we observed in introduced populations. Surprisingly, both sexes of the small Indian mongoose on Fajou resemble those on Adriatic islands and in the native region. As on all West Indies islands except for Trinidad, no other carnivore occurs on Fajou. However, Fajou is very small (115 ha). Some authors (Foster 1964, Lomolino 1985, Meiri *et al.* 2004, Van Valen 1973) have suggested that mammals tend to evolve smaller size on islands so as to reduce resource requirements and increase reproductive output and others (Grant 1965, Schoener 1969, Lomolino 1985, Meiri *et al.* 2004,) have contested this claim. Different populations likely evolve different sizes in response to local environmental conditions (Raia & Meiri 2006, Meiri *et al.* 2011). Fajou is just a single datum, but globally at least 64 islands, many of them very small, harbor introduced small Indian mongooses (Barun *et al.* in press), and it would be interesting to study mongoose sizes on the smallest of these.

The size of the small Indian mongoose on three Adriatic islands with martens is striking. On these islands the small Indian mongoose is similar in size to native populations where congeners and other carnivores co-occur and smaller than other introduced populations (Simberloff *et al.* 2000). Males are smaller in both skull length and canine diameter than other introduced populations, and they are similar in size to males from the three native regions. Females also have shorter skulls than those of other introduced island populations, but their skulls are even shorter than those from native regions. There is no pattern in canine diameter for females. On all other islands of

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introduction, except for Trinidad, no other small carnivorous mammals are present. It seems possible that the mongoose did not undergo character release on the Adriatic islands because of competition with the larger stone marten. In a pilot study in which we radio-tracked both species on Korčula island (AB and DS unpublished data) we found that when the two species encounter each other, the larger stone marten is dominant.

The mongoose was introduced to one Adriatic island lacking the stone marten, Čiovo. Skulls of both male and female mongooses on Čiovo are the shortest of all Adriatic islands and all three native Asian regions (but not significantly so). However, canines of Čiovo mongooses are larger than those of almost all Adriatic and native Asian populations. We cannot explain this discrepancy, because all prey species present on Čiovo are present on all other islands as well. On Čiovo, the regional hunting organization distributes "rat" poison for mongoose control during the annual autumn meeting (this procedure is illegal in Croatia), and a result of this aggressive multi-year campaign is that the mongoose population is very low. The mongoose on Čiovo might be subject to different selective pressures than on other islands of introduction, including Adriatic islands.

Stone Marten. Both males and females of the stone marten from three mongoose-free islands (Brač, Cres, and Lastovo) have shorter skulls than do those of several mainland European populations, three Danish islands, and neighboring, mongoose-infested Hvar. There is no clear pattern for male canine diameter size, but canines of female stone martens on Brač, Cres, and Lastovo are

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significantly smaller than on the one Adriatic island where the mongoose was introduced.

The stone marten tends to increase in size from west to east (Reig 1992) and from south to north (starting in Israel). In Asia, it has strong latitudinal gradients but no longitudinal ones (Meiri *et al.* 2005). These clines can confound a search for character displacement (Goldberg and Lande 2006, Adams and Collyer 2007, Meiri *et al.* 2011). The short skulls of the martens on Adriatic islands are not surprising: some carnivore species tend to be smaller on islands (Foster 1964) and others, including mustelids, do not (Meiri *et al.* 2004, 2008). In the absence of dietary information from the Adriatic populations, we cannot implicate a mechanism by which the small size in stone marten may have arisen. Because the stone marten is the only carnivore (except for feral *Felis catus*) on the islands we studied, release from competition from other mainland carnivore species is one possible explanation. For example, Dayan and Simberloff (1994) found that both sexes of the stoat (*Mustela erminea*) on Ireland, where the least weasel (*Mustela nivalis*) is absent, are smaller than on Great Britain, where the smaller least weasel is present.

On Hvar, one of the three Adriatic islands where the marten co-occurs with the mongoose, both male and female martens have significantly longer skulls than on the three mongoose-free islands; they are similar to martens of mainland Europe. It is possible that introduction of the small Indian mongoose displaced the stone marten on Hvar and very likely on two other islands, Korčula and Mljet. We were unable to collect large enough sample sizes for these two

islands.   However, preliminary data show that martens on both islands are similar to those on Hvar rather than to those on the three mongoose-free islands (Figure V-3 and V-4).

Conclusions

On Adriatic islands, interspecific competition between the small Indian mongoose and the stone marten is likely the factor leading to maintenance of small size in the mongoose and preventing the character release observed on other islands of introduction that lack mammalian competitors. In addition, our data suggest that the stone marten may have undergone character displacement as a result of the mongoose introduction on at least one Adriatic island and possibly on all three islands where the two species co-occur.

Acknowledgments

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Appendix V

Tables and Figures

Table V-1: Species of mammals (rows) on islands (columns). (X) indicates species historically present on an island, (-) indicates no recorded presence, (?) no recent records of species presence.

	Mongoose	Mongoose and Marten			Marten		
	Čiovo	**Mljet**	**Korčula**	**Hvar**	**Brač**	**Lastovo**	**Cres**
Rattus rattus	X	X	X	X	X	X	X
Apodemus sylvaticus	-	X	X	X	X	X	X
Apodemus epimelas	X	X	X	-	-	-	?
Mus musculus	X	X	X	X	X	X	X
Suncus etruscus	?	?	?	X	?	-	X
Crocidura suaveolens	-	X	X	X	X	X	X
Eliomys quercinus	-	?	X	X	X	X	-
Glis glis	-	X	X	X	X	?	-
Erinaceus concolor	-	X	X	X	X	X	X
Lepus europaeus	X	X	X	X	X	X	X
Felis domesticus	X	X	X	X	X	X	X
Canis aureus	-	-	X	-	-	-	-

Table V-2: Means, coefficients of variation (CV), and standard errors (SE) for small Indian mongoose upper canine diameter (CsupL) and condylobasal skull length (CBL) from three regions of Asia, four Adriatic islands, introduced mainland Guyana, and nine other introduced islands.

Island	Sex	CsupL (mm)				CBL (mm)			
		N	Mean	CV	SE	N	Mean	CV	SE
Asia III	F	20	2.68	7.92	0.05	18	59.56	7.92	1.11
	M	21	2.87	7.20	0.05	19	60.98	5.23	0.73
Asia V	F	3	2.74	8.02	0.13	3	62.85	8.68	3.15
	M	7	2.81	6.59	0.07	5	62.24	4.24	1.18
Asia VI	F	2	2.39	10.06	0.17	2	58.04	11.76	4.83
	M	2	2.65	4.54	0.09	2	61.94	2.61	1.15
Čiovo	F	12	2.69	5.75	0.04	12	56.05	4.54	0.73
	M	4	3.06	5.25	0.08	4	59.16	4.87	1.44
Hvar	F	15	2.69	4.75	0.03	15	57.21	2.81	0.42
	M	19	2.97	4.72	0.03	19	59.68	3.06	0.42
Korčula	F	25	2.63	6.56	0.03	25	57.86	2.56	0.30
	M	27	2.96	4.29	0.02	28	61.56	2.60	0.30
Mljet	F	17	2.66	5.10	0.03	17	58.55	2.52	0.36
	M	21	2.99	4.93	0.03	22	61.47	2.95	0.39
Guyana	F	3	2.57	3.84	0.06	3	59.83	2.03	0.70
	M	0				3	66.44	4.41	1.69
Fiji	F	14	2.86	6.66	0.05	15	61.37	4.36	0.69
	M	39	3.14	6.02	0.03	37	65.40	3.52	0.38
Mauritius	F	16	2.77	4.60	0.03	15	60.51	2.33	0.36
	M	41	3.15	3.40	0.02	43	65.48	2.41	0.24
Okinawa	F	10	2.81	2.74	0.02	11	59.98	1.86	0.34
	M	10	3.14	4.31	0.04	10	65.49	2.54	0.53
St. Croix	F	24	2.89	4.40	0.03	29	61.09	2.09	0.24
	M	18	3.26	4.85	0.04	19	65.73	2.80	0.42
Trinidad	F	0	.	.	.	0	.	.	.
	M	8	3.32	6.41	0.08	8	67.72	3.56	0.85
Maui	F	22	2.81	7.73	0.05	25	61.12	3.73	0.46
	M	44	3.07	6.12	0.03	77	64.31	3.41	0.25
Oahu	F	41	2.73	4.23	0.02	42	61.99	2.43	0.23
	M	45	3.09	3.93	0.02	45	66.55	2.62	0.26
Hawaii	F	27	2.70	5.66	0.03	31	60.52	2.95	0.32
	M	40	3.11	5.02	0.02	44	65.60	2.84	0.28
Fajou	F	27	2.69	5.81	0.03	33	59.88	2.52	0.26
	M	26	3.02	4.56	0.03	27	63.67	2.79	0.34

Table V-3: One-way ANOVAs for small Indian mongoose (A) male skull length, (B) female skull length (C) male canine diameter, and (D) female canine diameter.

A

Source	df	Sum of Squares	Mean Square	F Ratio	Prob > F
Island	16	1700.32	106.27	26.02	<.0001
Error	393	1604.57	4.08		
C. Total	409	3304.89			

B

Source	df	Sum of Squares	Mean Square	F Ratio	Prob > F
Island	15	762.69	50.84	11.34	<.0001
Error	280	1255.20	4.48		
C. Total	295	2017.90			

C

Source	df	Sum of Squares	Mean Square	F Ratio	Prob > F
Island	15	4.23	0.28	11.68	<.0001
Error	354	8.54	0.02		
C. Total	369	12.77			

D

Source	df	Sum of Squares	Mean Square	F Ratio	Prob > F
Island	15	1.84	0.12	5.01	<.0001
Error	262	6.44	0.02		
C. Total	277	8.29			

Table V-4: Means, coefficients of variation (CV), and standard errors (SE) for stone marten upper canine diameter (CsupL) and condylobasal skull length (CBL) from six Adriatic islands, Crete, several populations on mainland Europe, and three islands in Denmark.

Island/Country	Sex	CsupL (mm)				CBL (mm)			
		N	Mean	CV	SE	N	Mean	CV	SE
Brač	F	3	3.74	4.66	0.1	3	74.12	1.12	0.48
	M	9	4.12	2.37	0.03	7	79.83	1.76	0.53
Cres	F	27	3.69	4.06	0.03	28	73.53	2.48	0.34
	M	48	4.19	4.46	0.03	47	77.46	2.72	0.31
Lastovo	F	15	3.99	4.26	0.04	9	72.90	3.43	0.83
	M	17	4.49	3.25	0.04	9	76.67	3.38	0.86
Hvar	F	13	3.61	2.37	0.02	11	76.77	1.86	0.43
	M	16	4.2	3.78	0.04	16	81.26	2.99	0.61
Korčula	F	0	.	.	.	0	.	.	.
	M	2	4.16	6.98	0.21	2	80.97	3.64	2.09
Mljet	F	0	.	.	.	0	.	.	.
	M	2	4.54	3.59	0.12	0	.	.	.
Crete	F	2	3.92	4.15	0.12	2	74.36	4.23	2.23
	M	3	4.26	2.96	0.07	3	77.00	3.43	1.53
Italy	F	14	3.72	4.3	0.04	16	76.90	1.81	0.35
	M	18	4.16	5.53	0.05	18	79.98	3.52	0.66
Spain	F	9	3.71	4.85	0.06	10	75.63	2.68	0.64
	M	14	4.18	6.17	0.07	18	79.93	2.64	0.50
France	F	19	3.92	5.93	0.05	21	77.29	2.86	0.48
	M	18	4.16	4.69	0.05	20	80.55	3.46	0.62
Belgium	F	5	3.97	4.38	0.08	5	77.76	2.32	0.81
	M	6	4.39	3.56	0.06	7	82.06	1.54	0.48
Netherlands	F	9	3.81	3.86	0.05	12	77.54	2.40	0.54
	M	21	4.41	3.83	0.04	19	82.91	1.85	0.35
Germany	F	46	3.96	6.12	0.04	47	78.02	2.79	0.32
	M	50	4.31	4.87	0.03	49	81.37	2.72	0.32
Poland	F	6	3.97	2.46	0.04	6	78.79	1.21	0.39
	M	9	4.45	3.15	0.05	9	82.33	1.94	0.53
Israel	F	5	3.9	8.68	0.15	6	73.20	4.77	1.43
	M	5	4.23	1.72	0.03	9	79.67	1.71	0.45
Jutland	F	2	3.81	2.79	0.08	3	78.05	1.45	0.65
	M	6	4.3	3.09	0.05	5	82.90	2.49	0.92
Fyn	F	11	3.92	5.24	0.06	12	79.05	3.91	0.89
	M	15	4.35	4	0.04	16	82.36	2.61	0.54
Sjaelland	F	12	3.71	2.77	0.03	11	77.26	1.68	0.39
	M	10	4.19	4.97	0.07	10	80.93	2.57	0.66

Table V-5: One-way ANOVAs for stone marten (A) male skull length, (B) female
skull length (C) male canine diameter, and (D) female canine diameter.

A

Source	df	Sum of Squares	Mean Square	F Ratio	Prob > F
Island/Country	14	872.46	62.31	13.05	<.0001
Error	244	1164.48	4.77		
C. Total	258	2036.95			

B

Source	df	Sum of Squares	Mean Square	F Ratio	Prob > F
Island/Country	14	721.64	51.54	12.15	<.0001
Error	185	784.38	4.23		
C. Total	199	1506.03			

C

Source	df	Sum of Squares	Mean Square	F Ratio	Prob > F
Island/Country	14	3.00	0.21	6.03	<.0001
Error	247	8.77	0.03		
C. Total	261	11.77			

D

Source	df	Sum of Squares	Mean Square	F Ratio	Prob > F
Island/Country	14	3.33	0.23	6.43	<.0001
Error	181	6.69	0.03		
C. Total	195	10.02			

Figure V-1: Condylobasal skull length (CBL, mm) for (A) male and (B) female small Indian mongoose from three regions in its native range, four Adriatic islands, and several other introduced islands. The box and whiskers are interquartile ranges and 95% CI.
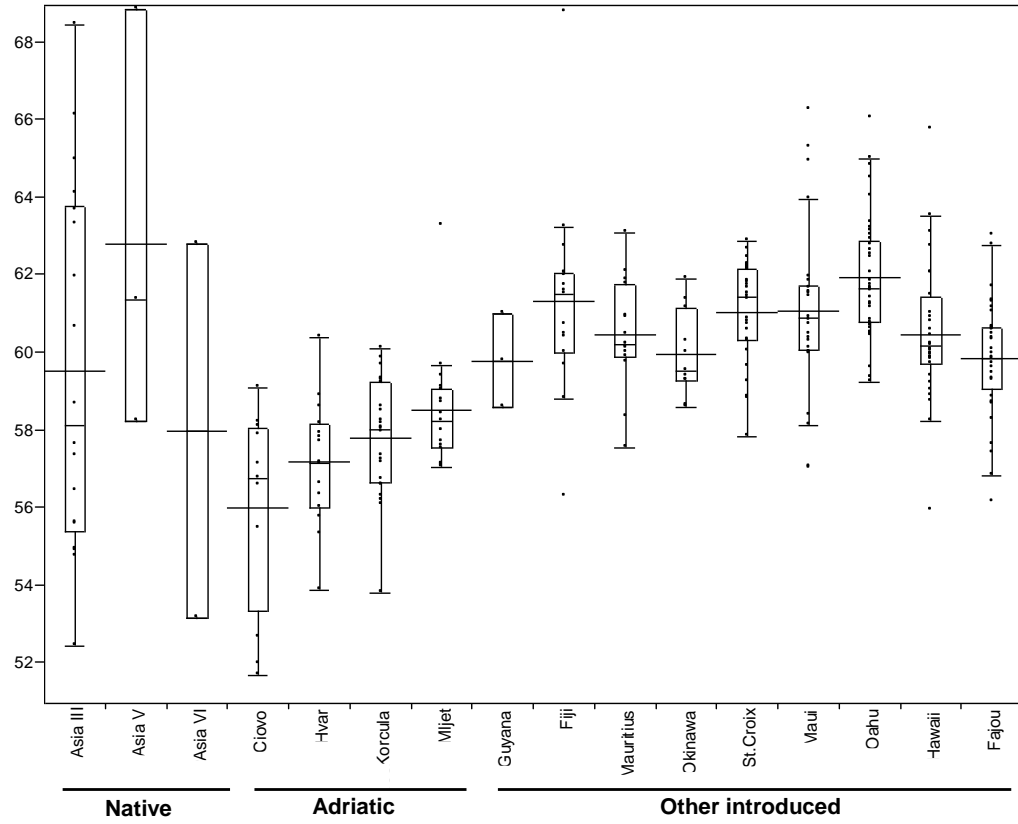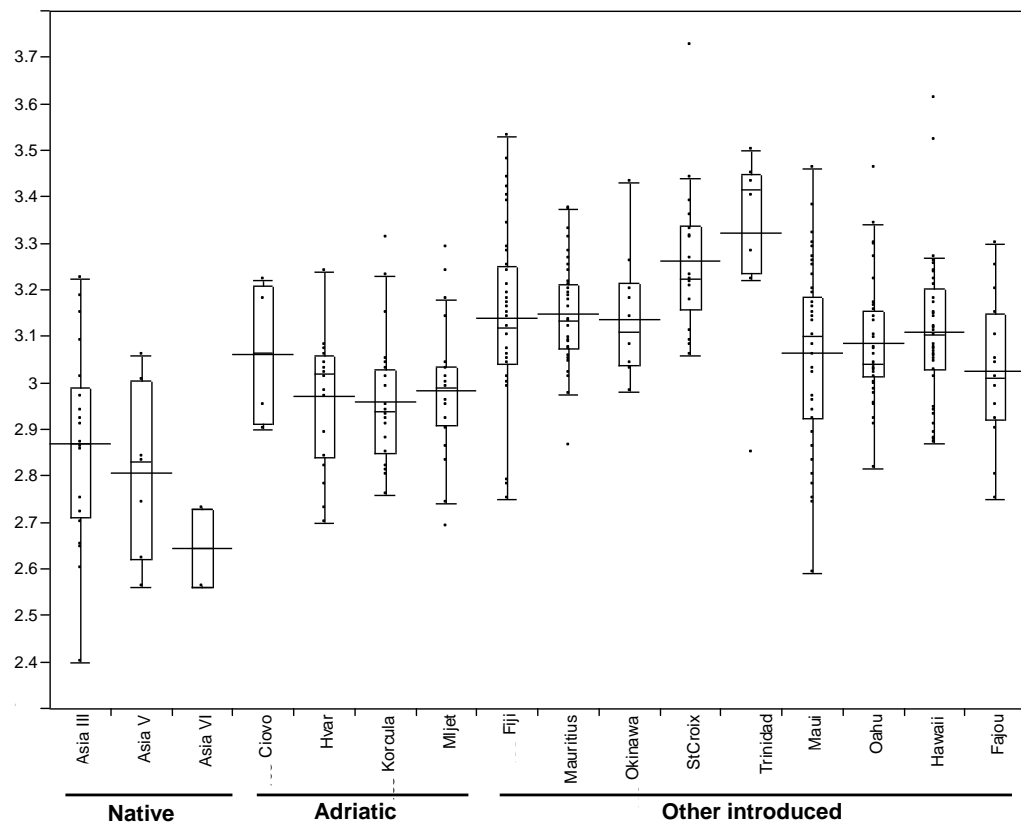
A
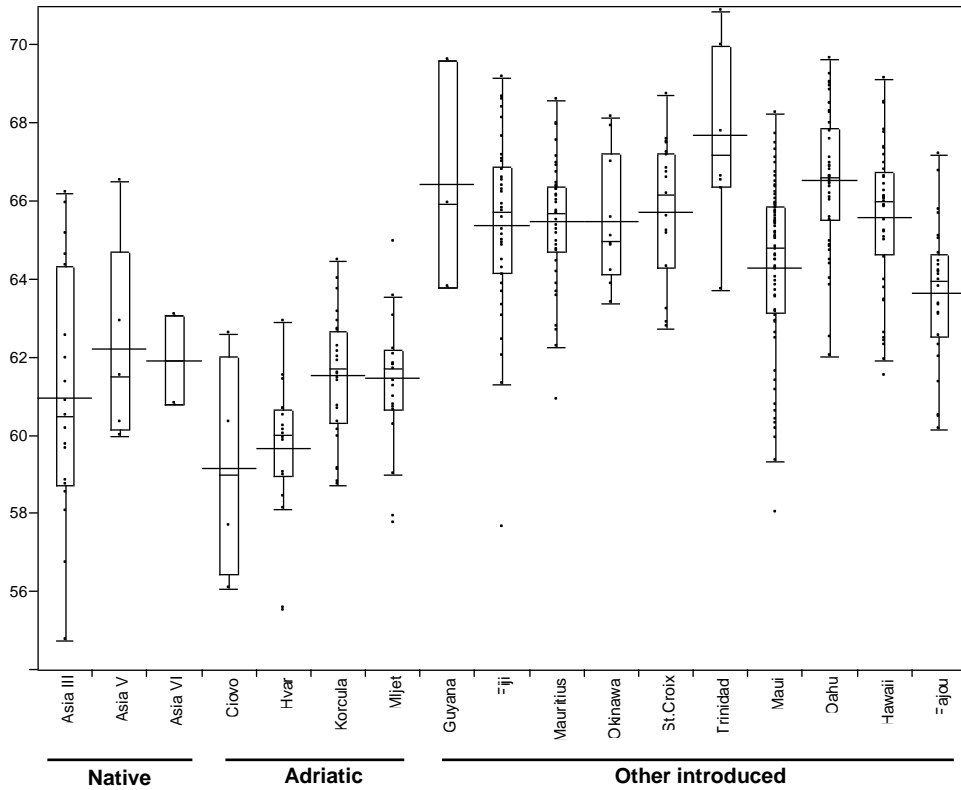
B

Figure V-2: Maximum diameter of upper canine (CsupL, mm) for (A) male and (B) female small Indian mongoose from three regions in its native range, four Adriatic islands, and several other introduced islands. The box and whiskers are interquartile ranges and 95% CI.
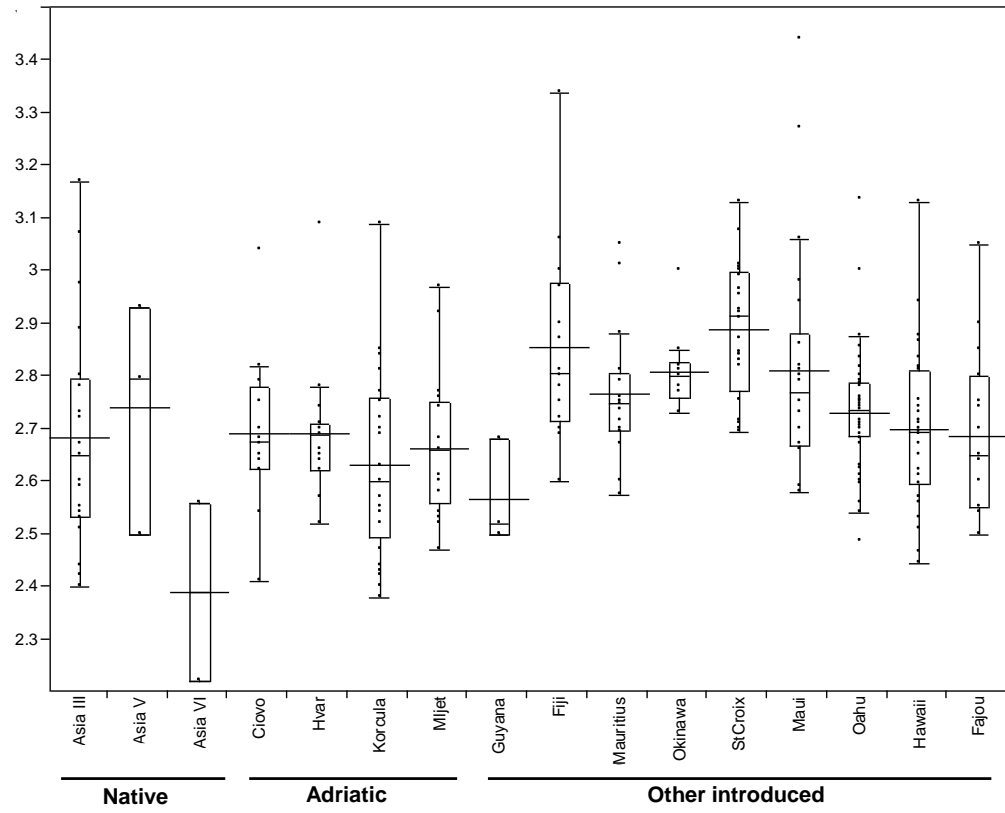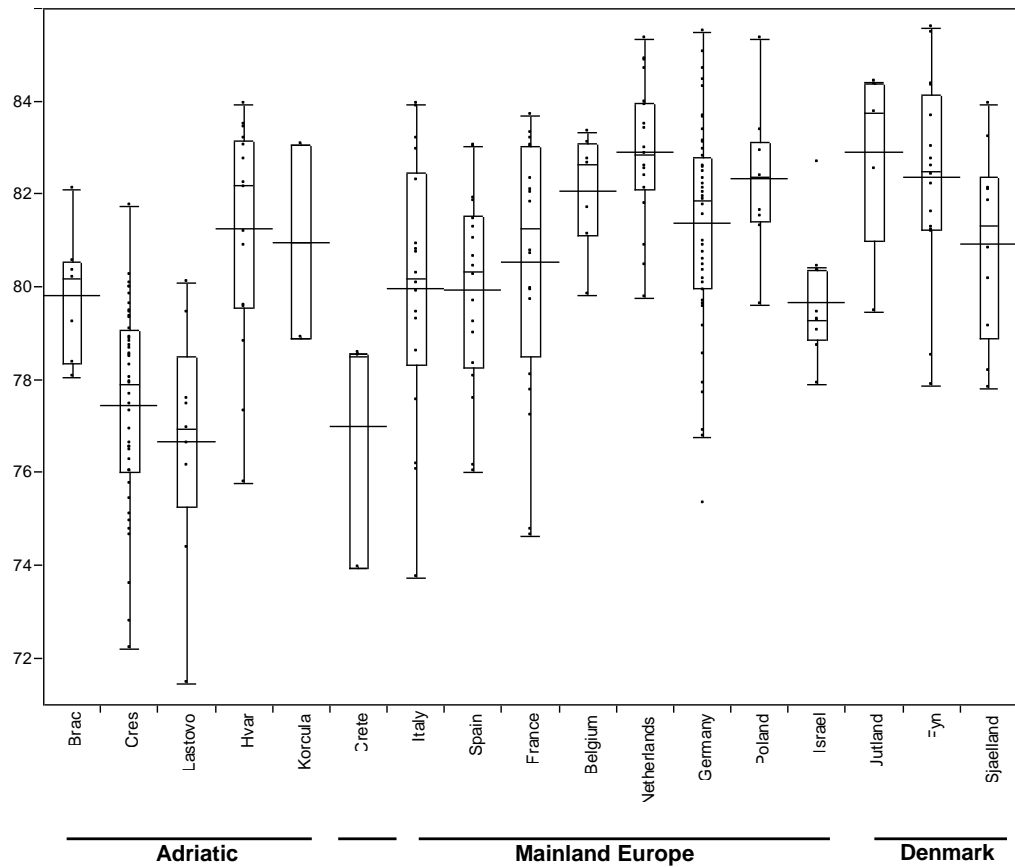
A

B

Figure V-3: Condylobasal skull length (CBL, mm) for (A) male and (B) female stone marten from six islands in Adriatic, several mainland European populations, and three Danish islands. The box and whiskers are interquartile ranges and 95% CI.
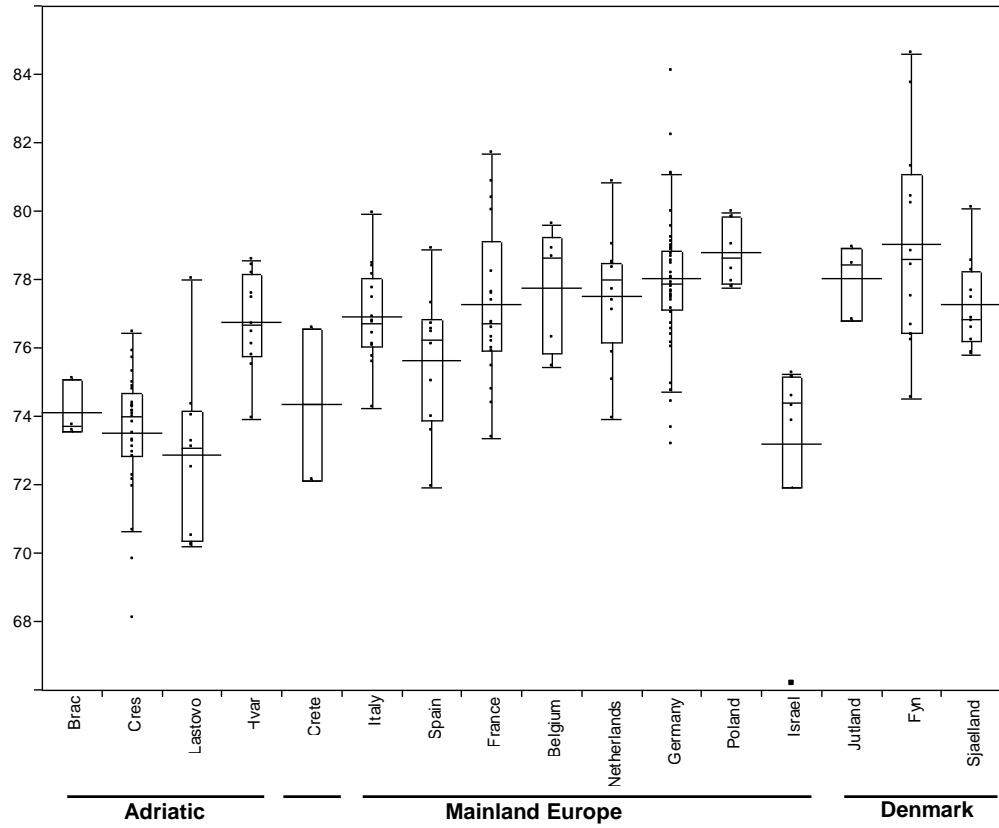
A

B

Figure V-4: Maximum diameter of upper canine (CsupL, mm) for (A) male and (B) female stone marten from six islands in Adriatic, several mainland European populations, and three Danish islands. The box and whiskers are interquartile ranges and 95% CI.

A

B

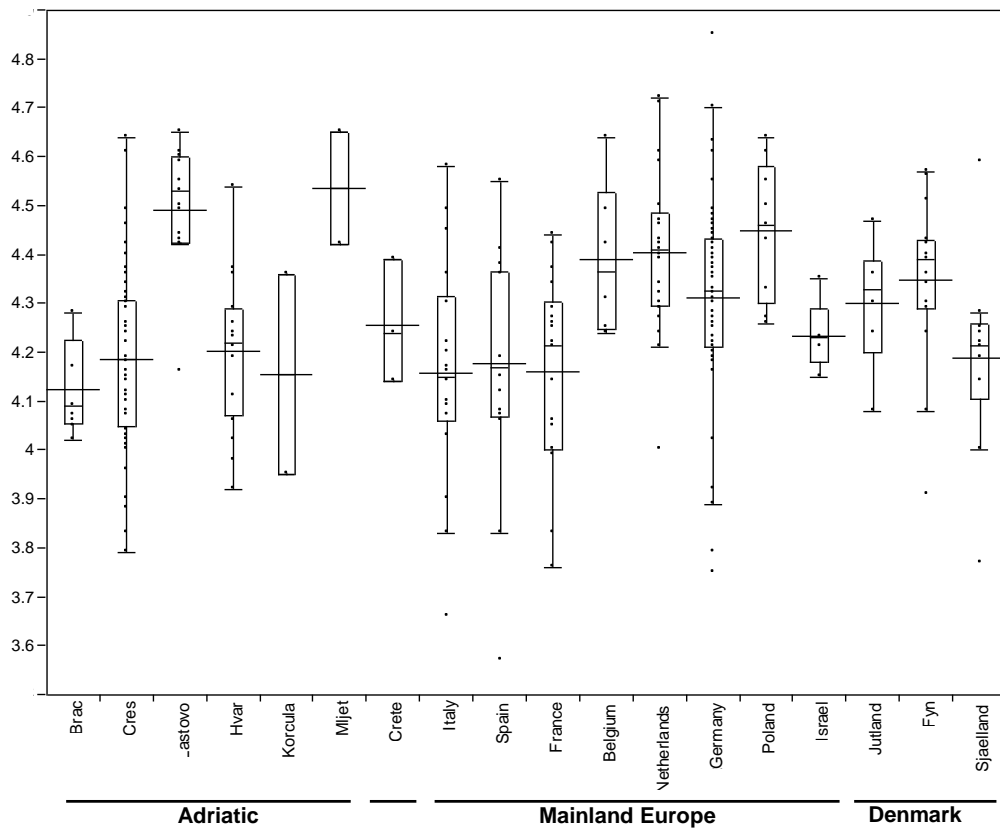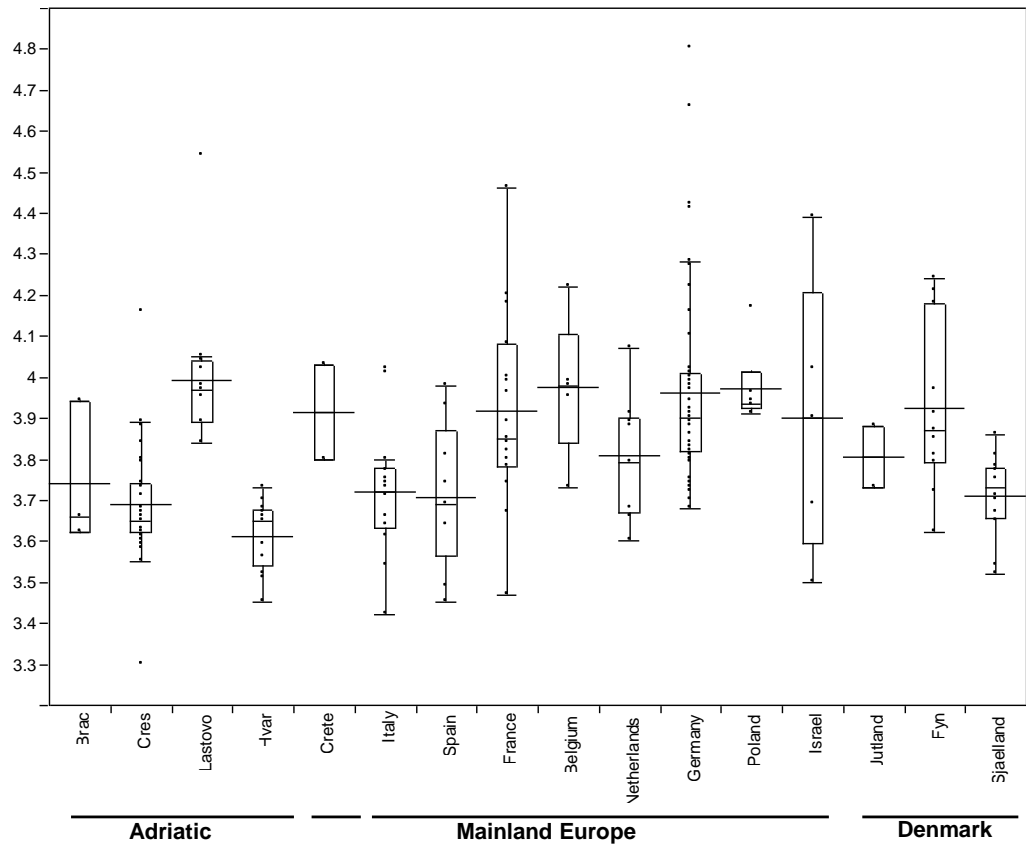# CHAPTER VI.

CAN GENETIC DATA CONFIRM OR REFUTE HISTORICAL RECORDS: THE ISLAND INVASION OF THE SMALL INDIAN MONGOOSE (*HERPESTES AUROPUNCTATUS*)

Co-authored by Matthew L. Niemiller, Benjamin M. Fitzpatrick, James A.

Fordyce, and Daniel Simberloff

Abstract

Several studies have attempted to infer the chronological order of introduction from variation in genetic diversity among populations within an introduced species' range. Such a pattern needs careful interpretation, however, because genetic variation can also reflect differences in the number of founders, variation in genetic diversity between groups of founders, or simply the standing variation in the native population. In this context, the serial introduction of the small Indian mongoose, *Herpestes auropunctatus*, was used to develop a simple simulation model to evaluate more broadly the potential for population genetic data to confirm or refute the completeness of other historical introduction records. We used already published microsatellite data to parameterize simulations and test the credibility of historical introduction records of *H. auropunctatus* to five islands (Fiji, Okinawa, Amami-Oshima, Jamaica and Mauritius). Based on our simulations and the number of alleles detected alone, the purported introduction history for the island of Fiji is inaccurate. Simulations revealed that the number of alleles observed was greater and expected heterozygosity was higher than expected for several loci, assuming the reported introduction data and a 12-month generation time. Although multilocus genotypes can sometimes be used to distinguish alternative sources of introduction, our findings show that we cannot use genetics to unambiguously describe introduction history or distinguish a wide range of founder population sizes.

Introduction

The evolutionary history of introduced populations typically involves complex changes in propagule size and number and, occasionally, genetic admixture between populations from different native regions (Kolbe *et al.* 2004; Dlugosch & Parker 2008; Simberloff 2009). Coalescent theory and population genetic data (e.g., microsatellites and AFLPs) have aided in inferring these historical population processes (reviewed by Beaumont [1999] and Stephens & Donnelly [2000]). The chronological order of introduced sites can predict variation in genetic diversity among populations within an introduced species' range (Estoup *et al.* 2001). After an initial founding event and genetic bottleneck, subsequent serial introductions (e.g., from site A to B, from site B to C, etc.) should result in a decline in genetic diversity with each successive introduction (Clegg *et al.* 2002). From this expected pattern of reduced genetic diversity, one potentially can infer the order of colonization (Estoup *et al.* 2001; Hufbauer *et al.* 2004; Kawamura *et al.* 2006).

Such a pattern needs careful interpretation, however, because genetic variation can also reflect differences in the number of founders (Nei *et al.* 1975; Chakraborty & Nei 1977; Lande 1988; Spencer *et al.* 2000; Simberloff 2009), random variation in genetic diversity between groups of founders, or natural variation among sources of founders (Kolbe *et al.* 2004). Furthermore, the initial population dynamics of introduced species may play a significant role in determining how much genetic diversity is retained. For example, a population that increases in size rapidly after a founder event will lose relatively little

variation, whereas substantial variation can be lost when a founder population remains small for several generations (Nei *et al.* 1975).

In this context, the serial introduction of the small Indian mongoose, *Herpestes auropunctatus*, to islands exemplifies a well-documented but complex historical process in which the credibility of historical records and hypothesized introduction routes can be tested by use of genetic data from introduced and native populations. The native distribution of *H. auropunctatus* ranges from Iraq in the Middle East eastward to Myanmar, and from northern Pakistan southward through the center but not the south of the Indian subcontinent (Veron *et al.* 2007). In the late 19th and early 20th centuries, *H. auropunctatus* was widely introduced to at least 64 islands in the Pacific and Indian Oceans, Caribbean and Adriatic Sea, and to two continental areas in the northeast coast of South America and Adriatic coast for control of rats and snakes (Barun *et al.* in press). This species is a generalist predator and is blamed for the decline and extirpation of many native island species (Hays & Conant 2007; Nellis & Everard 1983). Accordingly, *H. auropunctatus* has been listed as one of the world's 100 worst invaders (IUCN 2000).

The veracity of introduction records is critical to sound management recommendations for conservation purposes. For instance, knowing the sources, routes and timing of introductions allows authorities to plan effective methods of interdiction (e.g. Rollins *et al.* 2009) and to determine whether eradication, if achieved, would simply be redressed by recurrent invasion (e.g. Abdelkrim *et al.* 2007). At least superficially, *H. auropunctatus* would appear to meet these

criteria. In the late 19th and early 20th centuries, rats caused significant losses in sugar cane production, and any attempt to control these pests was widely publicized. Consequently, the introduction history of *H. auropunctatus* is often well-documented with the dates and numbers of individuals, including sex of individuals, available for many introductions (Simberloff *et al.* 2000 and Thulin *et al.* 2006). *Herpestes auropunctatus* was first introduced to Jamaica in 1872 (Espeut 1882) followed by several subsequent introductions from Jamaica to islands in the West Indies (Hoagland *et al.* 1989), the Hawaiian Islands (Bryan 1938), Mauritius (Cheke 1987), the Fijian Islands (Gorman 1975; Morley 2004), Japanese islands (Abe *et al.* 1991; Ishii 1998; Kishida 1931; Yamada 2002, 2004), Ngazidja in the Comoro islands (Louette 1987), and Adriatic islands (Tvrtković & Kryštufek 1990; Barun 2008). This species successfully reproduced and quickly spread throughout these islands and it is thought that subsequent undocumented introductions are unlikely. *Herpestes auropunctatus* is a poor swimmer and all known colonizations were deliberately performed by humans, except for possibly a single introduction to a small island in Fiji where *H. auropunctatus* is believed to have rafted from a nearby, larger island after a hurricane (Craig Morley, pers. comm.).

Thulin *et al.* (2006) investigated the extent of genetic differentiation within and between introduced and native populations of *H. auropunctatus* and how relationships inferred from genetic data relate to the documented history of introduction. In at least one case, their data conflict with a documented introduction scenario. The population on Fiji had more than 46 alleles at eight

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loci, but the documented introduction of only one male and one female predicts a maximum of four alleles per locus (barring an extraordinary mutation rate). This discrepancy could be explained if the single female was already pregnant with progeny of other males. However, analysis of mitochondrial DNA identified three unique haplotypes from Fiji, implying a minimum of three founding females (Barun *et al.* unpublished data).

In addition, there does not seem to be any relationship between estimates of gene diversity (expected heterozygosity) and the accepted story of founder population size for the mongoose introductions (Fig. VI-1). One would expect gene diversity to remain higher with larger founder size but this is not the case for any introduction of *H. auropunctatus* where the number of founders is known.

Given disproof of the introduction history on Fiji and no relationship between gene diversity and founder population size for several other mongoose introductions, we developed a simple simulation model to evaluate more broadly the potential for population genetic data to confirm or refute the completeness of other historical introduction records of *H. auropunctatus*. We use the published microsatellite data of Thulin *et al.* (2006) to parameterize simulations and test the credibility of historical introduction records of *H. auropunctatus* for five islands.

Materials and Methods

Population sampling and microsatellite scoring. Collection of samples and PCR procedures are described by Thulin *et al.* (2006). They report eight microsatellite primer pairs, but we found that three pairs could not be scored reliably by independent observers. Therefore, we retained only five previously reported microsatellite primer pairs (Hj34, Hj40, Hj45, Hj51 and Hj56) to score allelic differences.

Estimation procedure for demographic parameters. We conducted simulations using the R 2.2 environment (http://www.r-project.org) to follow the stochastic loss versus persistence of alleles for each microsatellite locus during the demographic growth of populations after introduction to determine whether reported data on an introduction were statistically consistent with the estimated genetic variation. Introduced populations were assumed to be derived from a parental population in Bangladesh and possessing the same initial frequency of alleles. Bangladesh is a source population for Okinawa population and is less then 100 km from Calcutta where all five populations are documented to have originated (except Mauritius, for which this origin is uncertain but suspected). Laws of India that disallow export of DNA materials prevented us from obtaining samples from the Calcutta region. Alleles sampled in the introduced populations but not in the Bangladesh source populations were assumed to have a source allele frequency of 1 divided by total number of source population alleles plus 1 observed $1/(2n+1)$.

Simulations were conducted only for Amami-Oshima, Fiji, Jamaica, Mauritius, and Okinawa because these were the only populations with apparently clear documentation of both the numbers and sexes of the founders (see Fig. VI-2). The only stepping stone introduction with adequate documentation is from Bangladesh to Okinawa to Amami-Oshima (in 1910, six male and six female *H. auropunctatus* were introduced to Okinawa and then in 1979, 30 mongooses were introduced to Amami-Oshima).

Each simulation consisted of a founder event of N_F diploid individuals followed by logistic population growth for T generations. For each locus, $2N_F$ alleles were initially drawn, with replacement, from the source population. N_F was calculated as the effective population size accounting for sex ratio (Wright 1931, Hartl and Clark 1997) based on historical records. Each generation t, genetic drift was simulated by sampling $2N_t$ alleles from the previous distribution of allele frequencies. Population size N_t was calculated from the logistic population growth equation with growth rate (r) of 3 and carrying capacity (K) of 1000. These numbers are based on the demography of *H. auropunctatus* (Nellis and Everard 1983). For most simulations, we used the same r and K in order to isolate the effects of variation in founder size on genetic diversity. Some islands have larger census population sizes, but preliminary trials with other values for carrying capacity (up to 10^6) yielded similar results (not shown).

We performed two sets of simulations using generation times of six and 12 months, respectively (Nellis and Everard 1983). At the end of each simulation, we recorded the number of remaining alleles in the introduced population and gene

diversity (H_e; Nei 1973) based on final allele frequencies in simulated samples according to the real sample sizes (Thulin *et al*. 2006). We also conducted a two-step introduction simulation for Amami-Oshima where an initial introduction to Okinawa in 1910 was simulated followed by an introduction in 1979 to Amami-Oshima as described above. We conducted 10,000 simulations for each locus of the introduced populations for each generation time. Values for demographic parameters used in simulations are found in Table VI-1. We then compared the distributions from simulation runs with the numbers of alleles and H_e estimated from the real populations. If an empirical estimate was greater or less than 97.5% of the simulation values, we infer that the data are inconsistent with the historical record, given the assumptions of the model. The *R* code implemented for conducting simulations can be found in Supplemental Materials.

Results

Five microsatellite loci exibited between three and nine alleles among the five islands investigated (Table VI-2). Based on the number of alleles detected alone, the purported introduction history for the island of Fiji is inaccurate. We detected more alleles at loci 1 and 5 than are theoretically possible based on a founding size of two individuals.

Simulations revealed that the number of alleles observed was greater than expected in a few instances: Jamaica (locus 1), Fiji (loci 1, 2, and 5), and Amami-Oshima (locus 1), assuming the reported introduction data and a 12-month

generation time (Table VI-2). Conversely, the number of alleles observed was fewer than expected for locus 3 for Mauritius and locus 5 for Okinawa and Amami-Oshima. However, other than Fiji, none of these discrepancies is significant after Bonferroni adjustment for 4 islands (excluding Fiji) times 5 loci (critical percentile values 0.125% and 99.875%). An exemplary plot of number of remaining alleles after demographic growth for locus 5 for Fiji is shown in Fig. VI-2a. Plots for all other loci and islands for both 6-month and 12-month generation times are found in Supplemental Figures VI-S1–S5.

Greater H_e than expected was detected by simulations only for loci 1, 2, and 5 for Fiji and locus 5 for Mauritius, assuming reported introduction data and a 12-month generation time (Table VI-3). No loci had significantly lower than expected H_e, although H_e for locus 3 for Mauritius was lower than 93.6% of simulations. Again, aside from Fiji, no significant discrepancies can be inferred after correction for multiple tests. A sample plot of H_e after demographic growth for locus 5 for Mauritius is shown in Fig. VI-2b. Plots for all other loci and islands for both 6-month and 12-month generation times are found in Supplemental Fig. VI-S1–S5.

Discussion

Many studies in recent years have used molecular data to examine the influence of propagule pressure on the establishment and subsequent spread of successful invasions (e.g. Genton *et al.* 2005; Kolbe *et al.* 2004; Lavergne and

Molofsky 2007; Roman and Darling 2007; Saltonstall 2002). Specifically, several studies used genetic diversity and simulations to address whether single or multiple introductions (i.e., propagule number) occurred, and the qualitative size of these introductions (i.e., propagule size) (Ficetola *et al.* 2008, Ross and Shoemaker 2008, Arntzen *et al.* 2010).

In the above studies, the authors did not address whether there was contradiction between the historical records of an introduction and molecular evidence, except in our current study of the mongoose introductions. According to documented introduction records, Fiji's mongoose population originated from a single mating pair. Our simulations are consistent with the suspicion of Thulin *et al.* (2006) that this introduction history is inaccurate so we are unable to exclude alternative introduction histories for Fiji introduction. We found more alleles than are theoretically possible at loci 1, 2 and 5 based on a founding size of two individuals (Table VI-2), and analysis of mtDNA for the Fiji population found three distinct haplotypes (Barun *et al.* in preparation). In addition, on other islands where the mongoose was introduced, our results are consistent with the accepted introduction history, but we are also not able to reject alternative introduction scenarios encompassing a wide range of founder population sizes.

Genetic variation of introduced populations is determined largely by the past history of the invasive species within its native range (Taylor and Keller 2007), as mutation has minimal influence given the age of most biological invasions (less than 500 years old, and often much younger). How this variation is represented in introduced populations is determined by propagule pressure

and can have a significant effect on establishment probability and expansion.

Therefore, an understanding of the evolutionary history of genetic diversity

within the native range is necessary to elucidate and understand factors affecting

genetic diversity during invasions (Taylor and Keller 2007). In our study, we

observed some discrepancy between our observed data and the simulations,

particularly for locus 1. This may be caused by inappropriate use of Bangladesh

samples as a proxy for Calcutta. As noted previously, most original founders are

documented from the Calcutta region but laws of India disallowing export of

DNA materials forced us to use Bangladesh as the "native" population. Although

Bangladesh is less then 100 km from Calcutta, our simulation results hint that

Bangladesh may not be an adequate surrogate source.

To identify the geographic source of introduced populations, determine

the number of introductions, and assess levels of genetic variation, the native

range of the species must be exhaustively sampled not just with regard to the

number of populations but also the number of individuals within populations.

Ultimately, the accuracy of the estimation of the number of introductions and

origins of introduced populations is determined by sampling intensity in the

introduced and native ranges, the resolution of the molecular markers employed,

and the scale of genetic differentiation across the native range (Dlugosch and

Parker 2008). Limited sampling with respect to coverage and sampling intensity

within native populations, as in our study, may fail to document haplotype

sharing among native populations and result in overestimation of the number of

introduction events. Moreover, high amounts of genetic variation across the

native range will complicate the estimation of the number of introduction events. Lack of geographic structure of genetic variation in the native range will also obfuscate the qualitative inference of the number of introduction events and identifying the source region in the native range.

A number of authors have debated whether a particular population was initiated by a small or large number of founders and how much genetic variation the introduced population would retain. For example, in a review of aquatic invasions, Roman and Darling (2007) provided evidence that reduced genetic diversity in invasive populations is not as common as one would expect despite small founder size. Despite the common belief that insect invasions must have arisen through large and even multiple invasions, Zayed et al. (2007) showed that the solitary bee *Lasioglossum leucozonium* invaded North America most likely through the introduction of a singly-mated female. For our simulation we selected only 5 populations for which the documented introduction history is for a single event only. However, the number of individuals introduced to each of the five populations varieed from 2 to 30 (Table VI-1). As we have observed previously, these different numbers of introduced individuals did not produce great variation in heterozygosity estimates for loci 1 through 5 in all five populations (Fig. VI-1). Based on this number of markers, it is unlikely that one can discriminate among various founding population size scenarios.

It is generally believed that stepping-stone introductions significantly reduce genetic diversity, but the stepping-stone introduction of *H. auropunctatus* from Calcutta to Okinawa Island to Amami-Oshima does not reflect such a

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reduction. Both islands are very large and *H. auropunctatus* reproduces very quickly, so there may have been insufficient time at the beginning of the introduction for genetic drift to eliminate alleles even in this serial introduction (Nei *et al.* 1975). In addition, results of Clegg *et al.* (2002) indicate that single founder events do not affect levels of allelic diversity but instead four to five serial founder events are required. We suspect that the drop of alleles may be substantial in a species with initial slow population growth. However, we were unable to obtain allelic data for a species that had initial slow population growth, small founder size, and a well-documented introduction history to test this hypothesis.

We cannot use genetics to define the history of introductions unambiguously or to indicate a large or small number of founders, but we can use sometimes use DNA analysis forensically to determine the source of introductions using multilocus genotypes of individuals. Recently, *H. auropunctatus* was discovered on two additional islands, Upolu and New Caledonia. This is not a unique case; new introductions of many other species are common worldwide and, unlike the introductions of *H. auropunctatus*, they are accidental (Varnham 2010). Also, many of these introduced species have enormous impact on native species and entire ecosystems, so resource agencies spend enormous amounts on their control. They would greatly benefit from having collection samples to be able to discriminate small from large numbers of founders. However, as our study shows, at present we lack the genetic tools to do so.

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Appendix VI

Tables and Figures

Table VI-1. Genetic data for the simulated populations. Founder N_e is the initial number of introduced mongooses, generations is the number of generations from initial introduction to the time of tissue collection (assuming 12 month generation time), and *n* of locus 1–5 is number of samples for each locus.

Parameters							
Island	Founder Ne	Generations[1]	n of Locus 1	n of Locus 2	n of Locus 3	n of Locus 4	n of Locus 5
Bangladesh (native range)	-	-	35	35	35	35	31
Pakistan (native range)	-	-	19	20	16	20	20
Jamaica[1]	9	130	44	47	46	42	46
Fiji[1]	2	119	35	35	35	35	35
Mauritius[1]	19	101	35	35	35	35	35
Okinawa[1]	12	92	93	93	85	91	90
Amami-Oshima[2]	30	18	43	32	39	42	39

1 assuming a 12 month generation time
2 two-step model: Calcutta to Okinawa and Okinawa to Amami-Oshima

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Table VI-2. Number of observed alleles for each population for loci 1–5. In parenthesis is percentile of simulated alleles that fall in 95% confidence interval (assuming 12-month generation time). A two-step model was simulated for Amami-Oshima: Bangladesh to Okinawa and Okinawa to Amami-Oshima.

Number of Alleles					
Island	**Locus 1**	**Locus 2**	**Locus 3**	**Locus 4**	**Locus 5**
Bangladesh	6	6	7	7	8
Pakistan	2	2	3	7	3
Jamaica[1]	**7 (98.4)**	4 (23.9)	7 (94.4)	5 (55.3)	7 (84.5)
Fiji[1]	**9 (100.0)**	**5 (100.0)**	3 (39.2)	4 (89.1)	**8 (100.0)**
Mauritius[1]	5 (55.9)	5 (51.7)	**3 (0.6)**	6 (75.3)	8 (92.6)
Okinawa[1]	5 (83.3)	4 (45.9)	5 (71.5)	4 (41.5)	**3 (2.1)**
Amami-Oshima[2]	**6 (98.5)**	3 (15.0)	4 (38.0)	4 (47.1)	**3 (3.1)**
[1] assuming a 12 month generation time [2] two-step model: Calcutta to Okinawa and Okinawa to Amami-Oshima					

Table VI-3. Expected heterozygosity for each population for loci 1–5. In parenthesis is percentile of simulated

heterozygosity that falls in 95% confidence interval (assuming 12-month generation time). A two-step model was

simulated for Amami-Oshima: Bangladesh to Okinawa and Okinawa to Amami-Oshima.

| He					
Island	**Locus 1**	**Locus 2**	**Locus 3**	**Locus 4**	**Locus 5**
Jamaica[1]	0.76 (93.9)	0.62 (46.9)	0.63 (35.7)	0.64 (49.0)	0.8 (93.6)
Fiji[1]	**0.78 (100.0)**	**0.72 (99.2)**	0.49 (47.8)	0.64 (88.3)	**0.84 (100.0)**
Mauritius[1]	0.76 (91.6)	0.72 (77.7)	0.49 (6.4)	0.78 (93.9)	0.84 (98.8)
Okinawa[1]	0.74 (94.5)	0.6 (52.5)	0.73 (86.6)	0.56 (37.7)	0.51 (12.8)
Amami-Oshima[2]	**0.74 (96.1)**	0.52 (36.3)	0.68 (73.6)	0.69 (81.0)	0.51 (15.2)
1 assuming a 12 month generation time 2 two-step model: Calcutta to Okinawa and Okinawa to Amami-Oshima					
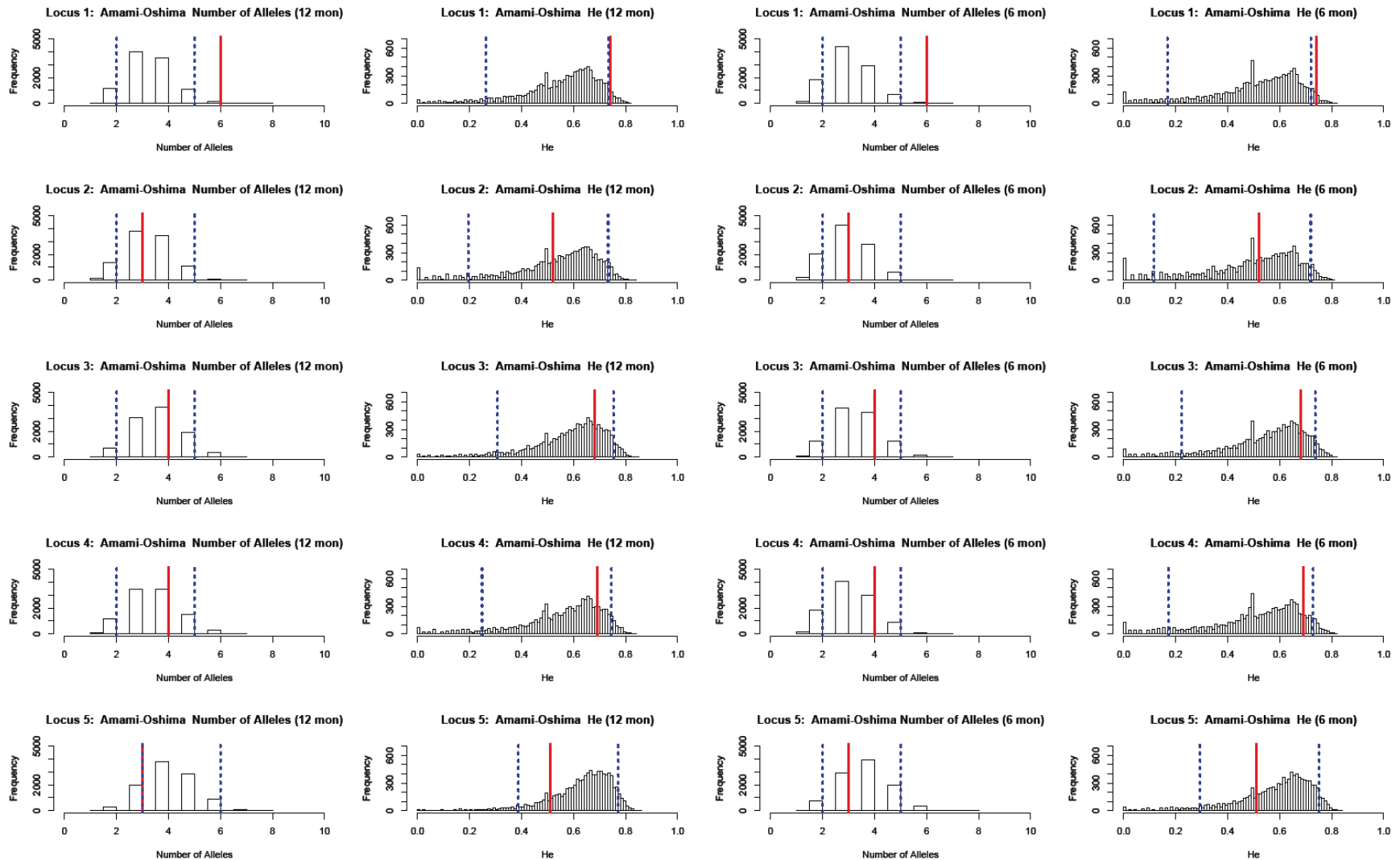
Figure VI-S1. Plots for loci 1-5 for Amami-Oshima for both 6-month and 12-month generation times. Red bar is observed and dashed blue bars are 95% confidence intervals for simulated number of alleles and heterozygosity, respectively.
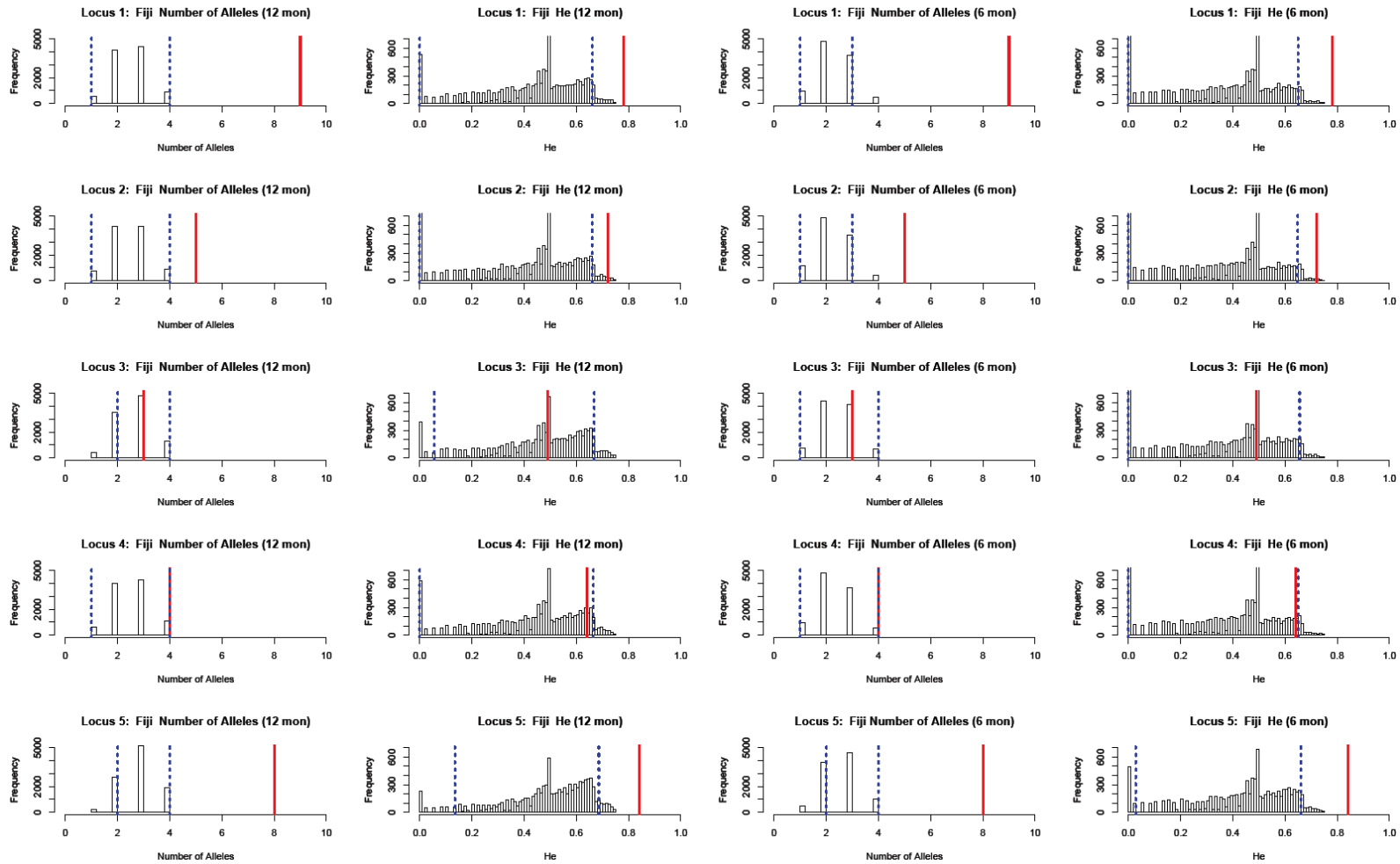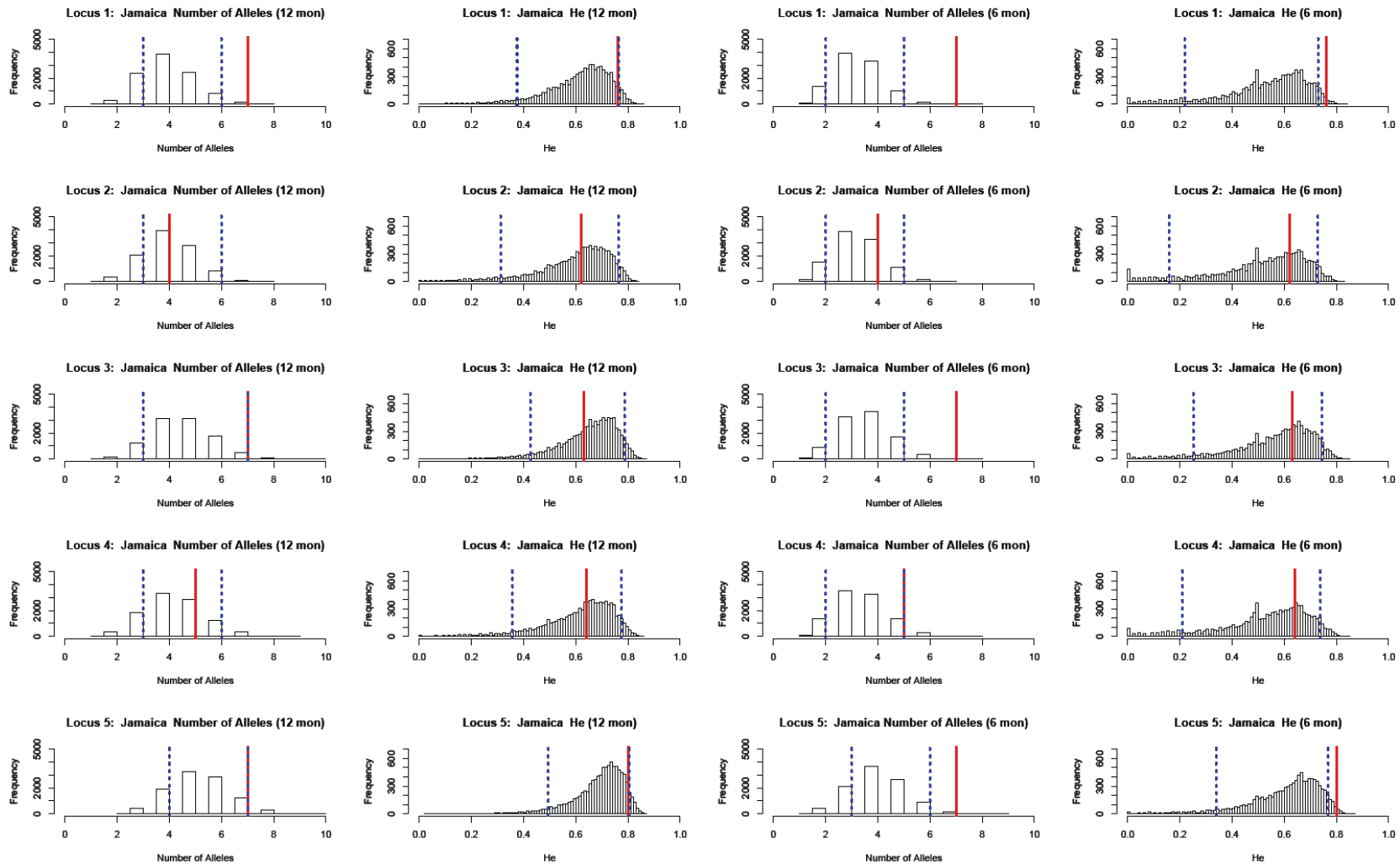
Figure VI-S2. Plots for loci 1-5 for Fiji for both 6-month and 12-month generation times. Red bar is observed and dashed blue bars are 95% confidence intervals for simulated number of alleles and heterozygosity, respectively.
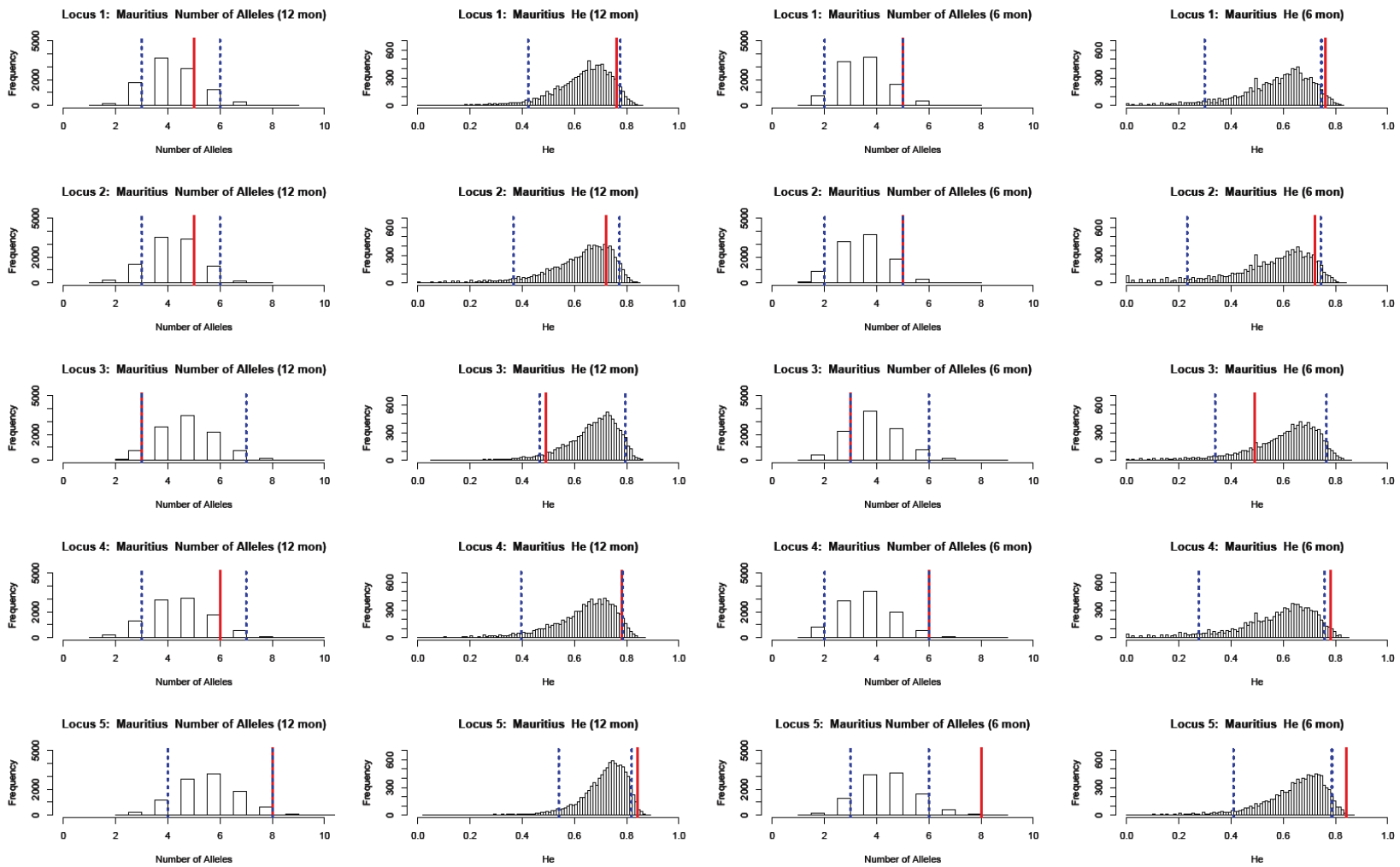
Figure VI-S3. Plots for loci 1-5 for Jamaica for both 6-month and 12-month generation times. Red bar is observed and dashed blue bars are 95% confidence intervals for simulated number of alleles and heterozygosity, respectively.

Figure VI-S4. Plots for loci 1-5 for Mauritius for both 6-month and 12-month generation times. Red bar is observed and dashed blue bars are 95% confidence intervals for simulated number of alleles and heterozygosity, respectively.
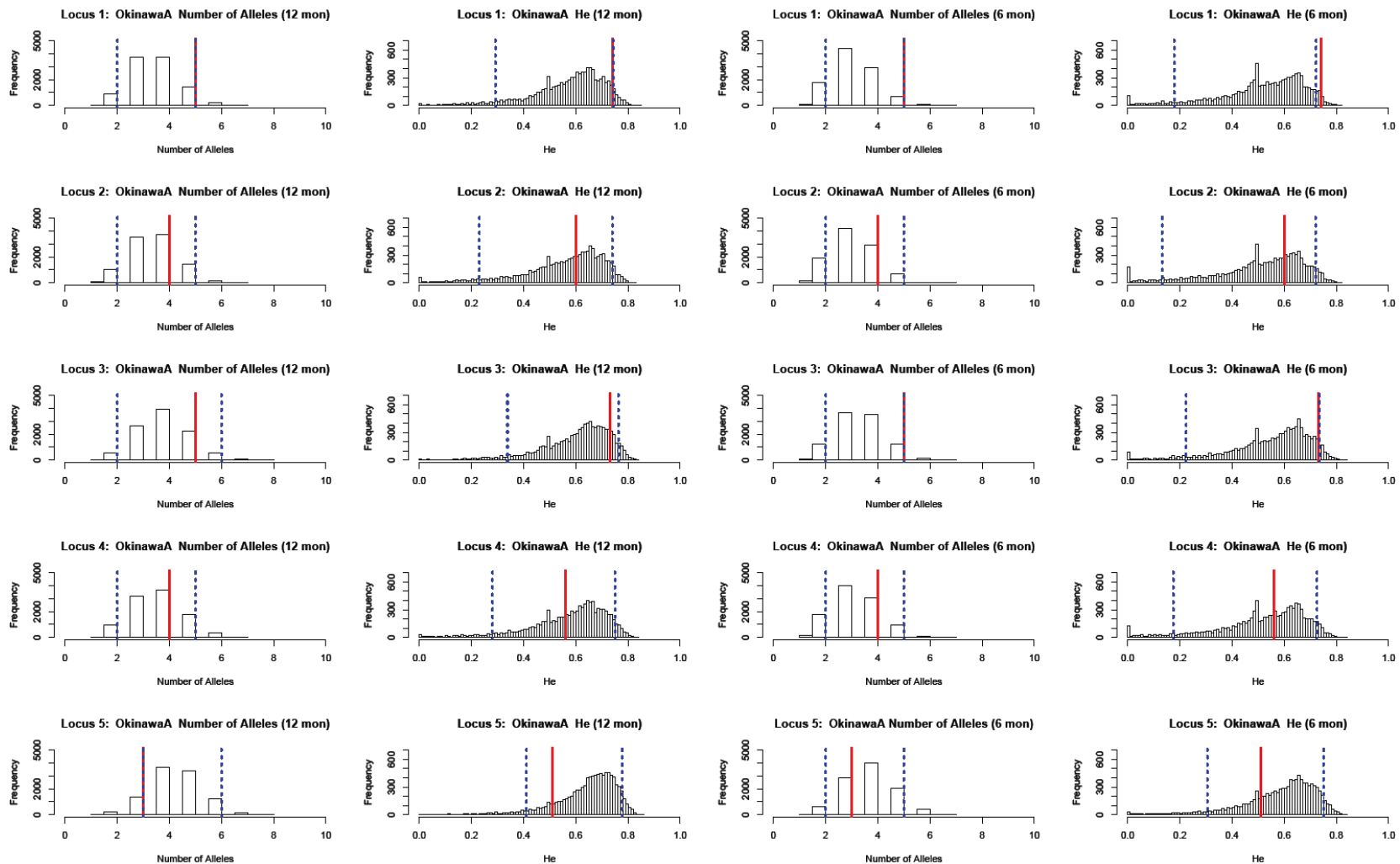
Figure VI-S5. Plots for loci 1-5 for Okinawa for both 6-month and 12-month generation times. Red bar is observed and dashed blue bars are 95% confidence intervals for simulated number of alleles and heterozygosity, respectively.
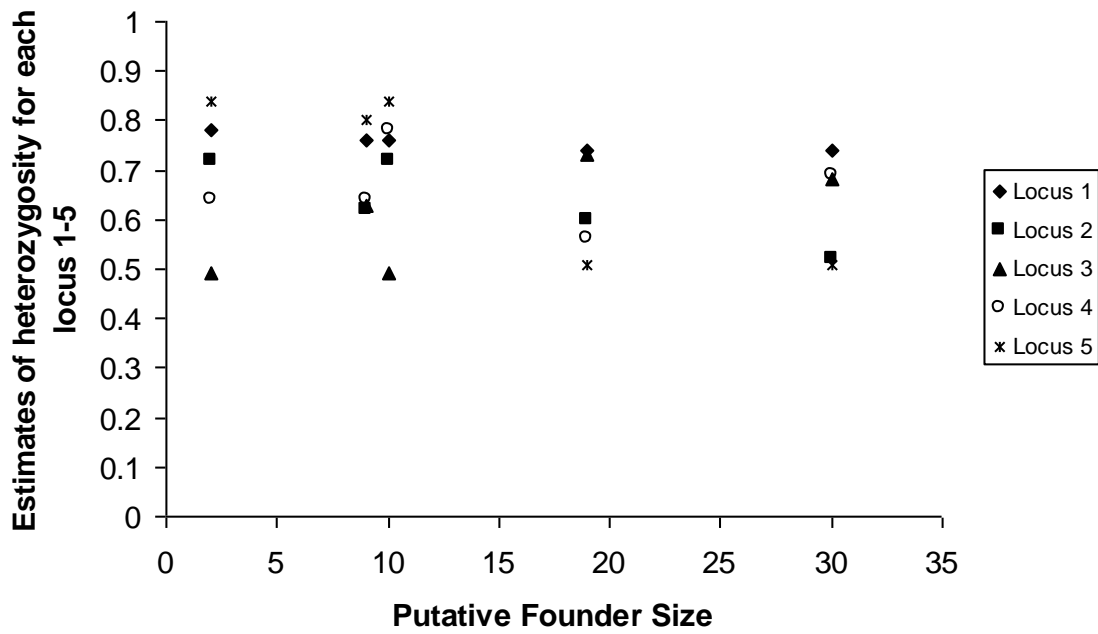
Figure VI-1. Graph of the founder size for each population and estimates of

heterozygosity for each locus (dashed line is observed Bangladesh
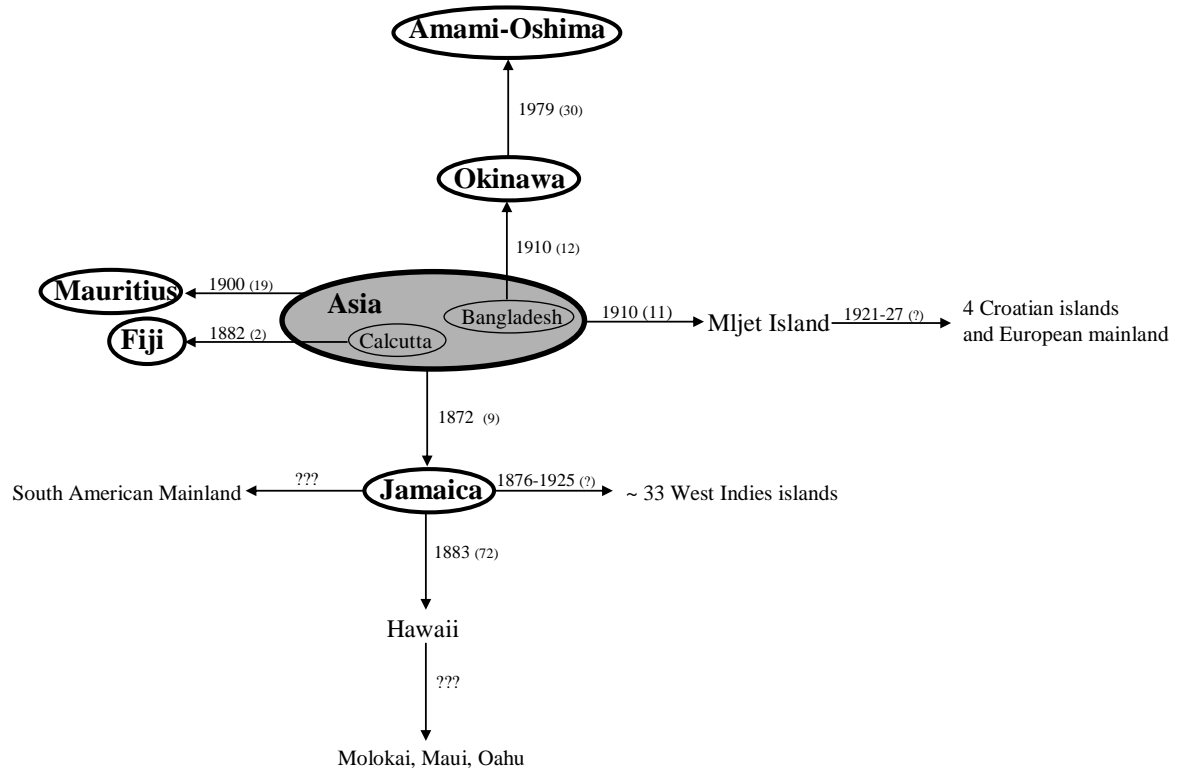
heterozygosity).

Figure VI-2. Schematic drawing of sequential founder events of the small Indian mongoose. In bold and circled are populations we simulated (modified from Thulin *et al.*, 2006). The numbers given are a year of introduction and in parenthesis is the number of individuals introduced.

Locus 5: Fiji Number of Alleles (12 mon)

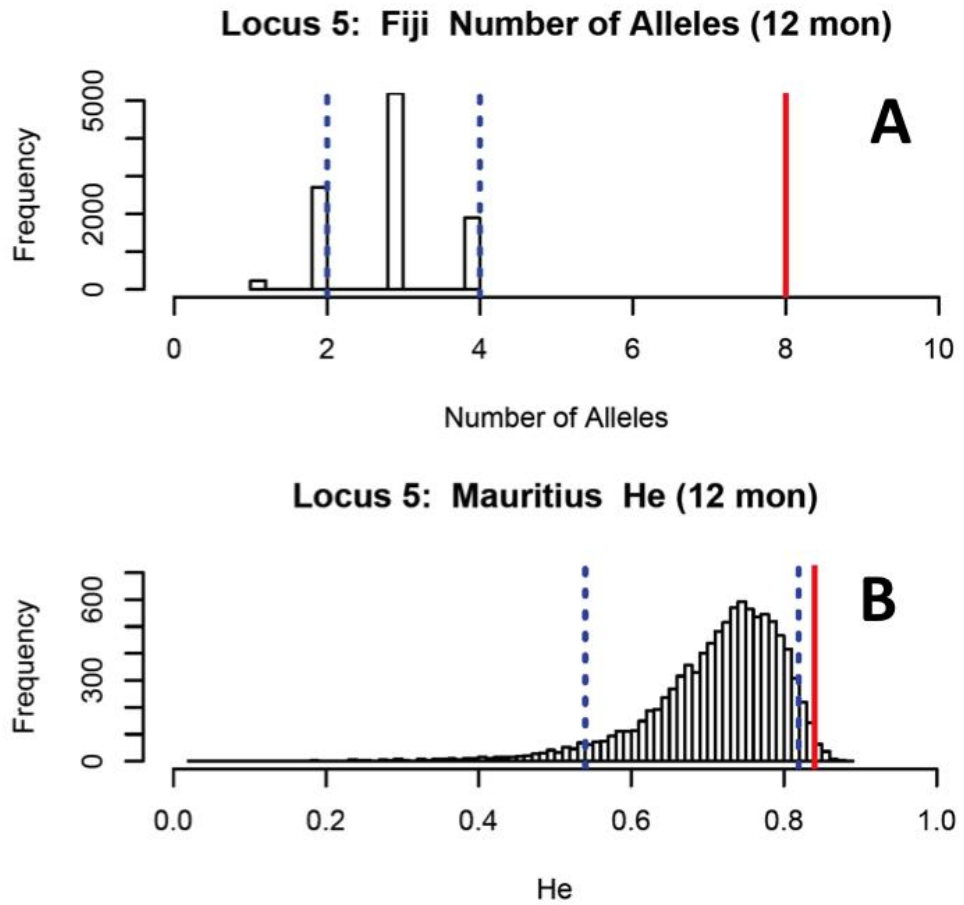**Locus 5: Mauritius He (12 mon)**

Figure VI-3. Example plots for (A) the number of remaining alleles after demographic growth for locus 5 of Fiji assuming a 12-month generation time, and (B) He after demographic growth for locus 5 of Mauritius assuming a 12-month generation time. Plots of all loci for all populations simulated can be found in Supplement Figures VI-S1 through S5 (both 6- and 12-month generation times). Red bar is observed and dashed blue bars is 95% confidence interval for simulated number of alleles and heterozygosity, respectively.

CONCLUSION

This dissertation illustrates how one introduced predator, the small Indian mongoose, might shape the prey community composition on Adriatic islands; it reviews current and past management practices for this carnivore, and is a good model to test putative introduction histories. It also suggests patterns of evolution in both the mongoose and a native carnivore, the stone marten. The main findings of the six parts of the dissertation are summarized below:

Chapter I: In my overview of introduced mammalian carnivores I conclude that many global declines and extinctions can be wholly or partially attributed to these populations. Carnivores were most often deliberately introduced to prey on pest animals, but many were also either escapes or intentional releases from fur farms. Predation by introduced carnivores is a major current threat to several species, but they have other impacts as well, affecting human health and economies and hybridizing with native species. Long-term carnivore control is required to prevent declines and possible extinctions of some endemic species. Successful eradication campaigns are increasingly being undertaken, though these have largely been restricted to islands to date.

Chapter II: In my study certain herpetofaunal species were either very scarce or completely absent on the three mongoose-infested islands but were present and even in high abundance on the three mongoose-free islands. I suggest that an expanded, systematic effort to eradicate or at least suppress small Indian

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mongoose populations on these islands, under the auspices of the Croatian government, would substantially and rapidly benefit some amphibian and reptile populations (Barun *et al.* 2010).

Chapter III: My results support an already large but mostly speculative literature that suggests inability of the small Indian mongoose to reduce high abundances of introduced *R. rattus*. Further, I suggest that the low abundance of certain native small mammals on mongoose-infested islands is probably not solely caused by the mongoose but also by high *R. rattus* populations on all six islands. In addition, I provide evidence that *R. rattus* has changed its activity time to become more nocturnal on mongoose-infested islands, possibly to avoid predation by the mongoose. I suggest that as *R. rattus* became more nocturnal, the diurnal mongoose may have become the main predator on amphibians, reptiles, and poultry.

Chapter IV: Research funding for mongoose eradication trials is urgently needed. The best opportunities for eradicating or containing an alien invasive species are often in sites were an invasion is in its early stages, when populations are small and localized and not yet well established. Priority for eradication should also be given to islands that can serve as sources for introduction to other areas and those that harbor endemic fauna. At present many islands inhabited by the mongoose are too large for eradication. Intensive localized control could benefit species that are at risk until eradication methods are developed.

Chapter V: My results suggest that the small Indian mongoose is significantly smaller in both the upper canine tooth and skull length on three Adriatic islands compared to other islands where it was introduced. It is not larger on one island where it is the sole carnivore. The stone marten appears to be smaller in skull length on three Adriatic islands without the mongoose, where it is the sole carnivore, as compared to one island where the mongoose is present, as well as the European mainland, where other carnivores are present. There is no pattern in canine diameter for male stone martens on Adriatic islands, but canines of females on the three mongoose-free islands are smaller than on a mongoose-infested island.

Chapter VI: Based solely on my simulations and the number of alleles detected, the purported introduction history for the island of Fiji is inaccurate. For other islands, simulations revealed that the number of alleles observed was greater and expected heterozygosity was either higher or lower than expected for several loci, assuming the reported introduction data and a 12-month generation time. My findings suggest that we usually cannot use genetics to define the history of introductions unambiguously or to indicate a large or small number of founders, but we can use genetics to determine the source of introductions using multilocus genotypes of individuals.

Arijana Barun was born in Čakovec, Croatia in 1972. She attended public elementary school from 1980 to 1988 at "Osnovna Škola Strahoninec" and high school from 1988 to 1992 at "Srednja Škola Josip Slavenski" in Čakovec. In September 1992 she entered the University of Zagreb, Varaždin, where in April 1994 she received an Associate degree in Data Processing. After graduation in June 1994 and until May 1996, Arijana lived in Sheffield, England and learned English at Hallam University.

She followed her husband to the USA in June 1996, and in January 1997 she entered Harper Community College, Schamburg, IL. In December of 1998 she received an Associate degree in Science and was selected for the All Illinois Academic Team. She represented HCC during an invited visit to the Illinois House of Representatives in Springfield. During that period Arijana enjoyed volunteering at the Lincoln Park Zoo, Chicago and decided to follow a career path of a biologist. In January 1999 she entered the University of Wisconsin, Madison, where in May 2000 she received a Bachelor of Science in Zoology with honors, with a major in Biological Aspects of Conservation. She volunteered in the laboratory of Dr. William Karasov, where she completed her Seniors Honors thesis on intestinal transport of putative passive probes in mice. As soon as she graduated, Arijana immersed herself in field work all over the USA and Caribbean: in New Mexico she studied movements and social behavior of brown-headed cowbirds; in Minnesota she studied ecology and surveys of the northern

goshawk; in Indiana she studied ecology and movements of the endangered copperbelly snake and the northern water snake; in Washington, DC she did an internship at the Smithsonian National Museum of Natural History in the Department of Systematic Biology. For several years now, Arijana has been participating in a long-term study of reptiles on Guana island, British Virgin Islands, which was summarized in a book by James Lazell, "Island: Fact and Theory in Nature".

In August 2003 Arijana entered the Ph.D. program in Ecology and Evolutionary Biology at the University of Tennessee, Knoxville in Daniel Simberloff's laboratory. During the field portion of her PhD, she enjoyed travelling to many Adriatic islands, planning her research, and meeting local people. Five years ago, Arijana became a United States citizen. Arijana's favorite activities are hiking, cooking and travelling with husband Vlado, 8 year old daughter Maria, and 4 year old son Lucas.