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„Factors facilitating the successful introduction of species of the mammalian order Carnivora on islands"

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A**bstract:** A major cause of ecosystem perturbation and biodiversity losses on islands is the introduction of alien species and more than any other vertebrate group introduced mammals have reportedly caused problems. In this study we focus on introduced terrestrial mammalian carnivores and the factors, which are crucial for colonizing islands. Therefore we collected data on the Carnivora fauna of 178 marine islands covering the southern and northern hemisphere, all ecoregions and climatic zones. Carnivora introduced on islands have lower mean female body weight and smaller mean litter size compared to native Carnivora species. We could show that island size has no effect on the occurrence and the number of species of non-native Carnivora. Our results indicate that the occurrence of native carnivores and human population density have a significant impact on the establishment of introduced carnivores on islands. The number of introduced species on islands decreased significantly with increasing number of native carnivores and was positively related to human population density. Our results confirm that one of the main reasons for the occurrence of non-native Carnivora on islands was and still is the presence of humans. As the human population is growing and therefore more native species will have to face the negative human impact on island ecosystems, the future seems to be not very bright. On the other hand, as conservationists and scientists are nowadays more connected to each other than ever in history, also the likelihood to find more effective control measures against introduced species will be higher.

Key words: island biogeography, introduced mammals, carnivores, human population, native species

Zusammenfassung: Größtenteils sind es eingeführte Arten die für die Störung diverser Ökosysteme und den weltweiten Verlust an Biodiversität verantwortlich gemacht werden können. Die größten Probleme innerhalb der Vertebrata verursachen Säugetiere. In dieser Arbeit beschäftigten wir uns mit auf Inseln eingeführten Landsäugern der Ordnung Carnivora und den Faktoren, welche invasive Prädatoren auf Inseln begünstigen. Dazu wurden insgesamt 178 Meeresinseln, der südlichen und nördlichen Erdhalbkugel, aller Ökoregionen und Klimazonen untersucht. Es stellte sich heraus, dass bezüglich der durchschnittlichen Körpergröße von Weibchen und der Wurfgröße, die eingeführten Arten sich signifikant von den heimischen Arten unterschieden. Invasive Beutegreifer auf Inseln sind im Durchschnitt kleiner und weisen eine höhere Wurfgröße auf als heimische Beutegreifer. Zwischen Inselgröße und eingeführten Arten gab es keinen Zusammenhang, weder was das Auftreten noch die Anzahl der eingeführten Arten auf den Inseln anbelangte. Unsere Ergebnisse zeigen, dass die Anwesenheit einheimischer Prädatoren und die menschliche Populationsdichte auf Inseln einen signifikanten Einfluss auf eingeführte Prädatoren ausüben. Die Anzahl an nicht heimischen Beutegreifern nahm mit der Zunahme heimischer Arten ab, während es eine positive Korrelation zwischen menschlicher Populationsdichte und eingeführter Arten gab. Unsere Studie zeigt, dass der Mensch immer noch der Hauptfaktor für die Einführung neuer Arten auf Inseln ist. Da die Weltbevölkerung stetig wächst, steigt auch der Druck auf einheimische Arten und erhöht die Wahrscheinlichkeit von eingeführten Arten auf Inseln. Die Zukunft scheint also nicht allzu rosig. Allerdings sind Biologen und Umweltschützer heute besser vernetzt als je zuvor, dadurch wird es auch leichter effiziente Methoden zum Schutz einheimischer Arten vor Exoten zu finden.

Schlagwörter: Inselbiogeographie, eingeführte Säugetiere, Carnivora, menschliche Besiedlung, heimische Arten

Introduction

There is no doubt that carnivores always fascinated people. Carnivores occur on every large landmass and inhabit every major habitat on earth (Hunter 2011). There are 245 species of terrestrial carnivores worldwide (Hunt 2011). Facilitated by humans approximately 30 species were introduced on islands (Long 2003).

In this study we evaluate which biological traits are characterizing Carnivora species successfully introduced on islands and which abiotic and biotic factors are the best predictors for their occurrence on islands. Carnivores span more than four orders of magnitude in body mass (Gittleman and Purvis 1998), with the Least Weasel (*Mustela nivalis*) as the smallest and the Polar Bear (*Ursus maritimus*) as the biggest species. Remarkably, there is no evidence for differences in body size distribution of carnivores on islands compared to carnivores on mainland (Meiri et al. 2005). However, we predict that Carnivora successfully introduced on islands are represented by r-selected species characterized by a smaller body size and a higher litter size than other carnivore species.

According to the Global Invasive Species Database 18 species of carnivores were introduced worldwide and cause problems in their new ecosystems (Global Invasive Species Database 2013). To understand factors facilitating the successful establishment of introduced Carnivora is particularly important, due to the enormous threat introduced carnivores can have to the native fauna. Introduced animals can have strong negative impact to their new ecosystem, especially on isolated habitats like islands. For example about 42% of island bird extinctions in the past were mainly caused by introduced animals (King 1985). Previous studies have shown that the introduction or colonization of an exotic species on an island can have dramatic consequences on the native species, which are, eradication or endangerment of native prey, competition with native carnivores, and transmission of diseases or genetic changes due to hybridization with closely related native populations (Kauhala 1996).

Why were so many mammals introduced by men? Long (2003) outlined nine different reasons: for aesthetic reasons, for food, hunting and sport, for commercial enterprises, for controlling pests, by accidental introduction, escapees and pet keeping. Pet keeping has a long tradition in many cultures. Two of the most favourite pets, are the domestic dog (*Canis lupus familiaris*) and the domestic cat (*Felis catus*). Today these two carnivore pets are found on many islands all over the world. Cats (*Felis catus*) have been and are still a strong biological threat to bird species, not only on islands but also on mainland (Nogales et al. 2004).

An example for a carnivore that was introduced for hunting purposes is the red fox (*Vulpes vulpes*) in Australia, where it is now a major threat for many native species, like rodents and marsupials (Global Invasive Species Database 2013).

In 1872 nine individuals of the small Indian Mongoose (*Herpestes auropunctatus*) were brought from Calcutta to Jamaica to control the rat population. It is supposed that these few animals were the source of all populations on 29 Caribbian and 4 Hawaiian islands (Lever 1994). Now *Herpestes auropunctatus* is found on the West Indies, Hawaiian island, South America, Fiji, Mafia Island and Africa (Long 2003). Unfortunately this small carnivore did not only hunt rats but started to feed on native amphibians, reptiles, birds and native mammals (Global Invasive Species Database 2013).

In recent times it was very common to introduce non-native carnivores to control agricultural crop pests (Long 2003). The small Indian mongoose (*Herpestes auropunctatus*) is a well known example for a carnivore that has been introduced to control other (non-native) species like rats (Global Invasive Species Database 2013)). Currently, the small Indian Mongoose belongs, along with *Felis catus*, *Vulpes vulpes* and *Mustela ermine,* to the 100 worst invasive alien species of the world (Global Invasive Species Database 2013).

One of our aims in this study was to examine the relationship between introduced carnivores and native carnivores on islands. Does the presence of native carnivore species affect the ability of non-native carnivores to establish on islands? For introduced species it may be easier to establish permanent populations on islands which are free of potential competitors. An increasing number of Carnivora species (with increasing island area and habitat diversity; e.g. for other taxa see Yu et al. 2012) may further decrease the likelihood of a successful establishment of introduced species on islands due to a higher niche packing leaving less “empty” niches for introduced Carnivora. Other important factors influencing the occurrence of introduced species on islands may be related to the human impact. This may be less pronounced in highly isolated islands, which are less frequently reached by boats and larger ships acting as potential vectors for introduced species. Also an increasing human population size on islands may increase the likelihood of occurrence of introduced species, which can be associated with human modified habitats or may profit form hunting activities reducing the density of native species acting as potential competitors.

Methods

Data on Carnivora on islands

We collected data from 174 marine islands covering the southern and northern hemispheres, all ecoregions and climatic zones (Figure 1). However, we did not include Australasian islands due to the fact that we did not include carnivore marsupials in this study. Because we were exclusively interested in factors explaining current patterns of richness and occurrence of island Carnivora, which may prevent or facilitate the establishment of introduced Carnivora, we did not consider species which became extinct during historic times (e.g. *Dusicyon australis* on the Falkland islands). Furthermore, we excluded all Pinnipeds due to their mainly aquatic life style. The complete list of references, from which we extracted distributional data on island Carnivora, is attached as Appendix. Data on body weight and average litter size were extracted from Wilson & Mittermeier (2009).

Data on islands features

For each island the following information was extracted from various references mainly from the United Nations Environment Programme Web site (http://islands.unep.ch/isldir.htm) and Google Earth Programme (2013): (1) distance to the nearest continent (in km), (2) island type (continental or oceanic islands; islands which were never connected by a land bridge to the mainland were defined as oceanic), (3) latitude (degree °), (4) maximum altitude (in m), (5) total area (in km^2), and (6) human population density. Furthermore, (7) each island was affiliated to one of the following ecoregions: Afrotropic, Australasia, Indomalaya, Nearctic, Neotropical, Oceania, and Palearctic and Antarctic.

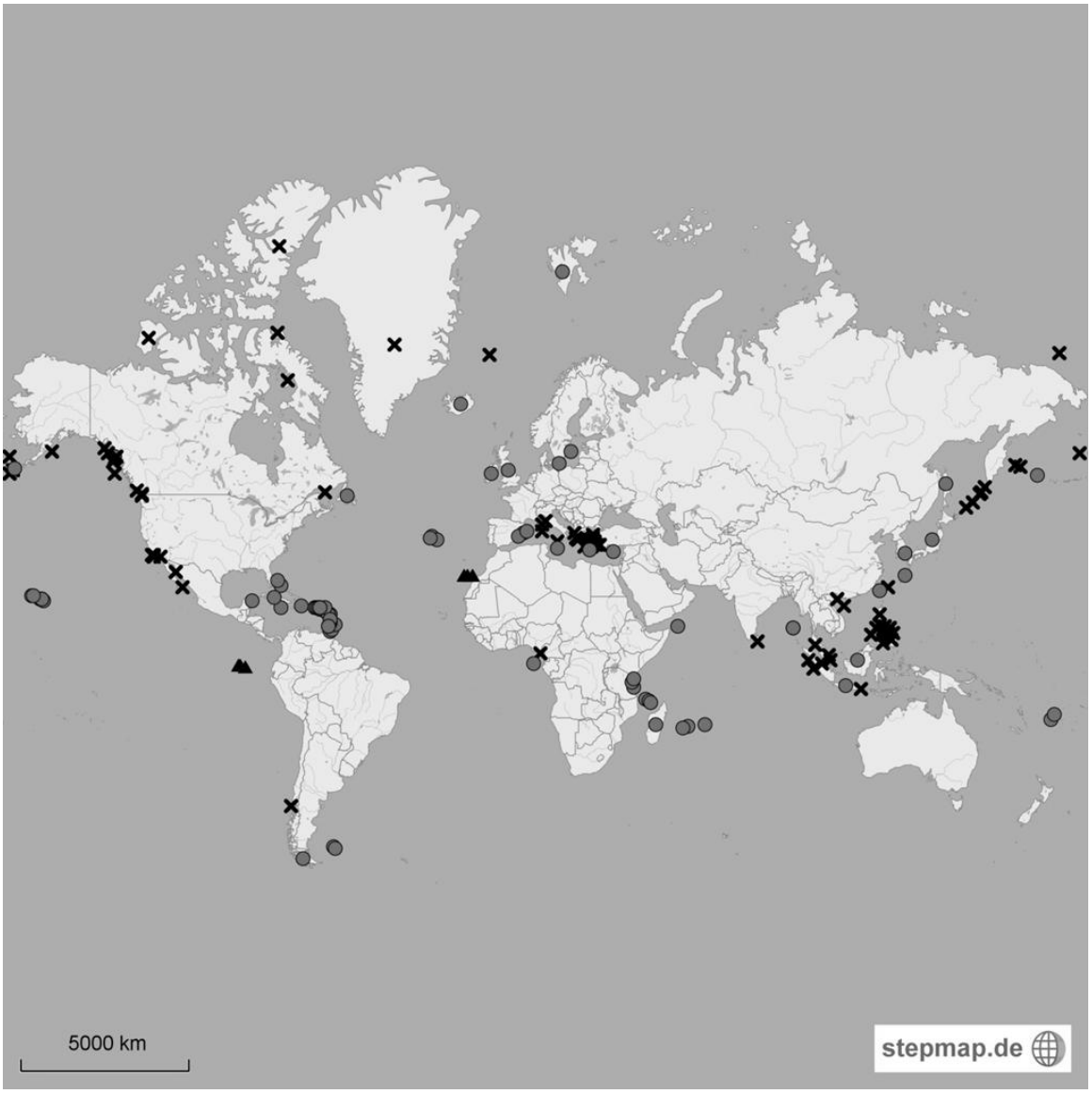

Figure 1. Islands that were considered in this study. ▲ – islands with no native or introduced carnivore species, • – islands with native and introduced carnivore species, × – islands with no introduced carnivore species.

Statistical analysis

Body weight and average litter size of species were log (x) transformed to approach normal distribution of data. To test for differences in body weight and litter size of introduced species and island species which were never successfully introduced, t-tests were calculated using the software Statistica vers. 7.1.

The effect of island size on the occurrence of native and introduced carnivore species was evaluated using logistic regressions. To test for effects of island size on the number of introduced and native species Spearman rank correlations were calculated.

To test for effects of the occurrence of native carnivore species on the occurrence of introduced species on islands a Chi-square test was calculated testing if introduced Carnivora successfully colonized a higher percentage of islands without native Carnivora compared to islands with native Carnivora only including islands which had a least one native or one introduced species.

Subsequently, we calculated a GLMM with a binomial error term and a log link function testing for effects of (1) the distance to the nearest continent (in km), (2) the latitude (degree °), (3) the human population size and (4) the number of native Carnivora on the occurrence of introduced species using the software SPSS version 20. The categorical variable ecoregion was included as random effect. To avoid zero inflation of our analyses only islands with native and/or introduced species were included (N = 168 islands). Because the number of native species was highly correlated with maximum altitude ($r = 0.25$, $p = 0.001$) and island area ($r = 0.48$, $p < 0.0001$), the latter two variables were excluded from the GLMM.

Results

Differences between native and introduced Carnivora species: body size and litter size

In total 115 species of Carnivora are recorded from the 168 islands considered in this study.

Of these, 13.9% were introduced on at least one of the selected islands. Introduced species had a significantly lower body weight (t-test: $t = -2.34$, df = 113, $p = 0.0210$; Figure 2a) and a higher litter size (t-test: $t = 2.49$, df = 97, $p = 0.0144$; Figure 2b) compared to the other island Carnivora.

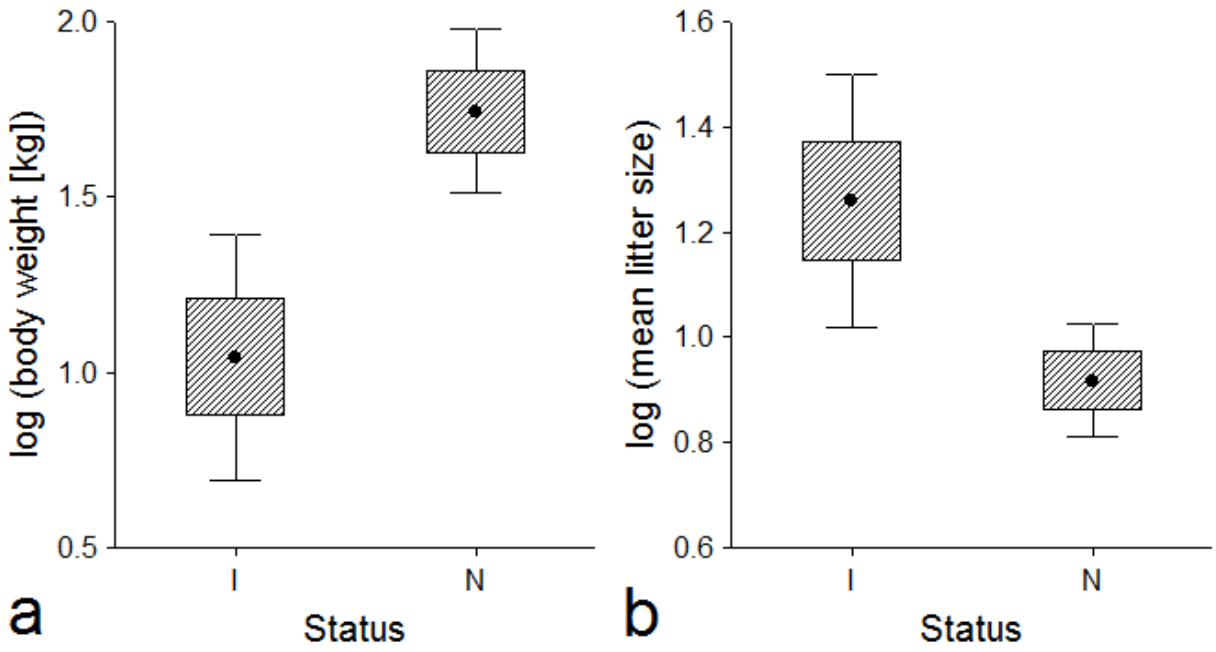

Figure 2. (a) Mean body weight and (b) mean litter size ± SE (box) and 95% CI (whiskers) of introduced (I) and non-introduced (N) island Carnivora.

Minimum island area requirements of carnivores

The likelihood of occurrence of native carnivore increased significantly with island size (logistic regression: $\chi^2 = 10.03$, $p = 0.0015$; Figure 3), while no significant effect of island size was found on the occurrence of introduced carnivores (logistic regression: $\chi^2 = 0.24$, $p = 0.6265$). Also the number of native carnivore species increased significantly with island size (Figure 4a), while again no effect of island size on non-native species was found (Figure 4b). A non-native Carnivora species even occurred on the smallest considered island, Jost Van Dyke with an area of only 9 km^2.

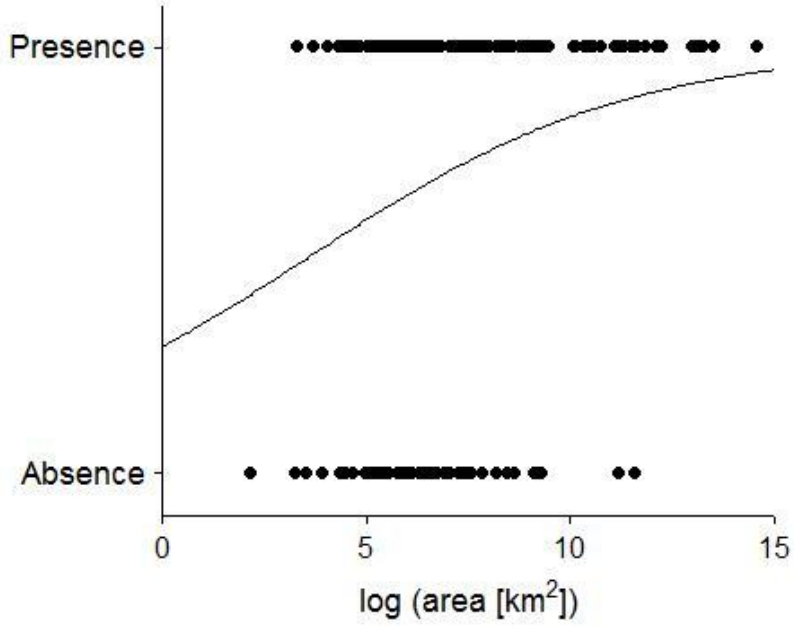

Figure 3. Likelihood of occurrence of native carnivores on islands depending on island area described by a logistic regression function.

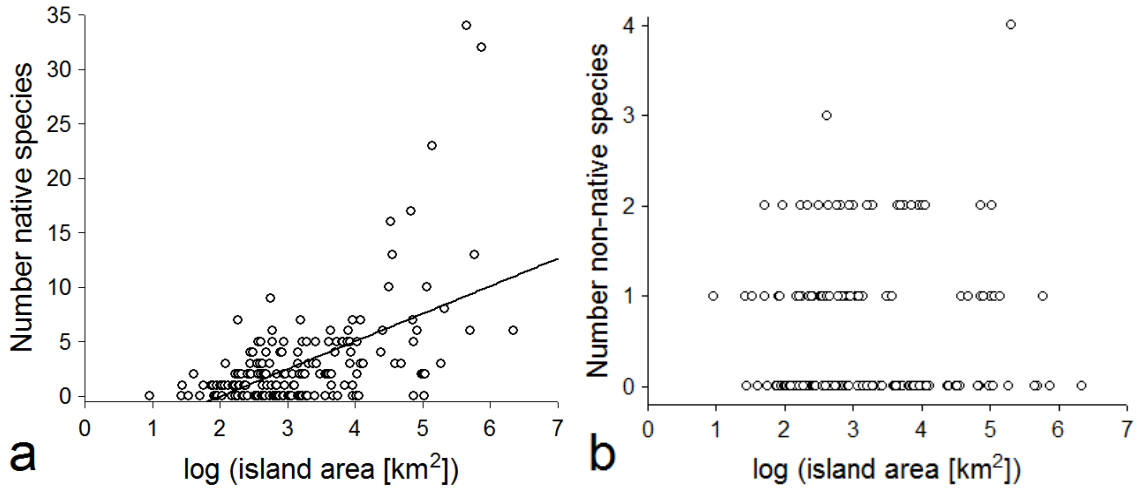

Figure 4. Relationship between the number of (a) native and (b) non-native (introduced) Carnivora species and island size.

Of the 174 islands considered in this study, a total of 6 islands (3 Canary Islands, 3 Galapagos islands) have neither native nor introduced carnivores. In all further analyses only islands (N = 168) are included which have at least one species of native or introduced carnivore.

Effect of native carnivores on occurrence and species richness of introduced species

Non-native species were able to colonize a higher percentage of islands without native carnivores compared to islands with at least one native carnivore species (Chi-square test: χ^2 = 58.31, $p < 0.0001$; Figure 5).

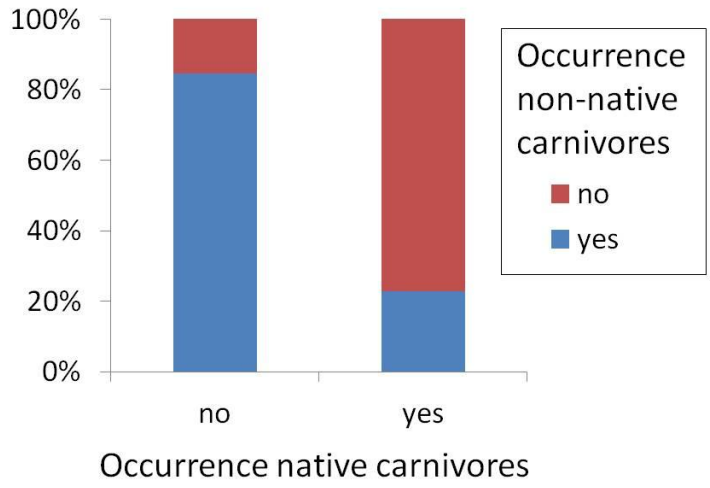

Figure 5. Percentage of islands with and without non-native Carnivora species depending on the occurrence of native Carnivora.

The number of introduced species on islands decreased significantly with increasing number of native carnivores (r_s = -0.55 $p < 0.0001$) and was positively related to human population density (r_s = 0.35, $p < 0.0001$). This was also indicated by the beta coefficients of a GLMM evaluating effects of native Carnivora species richness, human island population size, island latitude and distance to continent on the occurrence of introduced Carnivora (Table 1). Only the variables richness of native carnivore and human population size on islands proved to significantly affect the occurrence of introduced Carnivora species. The likelihood of occurrence decreased with increasing richness of native carnivores (Figure 6a) and increased with increased human population size (Figure 6b). With distance to mainland the likelihood of occurrence of introduced Carnivora increased significantly (Figure 6c).

Table 1. Results of GLMM evaluating effects of native Carnivora species richness, human island population size, island latitude and distance to continent on the occurrence of introduced Carnivora.

Variable	*F*	*P*	*Beta*
Number of native species (log x+1 transformed)	4.447	0.036	-1.033
Human population size (log x transformed)	12.465	0.001	0.328
Latitude	0.901	0.344	0.022
Distance to continent (log x transformed)	6.637	0.011	0.468

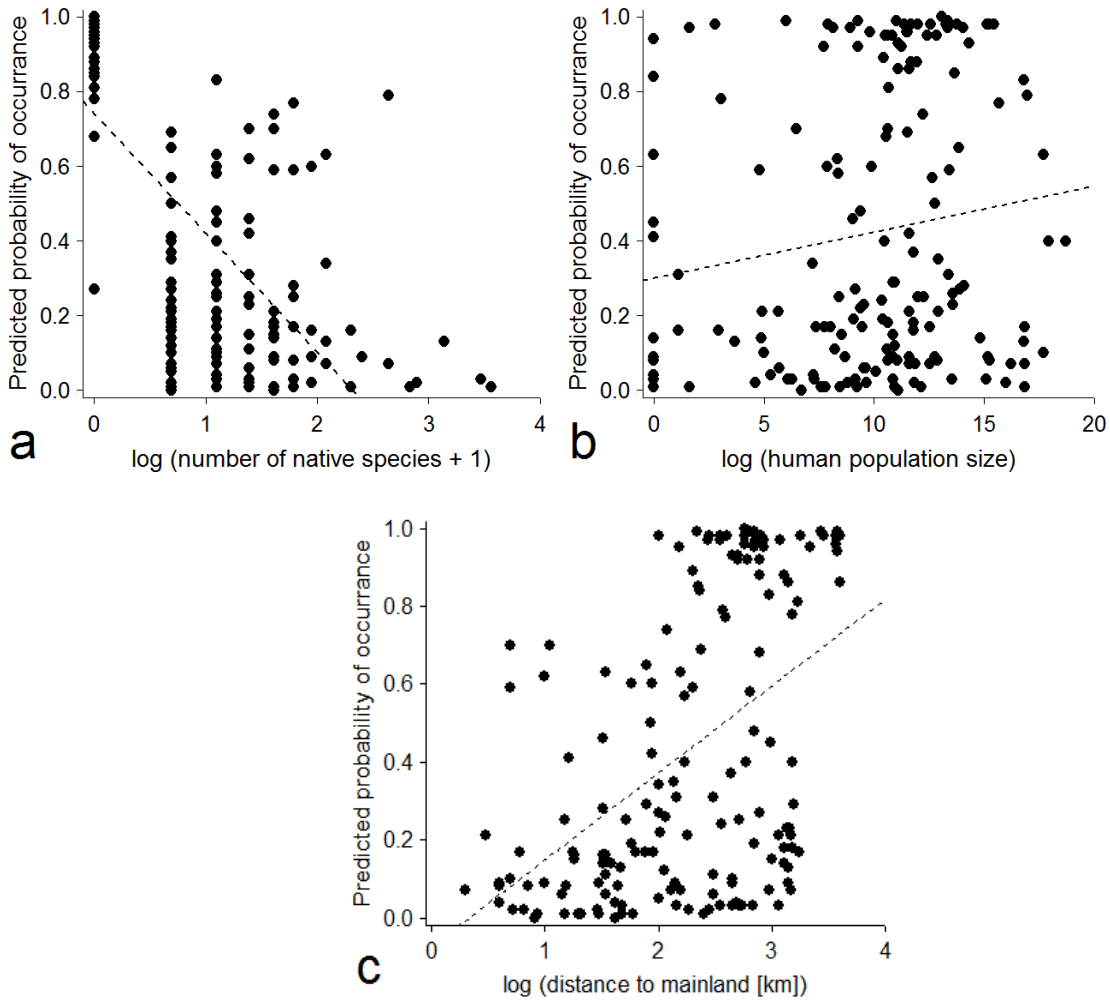

Figure 6. Predicted probability of non-native Carnivora species occurrence on islands in relationship to (a) the richness of native Carnivora, (b) human population size and (c) island isolation from continental mainland.

Discussion

Characteristics of introduced Carnivora

Why do some Carnivora species become invasive and others do not? Our results indicate that species (either originating from other islands or from the mainland) introduced on islands are smaller and have a larger litter size than island Carnivora not recorded becoming introduced on other islands. This result confirms also our hypothesis that introduced carnivore species are more r-selected species. It might also beneficial to be small, to escape prosecution by humans on islands. For Carnivora with a higher litter size it is probably also easier to invade a new ecosystem as only a few individuals can grow a population in a short time (Cardillo 2003). One example is the Least Weasel (*Mustela nivalis*), which has only about 0.138 kg mean female body mass and can has a litter size up 19 (Hunter 2011). The Least Weasel was introduced on the Azores Islands and New Zealand among others.

Factors affecting the successful establishment of introduced Carnivora on islands

A major cause of ecosystem perturbation and biodiversity losses on islands is the successful introduction of alien species (Atkinson 1985, Moors and Atkinson 1984, Lever 1994, Williamson 1996) and more than any other vertebrate group introduced mammals have reportedly caused problems (Ebenhard 1988, Lever 1994). About 20% of all introduced mammals are carnivores (Global Invasive Species Database 2013). One of our aims was to find out, which are the crucial factors, for non-native carnivores to establish on islands.

It appears that one important factor for a successful introduction of Carnivora on islands is the species richness of the native Carnivora fauna, which is related to island size (as shown in other taxonomic groups; e.g. MacArthur 1972, Simberloff 1974, Schoener 1976, Abbott 1980).

New Carnivora appeared to establish themselves more likely on islands without any native carnivores. This provides support for the, still controversial, concept of vacant niches (Lekevicius 2010). It is difficult for non-native carnivores to establish on islands, where most ecological the niches are already “occupied” by native carnivores. Non-native carnivores might

find more vacant niches on carnivore free islands and therefore less competition and more naive prey.

The concept that introduced species can “occupy” empty niches was also mentioned in studies of Mack (1996) or Levine and D´Antonio (1999) as there seems to be a negative relationship between diversity and invasibility of ecosystems.

These niches can also be “occupied” by other than mammal carnivore species (like monitor lizards), but we only considered terrestrial mammal carnivores in this study.

However, the occurrence of introduced carnivores on islands is apparently also affected by other factors. For example, the likelihood of occurrence of non-native carnivores was positively related the human population size on islands. This is not surprising as a great number of non-native mammals were introduced by humans, even on very remote islands, especially if they had a permanent settlement or were in a strategically important location for ships (Courchamp et al 2003). Humans can act as vectors for species potentially able to colonize new areas, including islands. Human activities on islands additionally caused an still cause massive habitat disturbance, which may facilitate the successful introduction of Canivora adapted to human-modified habitats (e.g. *Canis familiaris*). Furthermore, humans provide attractive food sources (garbage, domesticated animals as prey etc.) frequently exploited by introduced Carnivora. For example feral cats (*Felis catus*) that feed on fish waste at garbage sites in Japan (Duffy and Capece 2012) but also other introduced species can be part of the diet. It has been shown that rats and rabbits are regular prey for insular feral cats (Dilks 1979, Fitzgerald et al. 1991, Medina et al. 2006) however, when breeding seabirds are present on an island they can be the preferred prey (Rauzon 1983, Bloomer and Bester 1990, Keitt et al. 2002, Peck et al. 2008).

As such introduced prey is available the whole year round, cats can sustain a larger population and this can lead to a hyperpredation on native species (Keitt et al. 2002, Jones 2002, Oro et al. 2004).

Through husbandry activities that protect small and vulnerable non-native populations until they become larger and more resistant, humans can support the establishment of new species (Mack et al 2000). Especially on sensible ecosystems like islands even little habitat disturbance could have a strong effect.

The factor isolation (distance to continental mainland) appears also to influence the occurrence of introduced Carnivora positively. This could be caused by the fact, that remote islands often have no native mammal Carnivora and therefore provide “unoccupied niches” and naive prey.

Implications for the conservation of island faunas

The biodiversity crisis taking place on islands is mainly caused by biological invasions but the good news are, that it is easier to control or eradicate invasive and introduced species in a isolated and sometimes remote area as compared to the same surface area on a continent (Courchamp et al 2003). The eradication of non-native mammals from invaded ecosystems can clearly show us, by the recovery of native flora and fauna, how strong the impact of the alien species was (Newman 1994, Taylor et al 2000, Town et al 2001). One example is shown by the eradication of *Rattus rattus* on Mokoli´i island. Shortly after the eradication the survival of seabird chicks (*Puffinus pacificus*) increased and also the number of intertidal invertebrates and native plants appeared to increase (Smith et al 2006). But in recent times scientists are increasingly aware that removing a species from an ecosystem can have unexpected and unwanted consequences, like mesopredator release and prey switching (Murphy and Bradfield 1992, Dowding and Murphy 2001). These secondary effects can have a negative impact mainly in ecosystems with more than one introduced species and this is true for the great majority of islands (Zavaleta et al 2001). This complex pattern of direct and indirect effects was described as the Sisyphus effect (Mack and Lonsdale 2002). Accordingly, we suggest, before eradicating a single introduced carnivore from an island, to study how this species interacts with other exotic or native species to avoid negative secondary effects. Although we are aware, that there is mostly very little time for taking action to save native species, it is important to study the relationships of the introduced species with other introduced species and with the native species before trying to eradicate them.

Our results confirm that one of the main reasons for the occurrence of non-native Carnivora on islands was and still is the presence of humans. As the human population is growing and therefore more native species will have to face the negative human impact on island ecosystems, the future seems to be not very bright. On the other hand, as conservationists and scientists are nowadays more connected to each other than ever in history, also the likelihood to find more effective control measures against introduced species will be higher.

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Curriculum vitae

Name: Marko Ascher

Education

1987 – 1991	Elementary school Landeck/Bruggen
1991 – 2000	Bundesrealgymnasium Landeck
2000 - 2001	Graduation Wirtschaftskundliches Bundesrealgymnasium für Berufstätige Innsbruck

Military

2001 – 2002	military service

University

2002 - 2005	Biology studies at University Innsbruck
2005 - 2013	Biology studies at University Vienna (Zoology/Ethology)

Occupational data

2007 - 2010	minor employment in the Zoo Schönbrunn as educational consultant
2010 - 2011	part-time employment as animal keeper in the Zoo Schönbrunn, Department Sealions
Since - 2011	full-time animal keeper in the Zoo Schönbrunn, Department Neptun

Career

2004(July-September)	3-months internship at Wolfpark in Indiana/USA as animal keeper and tourist guide
2005(September)	Ethology course at the Konrad-Lorenz-Researchstation in Grünau
2006(September)	Etholgy course at Bärenpark Worbis/Germany
2007(August)	Seminar about Mammal behaviour with Dr. Udo Gansloßer in the Zoo Nürnberg/Germany
2008(July-August)	animal keeper internship in the Zoo Schönbrunn, Department Neptun and Rainforest house