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SPECIAL PAPER

Possible character displacement of an introduced mongoose and native marten on Adriatic Islands, Croatia

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ABSTRACT

Aim Character displacement and release can occur quickly in novel environments and communities. Species introductions are 'natural experiments' in which evolutionary changes can be studied as community composition varies. We asked whether morphologies of the introduced small Indian mongoose (*Herpestes auropunctatus*) and the larger native stone marten (*Martes foina*) on Adriatic islands where they are sympatric or allopatric are consistent with hypotheses of character displacement and release, respectively.

Location The mongoose is native to Asia and has been introduced to over 60 islands. We measured specimens from several island groups and the native region. The marten is native to Eurasia and several European islands, and we have measurements throughout most of its native range.

Methods We measured skull length and the maximum diameter of the upper canine tooth in both species on Adriatic islands and compared these traits with those in other sites.

Results The mongoose has smaller canines and skulls on the three Adriatic islands it co-occupies with the marten compared with other islands of introduction, consistent with the hypothesis of character displacement. It is not larger on the Adriatic island where it is the sole carnivore than on other Adriatic islands, which contradicts the hypothesis of character release. Marten skulls are shorter on three islands with no mongooses than on one island where the mongoose is present, consistent with the hypothesis of character release. However, marten canine diameters are similar across Adriatic islands.

Main conclusions On Adriatic islands, interspecific competition between the mongoose and the marten is most likely what maintains small size in the mongoose and prevents the character release observed on other islands of introduction lacking mammalian competitors. The marten may have undergone character displacement because of the mongoose introduction on at least one Adriatic island and possibly all three islands where the species co-occur.

Keywords

Adriatic islands, body size, character release, co-existence, competition, *Herpestes auropunctatus*, insular carnivores, mammals, *Martes foina*, sexual dimorphism

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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; Hubbell, 2001; Meiri *et al.*, 2011; Dhondt, 2012). Brown & Wilson (1956) suggested that species with overlapping ranges might evolve under the selective pressure of competition to avoid hybridization ('reproductive character displacement') or resource use overlap ('ecological character displacement'). The opposite phenomenon, termed 'character release' by Grant (1972), is predicted to occur where either species

occurs alone and converges towards traits of the other species. Many studies have sought morphological patterns of ecological character displacement and release (reviewed by Simberloff & Dayan, 1998; Dayan & Simberloff, 2005). Among mammals, carnivores have featured in such analyses because of their large morphological variation; moreover, the advantages of different body sizes in capturing prey of various sizes seem obvious (Dayan *et al.*, 1989; Dayan & Simberloff, 1994; Davies *et al.*, 2007).

Several studies have examined introduced species to determine whether character displacement and release can occur relatively quickly in response to novel environments and communities (Dayan & Simberloff, 2005; Strauss *et al.*, 2006; cf. Robinson & Parsons, 2002). Introductions are 'natural experiments' in which size changes can be examined as community composition varies. Studies of introductions of murids to Pacific and New Zealand islands (Yom-Tov *et al.*, 1999) and of sticklebacks (Schluter, 1994; Pritchard & Schluter, 2001; Gray & Robinson, 2002) are examples.

Not only do introduced species evolve in response to novel environments and competitors, they can also affect the distribution, abundance, reproduction, behaviour and morphology of native species. Strauss *et al.* (2006) provide examples of native species that have evolved in response to introductions. Of 33 examples, 21 manifested morphological or physiological change, including character displacement. For example, decrease in population size of benthic-feeding morphs of native brook char occurred after introduction of benthic-feeding competitors (Bourke *et al.*, 1999). As another example, soon after American mink (*Neovison vison*) were introduced to Belarus, native European mink (*Mustela lutreola*) increased in size while *N. vison* decreased (Sidorovich *et al.*, 1999).

Simberloff *et al.* (2000) examined size variation in mongoose (Herpestidae) species, including introduced island populations of the small Indian mongoose, *Herpestes auropunctatus* (Hodgson, 1836), hereafter called 'mongoose' (Veron *et al.*, 2007; Patou *et al.*, 2009). In its native Asian range, this mongoose is sympatric with one or two larger congeners as well as other larger carnivores (Simberloff *et al.*, 2000). On many previously carnivore-free islands to which it had been introduced, the mongoose increased in size in only 100–200 generations (Simberloff *et al.*, 2000), a morphological change consistent with ecological release from competition.

Here, we examine morphology of the introduced mongoose and the native stone marten, *Martes foina* (Erxleben, 1777) (hereafter called 'marten') on Adriatic islands in Croatia. Adriatic islands are, with one exception, the only islands where the mongoose was introduced that contain a native small carnivore, the marten. Trinidad has native tayra, *Eira barbara* (Linnaeus, 1758), ocelot, *Leopardus pardalis* (Linnaeus, 1758), crab-eating raccoon, *Procyon cancrivorus* (Cuvier, 1798) and Neotropical river otter, *Lontra longicaudis* (Olfers, 1818).

The mongoose is a small (350–1250 g, mean *c.* 600 g; S. Meiri, unpublished data), terrestrial, diurnal carnivore, native to southern Asia from Myanmar west through northern peninsular India to Iraq (Veron *et al.*, 2007). It has sometimes been treated as a synonym of a more easterly, larger congener *Herpestes javanicus* (Geoffroy Saint-Hilaire, 1818), but the two forms are genetically distinct (Veron *et al.*, 2007). Patou *et al.* (2009) found *Herpestes* to be paraphyletic and tentatively suggested restricting the name *Herpestes* to African forms, while placing Asian forms in the genus *Urva*. To avoid taxonomic uncertainties we refer to it simply as the 'mongoose' throughout.

This mongoose was introduced in 1910 to Mljet Island in the Adriatic to control the native horned viper, *Vipera ammodytes* (Tvrtković & Kryštufek, 1990). Thereafter, it was introduced to the island of Korčula and to the mainland Pelješac Peninsula in 1927 and by unknown means to the islands of Hvar in the 1950s, Čiovo in the 1970s and Škrda (date unknown) (Tvrtković & Kryštufek, 1990). It is spreading along the Dalmatian coast and has reached the Neretva River in the north and Albania in the south (Barun *et al.*, 2008; Ćirović *et al.*, 2010). The introduction history, diet and behaviour of the mongoose are well known in parts of its introduced range (Nellis & Everard, 1983; Simberloff *et al.*, 2000; Hays & Conant, 2007). The mongoose's diet in its native range has only recently been studied, in agricultural and not natural settings (Rana *et al.*, 2005). The diet resembled those in the areas of introduction. The mongoose eats mainly small vertebrates, fruits, seeds and insects on islands of introduction: Hawaiian Islands (Baldwin *et al.*, 1952; Hinton & Dunn, 1967), Antilles (Williams, 1918; Nellis & Everard, 1983), Mauritius (Carié, 1916) and Croatia (Cavallini & Serafini, 1995; Barun *et al.*, 2010).

All large Croatian islands have a native carnivore, the marten, which reached Europe from the Middle East after the last glacial retreat (Kurtén, 1968; Anderson, 1970). This marten inhabits central and southern Europe to the Caucasus and western Russia, and the Middle East to Afghanistan, Tibet and Mongolia. In Mediterranean areas it prefers rocky or forest habitats (Virgós & Casanovas, 1998; Virgós *et al.*, 2000). Its diet consists of many wild animal and plant species (Clevenger, 1994; Baghli *et al.*, 2002; Padial *et al.*, 2002; Lanszki, 2003; Carvalho & Gomes, 2004; Zhou *et al.*, 2010). Diet varies seasonally, with small 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 appear in a small percentage of faeces during spring and summer (Delibes, 1978). The Adriatic islands are towards the southern limit of the marten range in Europe.

Ecological similarities of these two species and their sympatry on some, but not all, islands suggest the following questions.

1. On Adriatic islands where the larger marten is present, is the mongoose smaller than on other islands to which it has been introduced, and is its size similar to that in its native range?

2. On the sole mongoose-inhabited Adriatic island lacking the marten, is the mongoose larger than on islands where the marten is present?

3. On Adriatic islands lacking the mongoose, where the marten is the only small carnivore, is it smaller than in other mainland and island areas in Europe with even smaller carnivores (*Mustela* spp.)?

4. On Adriatic islands, in the presence of a smaller introduced carnivore, the mongoose, has the marten increased in size?

MATERIALS AND METHODS

Island habitat characteristics

All studied islands are large and inhabited: Mljet 98 km^2, Korčula 279 km^2, Hvar 297 km^2, Lastovo 46 km^2, Brač 396 km^2, Cres 405 km^2, Čiovo 29 km^2 (Fig. 1). 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 agricultural fields. Shrublands (maquis) are dense thickets of evergreen sclerophyll shrubs and small trees. Forests are dominated mostly by *Pinus halepensis*. All but one of the islands reported above have only these four vegetation types, but proportions of the various types may vary (Trinajstic *et al.*, 1992). The only exception is Cres, which has several continental plant species (Trinajstic *et al.*, 1992). Therefore, marten collection on Cres was limited to the middle of the island, where the vegetation is a mosaic of the four vegetation types mentioned above. 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 (when present) and the marten are frequently observed. In addition, all islands have similar native mammals (see Appendix S1 in Supporting Information) and timing of introduction of most non-native mammals, all of which were present before the mongoose arrived (Kryštufek & Kletečki, 2007).

Skull collection and measurements

Mongooses were collected on Mljet, Korčula and Hvar by hunters from 2004 through 2008 and by A.B. during 2008 spring and summer surveys. Mongooses on Čiovo were collected either by local hunters, by A.B. or by Ivan Budinski between 2005 and 2008. Hunters trapped live martens or collected road-killed individuals on Brač, Cres, Lastovo, Mljet, Korčula and Hvar from 2005 to 2009. All skulls were cleaned by dermestid beetles in Z.T.'s laboratory except for several marten skulls from Cres and Hvar in the Croatian Natural History Museum collected in 1997–1998.

Measurements reported here for the mongoose were previously reported by Simberloff *et al.* (2000) except for those of specimens from the Adriatic islands, Fajou, Maui, Trinidad and Guyana, which were recently measured in museum collections. For comparisons of mongooses from the Adriatic and other areas of introduction, we represented the native population by the broad region of India and Bangladesh surrounding Calcutta, the ultimate source for all introductions for which source is known ('Asia III, V and VI' in Simberloff *et al.*, 2000). Marten specimens from European and Middle Eastern populations were measured in museum collections and were previously reported by Meiri *et al.* (2007).

Island sizes for comparison in the mongoose introduced range range from 1.15 km^2 (Fajou) to 10,432 km^2 (Hawaii). Areas of St Croix (215 km^2), St Kitts (168 km^2) and St John (51 km^2) are similar to the range of areas for our Adriatic islands (29–297 km^2).
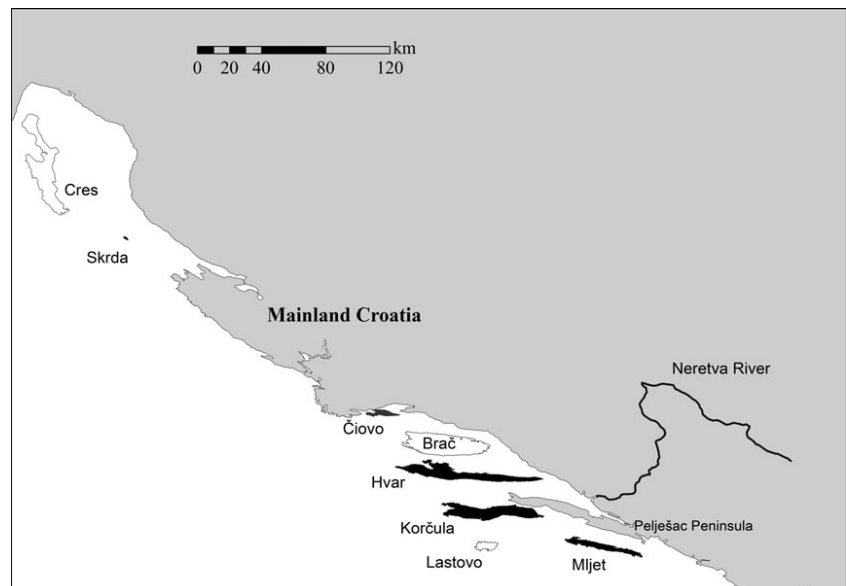

Figure 1 Map of the Adriatic Sea showing islands (in white) with the stone marten (*Martes foina*), one island (Čiovo; in dark grey) with only the small Indian mongoose (*Herpestes auropunctatus*) and islands with both the marten and the mongoose (in black).

We measured the maximum diameter of the upper canine teeth (C^{sup}L) and the condylobasal skull length (CBL) of the mongooses and martens, as in Dayan *et al.* (1989), Dayan & Simberloff (1994), Simberloff *et al.* (2000) and Meiri *et al.* (2007), with digital callipers (precision 0.01 mm). We omitted juveniles and unsexed adults with unfused cranial sutures. We used subadult marten canine measurements but not skull length because mammalian permanent dentition erupts before adulthood. Worn or cracked teeth were not measured. We measured skull length because it is often taken as a measure of size in carnivores (Ralls & Harvey, 1985; Gittleman & Van Valkenburgh, 1997; Meiri *et al.*, 2005a). For mustelids and herpestids, the upper canine tooth is used with great speed and accuracy to kill normal vertebrate prey, and the maximum diameter of this tooth may adapt each species to a particular array of prey sizes (Ewer, 1973; Dayan *et al.*, 1989; Dayan & Simberloff, 1994; Simberloff *et al.*, 2000).

To address whether presence of the marten has influenced size of the mongoose on Adriatic islands and vice versa, we ran generalized linear models (GLMs) with normal error structure and identity link function with either skull length or canine diameter as the response variable and site as the explanatory factor. We used least squares difference of means (5%) tests to compare one group of island/mainland populations with another group. All analyses were carried out in GENSTAT, version 16 (VSN International, Hemel Hempstead, UK).

RESULTS

Mongoose

Maximum upper canine diameters and condylobasal skull lengths are listed in Appendix S2 for all mongoose populations. Skull lengths and canine diameters for each location are depicted in Figs 2 and 3, respectively. The overall coefficient of determination for the correlation between upper canine diameter and skull length (all locations, both sexes) is 0.507 (n = 309). However, within location and sex, the correlation is much lower. For all samples with $n \geq 18$, for males the two samples have r^2 = 0.015 and 0.121, respectively, while for females the two samples have r^2 = 0.002 and 0.217, respectively. Thus, although both measurements are likely to be selected for, to some extent, by diet, they clearly respond to different net selective pressures. Upper canine diameter is probably selected for by the frequency and type of live vertebrate prey, while skull length may reflect a variety of dietary and other selective forces in a notably omnivorous carnivore.

Skull length for both sexes varies geographically (males: $F_{17,409}$ = 26.34, P < 0.001; females: $F_{16,288}$ = 10.20, P < 0.001). Males from the three Adriatic islands with the marten ($\bar{x}$ = 61.01, $\pm$ 1 SE = 0.26) are smaller than males from all other islands of introduction ($\bar{x}$ = 65.30 $\pm$ 0.12), not different from males from Asia ($\bar{x}$ = 61.29 $\pm$ 0.42), not different from males from the one Adriatic island lacking the marten ($\bar{x}$ = 59.16 $\pm$ 1.08), and smaller than males from South America ($\bar{x}$ = 66.07 $\pm$ 0.82). Females from three Adriatic islands with the marten ($\bar{x}$ = 57.89 $\pm$ 0.29) are smaller than females of all other islands of introduction ($\bar{x}$ = 60.96 $\pm$ 0.15), do not differ from those in Asia ($\bar{x}$ = 59.86 $\pm$ 0.46), are larger than females from the one Adriatic island lacking the marten ($\bar{x}$ = 56.05 $\pm$ 0.64) and do not differ from females from South America ($\bar{x}$ = 59.83 $\pm$ 1.28).

GLMs show similar patterns for mongoose canine diameters (Fig. 3a,b). Both sexes vary geographically (males: $F_{17,368}$ = 10.45, P < 0.001; females: $F_{16,268}$ = 4.54, P < 0.001). Males of three Adriatic islands with the marten ($\bar{x}$ = 2.971 $\pm$ 0.02) are smaller than males of all other islands of introduction ($\bar{x}$ = 3.12 $\pm$ 0.01), not different than males from the native Asian region ($\bar{x}$ = 2.84 $\pm$ 0.03), not different from males from the island that lacks the marten ($\bar{x}$ = 3.06 $\pm$ 0.08) and smaller than males from South America ($\bar{x}$ = 3.17 $\pm$ 0.07). Females from the three Adriatic islands with the marten ($\bar{x}$ = 2.66 $\pm$ 0.02) are smaller than females from all other islands of introduction ($\bar{x}$ = 2.77 $\pm$ 0.01), but do not differ from those in the native Asian region ($\bar{x}$ = 2.67 $\pm$ 0.03) or from females from the one Adriatic island lacking the marten ($\bar{x}$ = 2.69 $\pm$ 0.05). They are larger than females from South America ($\bar{x}$ = 2.57 $\pm$ 0.10).

Marten

Maximum upper canine diameters and condylobasal skull lengths are listed in Appendix S3 for all marten populations. Figures 4 and 5 depict skull lengths and maximum upper canine diameters for each location for males and females, respectively. We were unable to collect female martens on Korčula and Mljet. The overall coefficient of determination for the correlation between upper canine diameter and skull length (all locations, both sexes) is 0.488 (n = 412). However, as with the mongoose, within location and sex, the correlation is almost always much lower. For all samples with $n \geq 18$, r^2 values range between 0.058 and 0.290 for males (mean = 0.173, n = 7) and between 0.116 and 0.490 for females (mean = 0.333, n = 4). As with the mongoose these low correlations suggest that, for this omnivorous carnivore, upper canine diameter and skull length reflect differing sets of selective pressures.

A GLM shows the same pattern for male and female skull length of the marten (Fig. 4a,b). Skull lengths vary geographically (males: $F_{14,249}$ = 13.12, P < 0.001; females: $F_{14,187}$ = 11.72, P < 0.001). Skulls of males of three mongoose-free Adriatic islands ($\bar{x}$ = 77.61 $\pm$ 0.30) are shorter than those on mongoose-infested Hvar and Korčula ($\bar{x}$ = 81.23 $\pm$ 0.55). Skull lengths of male martens from Hvar and Korčula do not differ from those of mainland European populations ($\bar{x}$ = 81.25 $\pm$ 0.17). Male marten skulls are shorter on Brač, Cres and Lastovo, where the mongoose is absent ($\bar{x}$ = 77.61 $\pm$ 0.30), than those of populations of
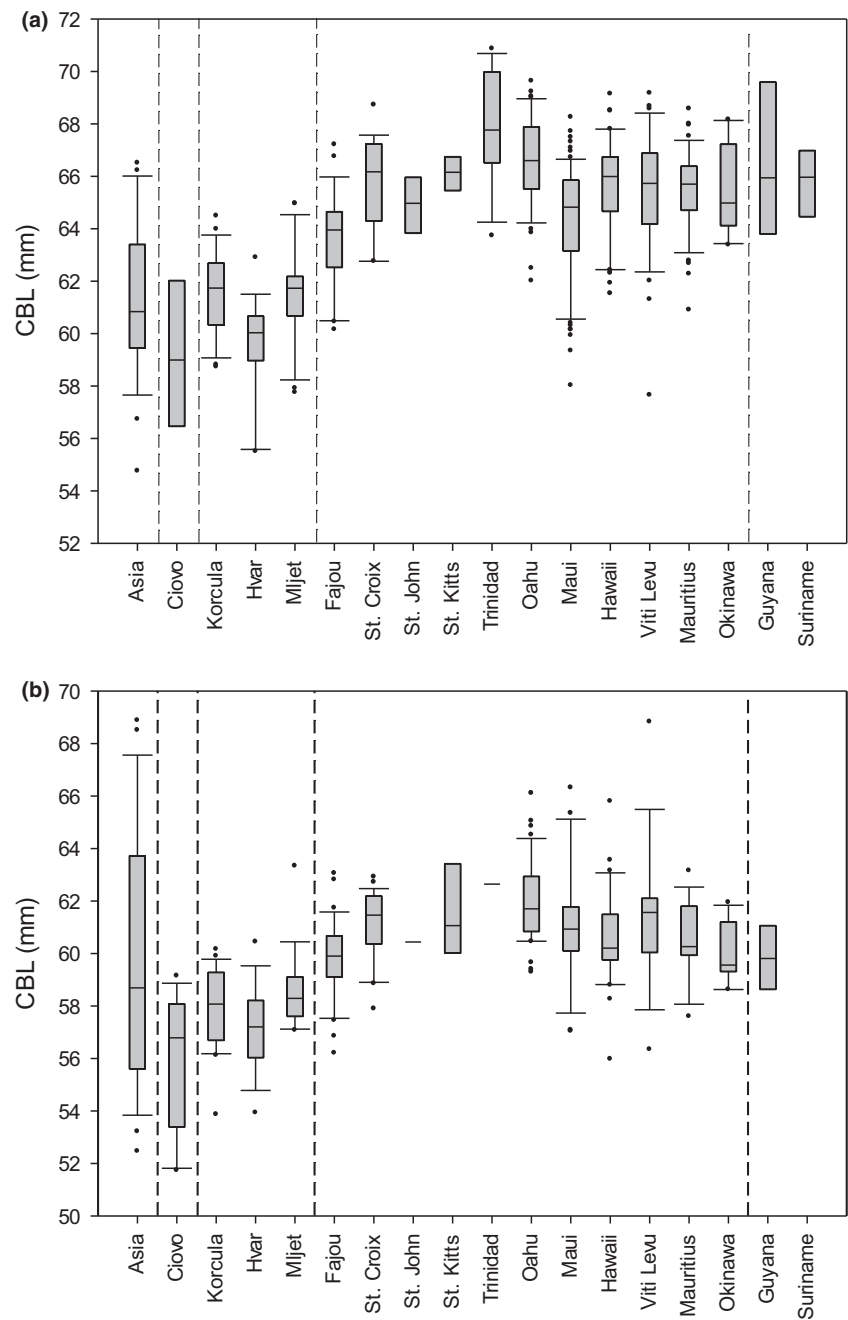
Figure 2 Left to right: condylobasal skull length (CBL, mm) for (a) male and (b) female mongoose (*Herpestes auropunctatus*) from its native range in Asia, four Adriatic islands and 11 other introduced islands and two introduced continental areas in South America. The box and whiskers are interquartile ranges and 95% confidence intervals.

mainland Europe ($\bar{x}$ = 81.25 ± 0.17) and similar to marten skulls on Crete ($\bar{x}$ = 77.00 ± 1.35). Female skulls on three mongoose-free Adriatic islands (Brač, Cres, Lastovo) are shorter ($\bar{x}$ = 73.43 ± 0.36) than on mongoose-infested Hvar ($\bar{x}$ = 76.77 ± 0.68) and shorter than in mainland European populations ($\bar{x}$ = 77.46 ± 0.18) but not different from the population on Crete ($\bar{x}$ = 74.36 ± 1.59).

The pattern for skull length does not hold for maximum upper canine diameter of males (Fig. 5a). There are geographical differences ($F_{15,253}$ = 5.63, P < 0.001), but they do not arise from differences between the mongoose-free Adriatic islands and other comparison groups. Male canines on three mongoose-free Adriatic islands (Brač, Cres, Lastovo) do not differ ($\bar{x}$ = 4.25 ± 0.02) from those on mongoose-

infested Hvar and Korčula ($\bar{x}$ = 4.23 ± 0.05) or from those of populations from mainland Europe ($\bar{x}$ = 4.28 ± 0.02) or Crete ($\bar{x}$ = 4.26 ± 0.12). Female canine diameter (Fig. 5b) varies geographically ($F_{13,184}$ = 6.27, P < 0.001). Female canine diameters on three mongoose-free Adriatic islands (Brač, Cres, Lastovo) are larger ($\bar{x}$ = 3.79 ± 0.03) than on mongoose-infested Hvar ($\bar{x}$ = 3.61 ± 0.06) and do not differ from those of populations of mainland Europe ($\bar{x}$ = 3.88 ± 0.02) or Crete ($\bar{x}$ = 3.92 ± 0.15).

DISCUSSION

The size of the mongoose on three Adriatic islands with martens is striking: they are similar in size there in both
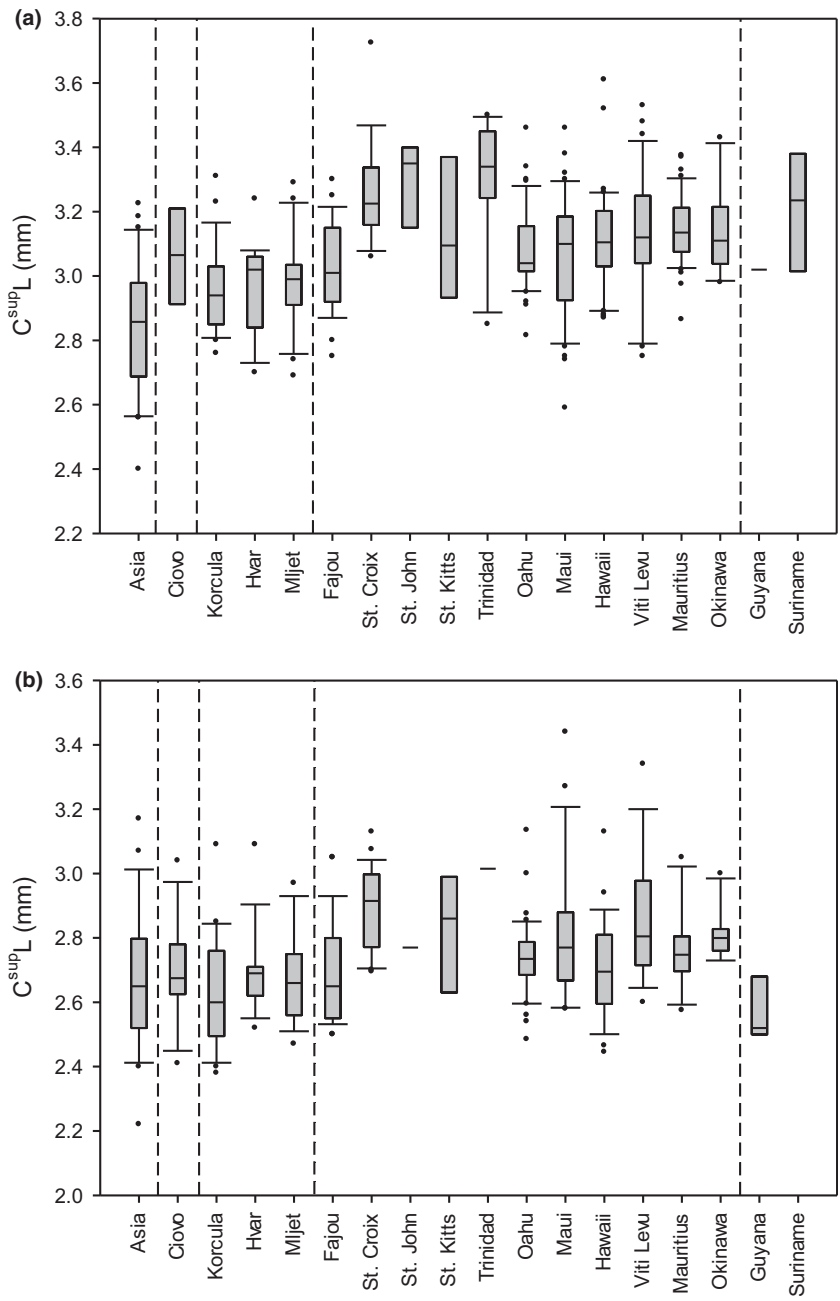
Figure 3 Left to right: maximum diameter of upper canine (C^{sup}L, mm) for (a) male and (b) female mongoose (*Herpestes auropunctatus*) from its native range in Asia, four Adriatic islands and 11 other introduced islands and two introduced continental areas in South America. The box and whiskers are interquartile ranges and 95% confidence intervals.

measured traits to native populations, where congeners and other carnivores co-occur, and smaller than in other introduced populations reported by Simberloff *et al.* (2000) and here except for Fajou. Males are smaller in both skull length and canine diameter than in other introduced populations except that on Fajou, and they are similar in skull length and canine diameter to males from native regions. Females also have shorter skulls than those of other introduced island populations except for that on Fajou, but their skulls are even shorter than those from native regions. There is no pattern in canine diameter for females. One might have expected exactly the opposite result – larger mongooses in the Adriatic than elsewhere – if Bergmann's rule applied. These islands are at far higher latitudes (42.44° N or higher)

and have cooler winters than any other islands of introduction (all these are within the tropics or subtropics) and than the entire native range, all of which is within the tropics or subtropics (Veron *et al.*, 2007). The highest native latitude is 36.25° N in Iraq (Al-Sheikhly & Mallon, 2013). A previous report that mongoose size declines with latitude (Meiri *et al.*, 2004b) is incorrect, because it lumped larger *Herpestes javanicus* with *H. auropunctatus*; they are now known to be separate species (Veron *et al.*, 2007).

On all other islands of introduction, except for Trinidad, no other small carnivorous mammals are present. It seems possible that the mongoose did not undergo character release on Adriatic islands because of competition with the larger marten. In a pilot study in which we radio-tracked individuals of both
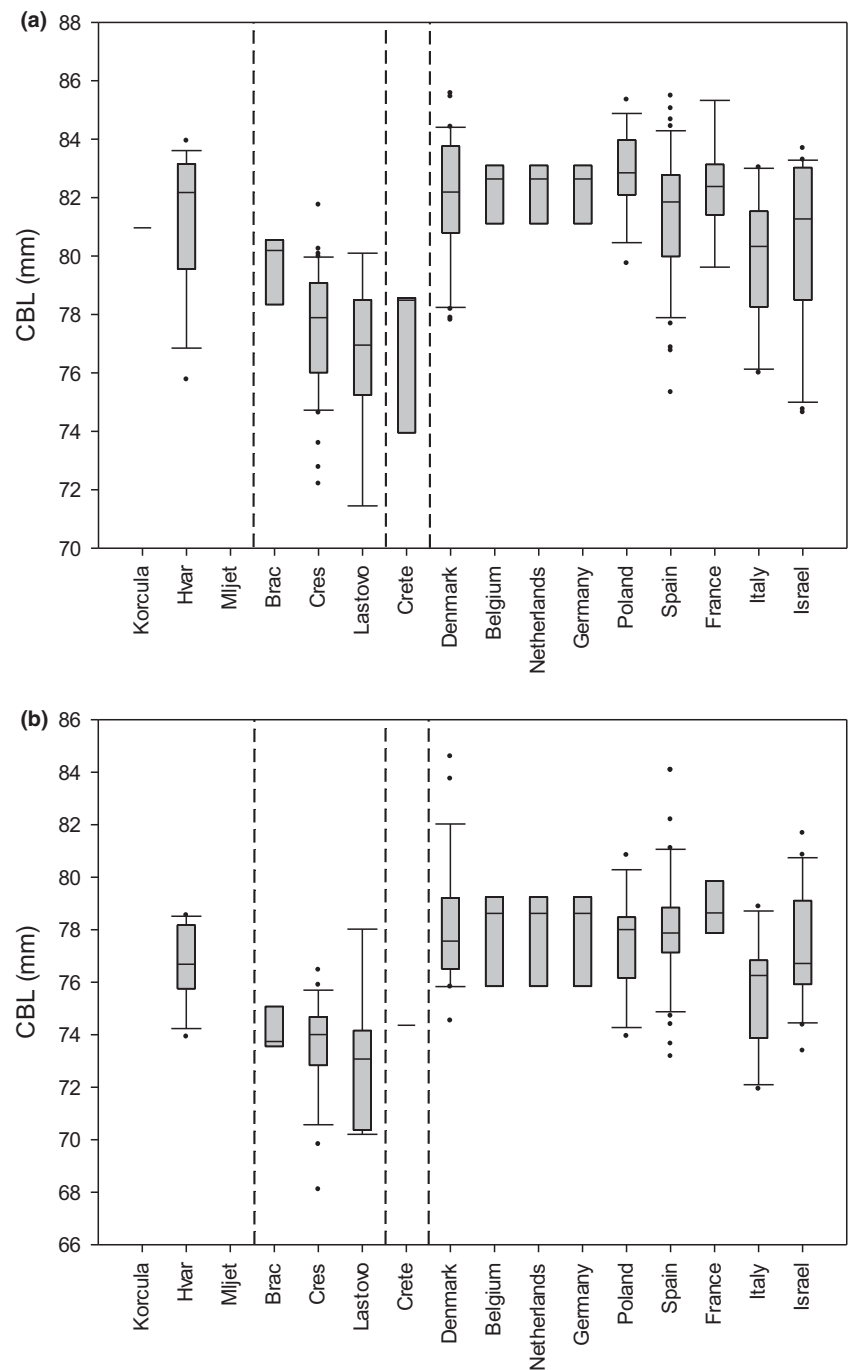
Figure 4 Left to right: condylobasal skull length (CBL, mm) for (a) male and (b) female marten (*Martes foina*) from three islands in the Adriatic where mongoose (*Herpestes auropunctatus*) is present as well, three islands where it is the sole carnivore, Crete, eight European populations and Israel. The box and whiskers are interquartile ranges and 95% confidence interval.

species on Korčula (A.B. & D.S., unpublished data), when the two species encountered each other, the marten was dominant. Thus, our observations are consistent with the hypothesis of Simberloff *et al.* (2000) that the mongoose has undergone character release in regions of introduction.

The mongoose was introduced to one Adriatic island lacking the marten, Čiovo. Skulls of both males and females on Čiovo are the shortest of all Adriatic islands and the native Asian region (but not significantly so). However, canines of Čiovo mongooses are larger than those of almost all Adriatic populations and the native Asian one. We cannot explain this discrepancy, because all prey species present on Čiovo are present on all other islands. On Čiovo, the regional hunting organization distributes 'rat' poison for mongoose control during its annual autumn meeting (although this procedure is illegal in Croatia), and a result of this aggressive multi-year campaign is a minuscule mongoose population. To our knowledge, no similar effort is undertaken on other islands. The mongoose on Čiovo might be subject to different selective pressures than on other islands of introduction, including Adriatic islands. Additionally, genetic drift could have caused Čiovo mongooses to be remarkably small. The initial propagule arriving on Mljet consisted of only seven males and four females (Tvrtković & Kryštufek, 1990). Subsequent introduc-
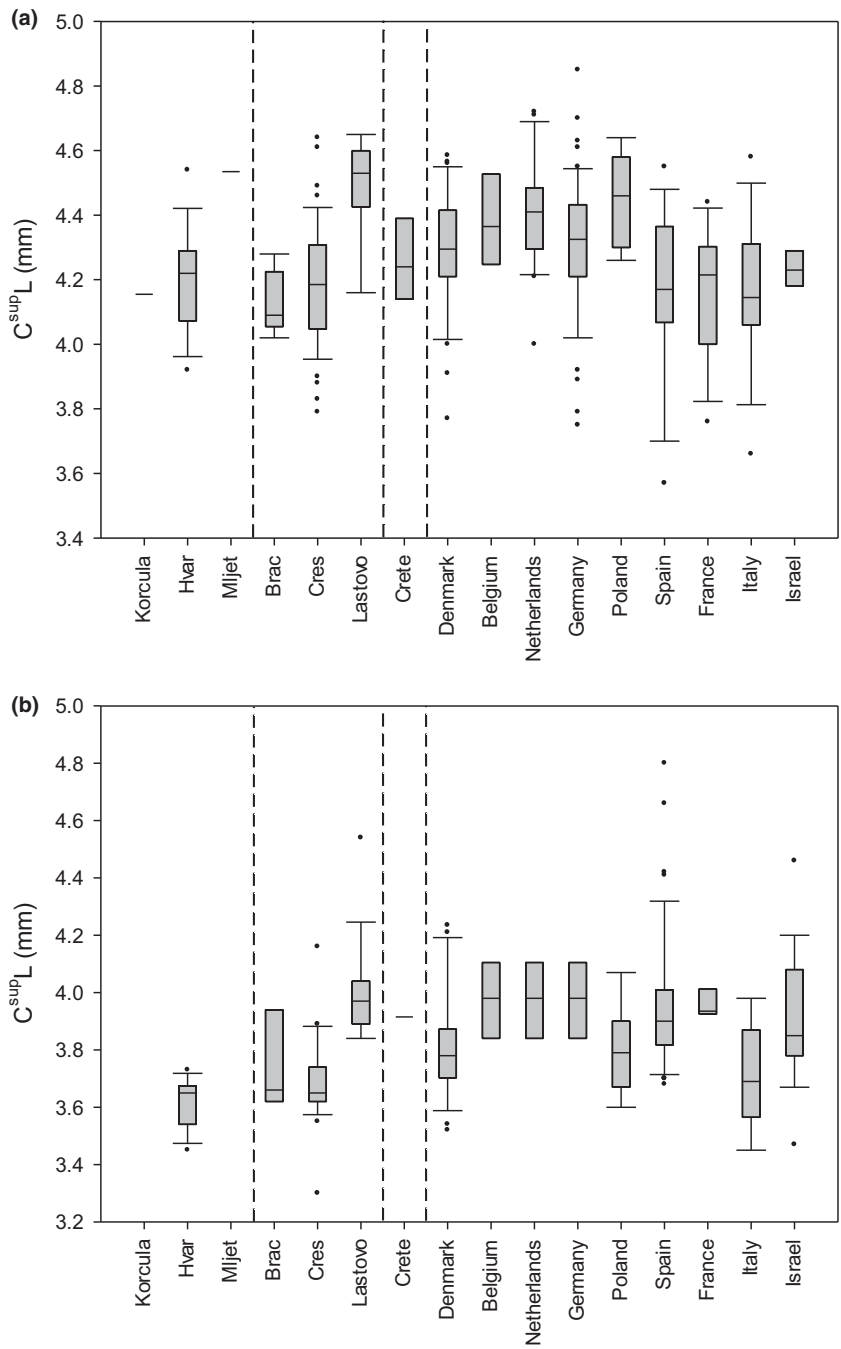
Figure 5 Left to right: maximum diameter of upper canine ($C^{sup}L$, mm) for (a) male and (b) female marten (*Martes foina*) from three islands in the Adriatic where mongoose (*Herpestes auropunctatus*) is present as well, three islands where it is the sole carnivore, Crete, eight mainland European populations and Israel. The box and whiskers are interquartile ranges and 95% confidence interval.

tions to other islands (and the mainland) are believed to have consisted of very small numbers of individuals deliberately introduced (Korčula) or carried inadvertently by motor vehicles on ferries. There is no reason to think that mongooses have been moved between islands or between islands and the mainland even sporadically since the initial introductions. Thus, a bottleneck effect could have limited genetic diversity and enhanced the role of drift on all of these islands, but particularly on Čiovo, by far the smallest. We have no genetic data with which to test this hypothesis.

Our comparisons include measurements of four additional mongoose populations not treated in previous literature:

Fajou, Maui, Trinidad and Guyana. For two of them, Maui and Guyana, results are consistent with previous ones (Simberloff *et al.*, 2000) and accord with our hypotheses of character displacement in the presence of larger carnivores of similar ecology and character release in their absence. On Maui, mongooses of both sexes resemble those on other Hawaiian islands and are larger than those in its native area in Asia, in both traits. In Guyana, on the South American mainland, the female mongoose is smaller than on islands of introduction and similar in size to the mongoose in its native range; it is noteworthy that, like three of our Adriatic islands, Guyana has native carnivores larger than the mon-

goose, including mustelids: the greater grison, *Galictis vittata* (Schreber, 1776) and tayra, *Eira barbara*. However, our small sample size (three males, three females) prevents further analysis and speculation.

Mongoose populations of Fajou and Trinidad are exceptions to character displacement and release patterns we hypothesized and observed in other introduced populations. Both sexes on Fajou resemble those on Adriatic islands and in the native region. No other carnivore occurs on Fajou. However, Fajou is far smaller (1.15 km^2) than any other island on which the mongoose has been measured. Some authors (Foster, 1964; Van Valen, 1973; Lomolino, 1985) have suggested that mammals tend to evolve smaller size on islands so as to reduce resource requirements and increase reproductive output; others (Grant, 1965; Schoener, 1969; Meiri *et al.*, 2004b) have contested this claim. Different populations probably evolve different sizes in response to local environmental conditions (Raia & Meiri, 2006; Meiri *et al.*, 2011). Fajou is just one datum, but globally at least 64 islands, many very small, harbour introduced mongooses (Barun *et al.*, 2011), and it would be interesting to study mongoose sizes on the smallest of these. On Trinidad, male canines and skulls (we are unable to locate females in collections) are larger than those in the native range and on the Adriatic islands, as on other islands of introduction, although Trinidad has native carnivores (listed above). These are all much larger than the mongoose, and at least the raccoon and river otter do not share habitats with it. Only the tayra has a similar diet. Perhaps these species differ too much from the mongoose to compete with it; there is insufficient research, especially on Trinidad, to explore this conjecture.

Although we interpret the mongoose data from the Adriatic islands as reflecting character displacement, other factors that differ between islands and mainland as well as between different islands can come into play. Climate, area, isolation and habitat diversity are all believed to influence directly or indirectly the evolution of body size for a mainland species colonizing an island (Lomolino *et al.*, 2012; van der Geer *et al.*, 2013; cf. Meiri *et al.*, 2005b). Because the mongoose was introduced by humans to all islands we examined, isolation can be ruled out as a factor directly influencing body size. Resource limitation sometimes implicated in island dwarfism of large mammals (e.g. Sondaar, 1977; Wasserzug *et al.*, 1979) would be unlikely to play a role in a mammal as small as this mongoose on islands the size of those in the Adriatic or on all other islands of introduction except perhaps the very smallest – a few hectares (Barun *et al.*, 2011) – in the Caribbean. The mongoose is a particularly omnivorous carnivore, eating both plants and carrion in great quantities in some locations (Simberloff *et al.*, 2000). In general, Meiri *et al.* (2005b, 2006, 2008) and Lomolino *et al.* (2012) found that area *per se* was not strongly implicated as a means by which resource limitation on islands may influence body size evolution.

Raia & Meiri (2006) and Palombo (2009) point to the size distribution of available prey as probably having been the key factor selecting for carnivore body size in both recent and Pleistocene Mediterranean island communities. We have no data on the spectrum of available prey size and use for Adriatic islands or any others inhabited by this mongoose.

It is tempting to try to interpret mongoose body size on Adriatic islands in terms of the classical 'island rule' (Foster, 1964; Lomolino *et al.*, 2013) whereby, at least in some mammalian groups, small species tend to become larger on islands and large species tend to become smaller. However, mean body weight of the mongoose is roughly 500–600 g (Hays & Simberloff, 2006; S. Meiri, unpublished data), the approximate break point for these expectations (Lomolino, 1985), so it is unclear what the island rule would predict. In addition, examinations of large numbers of species show tremendous scatter, to the extent that the generality of the rule is controversial (Meiri *et al.*, 2004a, 2006, 2008; Lomolino, 2005; Lomolino *et al.*, 2012, 2013).

The presence of a larger potential competitor on most Adriatic islands and their temperate location are the most striking ecological features separating these islands from other islands with introduced mongooses. The resultant pattern is consistent with a competitive influence by the marten (and inconsistent with a major climatic role), with the observed pattern of mongoose sizes on other islands of introduction and in the native range, and with other observations of island carnivores. For British mustelids, Dayan & Simberloff (1994) similarly implicated the absence of certain species on Ireland in apparent character release of species that were present, while van der Geer *et al.* (2013) for palaeo-insular mammals of very large Mediterranean islands argued that presence of competitors and/or predators greatly affected sizes that would otherwise have been determined by climate, habitat and food spectrum.

Both male and female martens from three mongoose-free islands (Brač, Cres and Lastovo) have shorter skulls than those of several mainland European populations and neighbouring, mongoose-infested Hvar. There is no clear pattern for male canine diameter, but canines of female martens on these three islands are larger than on Hvar, the one mongoose-infested Adriatic island for which we have adequate data.

The marten tends to increase in size from west to east (Reig, 1992) and from south to north (starting in Israel). These clines can confound a search for character displacement (Goldberg & Lande, 2006; Adams & Collyer, 2007; Meiri *et al.*, 2011). In the absence of dietary information for Adriatic populations, we cannot infer a mechanism by which small marten size may have arisen. Because the marten is the only carnivore (except for feral cats, *Felis catus*, on all islands and golden jackals, *Canis aureus*, on Korčula) on the islands we studied, release from competition from other mainland carnivore species is a possible explanation. For example, Dayan & Simberloff (1994) found that both sexes of the stoat (*Mustela erminea*) in Ireland, which lacks the least weasel (*Mustela nivalis*), are smaller than in Great Britain, where the smaller least weasel is present.

On Hvar, one of three Adriatic islands where the martens and mongooses co-occur, both male and female martens

have longer skulls than on the three mongoose-free islands; they are similar to martens of mainland Europe. Introduction of the mongoose may have displaced the marten on Hvar and possibly on Korčula and Mljet, for which we were unable to collect adequate samples. Preliminary data based on small samples show that martens on both islands resemble those on Hvar rather than those on the three mongoose-free islands (Figs 4 & 5). The marten is found on many other islands of various sizes in the eastern Mediterranean (Masseti, 1995); several of these contain the much smaller least weasel (*Mustela nivalis*) (Masseti, 1995). None of these, except for Crete in the current study, have been examined for character displacement or release.

The average weight of the marten is *c.* 1.9 kg for males and 1.3 kg for females (D.S. & S.M., unpublished data), larger than that of the mongoose but still near the breakpoint for island mammals to increase or decrease in size according to Lomolino (1985). Thus, no prediction derives from the island rule. If Bergmann's rule holds, climatic patterns would predict the marten to be smaller on Adriatic islands then in the rest of mainland Europe (but larger than on Crete and in Israel), and it is smaller on the islands lacking the mongoose, but about the same size as other European populations on Hvar, where it co-exists with the mongoose. The reasons it is smaller on mongoose-free islands than in the rest of Europe could reside in any combination of the factors discussed above with respect to the mongoose. Like the mongoose, this marten is omnivorous, making resource limitation an unlikely explanation. We have very few data on this species from other islands. In Denmark (D.S. & S.M., unpublished data) it occupies the mainland Jutland Peninsula and the islands Sjaelland and Fyn. The mainland and Sjaelland also have the slightly larger pine marten, *Martes martes* (Linnaeus, 1758), which Fyn lacks. The sizes do not differ significantly among all three sites for either males or females (Meiri *et al.*, 2007).

CONCLUSIONS

On Adriatic islands, interspecific competition between the mongoose and the marten is most likely what maintains small size in the mongoose and prevents the character release observed on other islands of introduction that lack mammalian competitors. Compared with martens on mainland Europe, martens on mongoose-free Adriatic islands have shorter skulls, a result consistent with Bergmann's rule given that the islands have a warmer climate than mainland Europe. Martens do not have shorter skulls on the islands with mongooses, consistent with the possibility that the smaller competitor displaces martens towards having larger skulls compared with martens on islands without competitive pressure from mongooses.

Any species with a large geographical range will encounter different sets of potentially interacting species (including predators, prey and competitors) and different physical conditions in different parts of that range. For a widely introduced species, such as the mongoose, these shifting contexts will probably be even more varied. Furthermore, the different components of the physical and biotic environments will vary to some extent independently. The resultant patterns of multiple selective pressures must be extraordinarily complex. Nevertheless, for certain species – and the mongoose is one – a persistent pattern may be manifested in such geographically distant and biologically and physically varied circumstances that it can be recognized as signalling one important type of selective pressure. For the mongoose, character displacement and release are so frequently seen that they strongly implicate competitive pressure from co-existing larger small carnivores. It seems likely that close morphological study of other widely introduced species might similarly reveal dominant selective forces.

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REFERENCES

Adams, D.C. & Collyer, M.L. (2007) Analysis of character divergence along environmental gradients and other covariates. *Evolution*, **61**, 510–515.

Al-Sheikhly, O.F. & Mallon, D. (2013) The small Asian mongoose *Herpestes javanicus* and the Indian grey mongoose *Herpestes edwardsii* in Iraq (Mammalia: Carnivora: Herpestidae). *Zoology in the Middle East*, **59**, 173–175.

Anderson, E. (1970) Quaternary evolution of the genus *Martes* (Carnivora, Mustelidae). *Acta Zoologica Fennica*, **130**, 1–132.

Baghli, A., Engel, E. & Verhagen, R. (2002) Feeding habits and trophic niche overlap of two sympatric Mustelidae, the polecat *Mustela putorius* and the beech marten *Martes foina*. *Zeitschrift für Jagdwissenschaft*, **48**, 217–225.

Baldwin, P.H., Schwartz, C.W. & Schwartz, E.R. (1952) Life history and economic status of the mongoose in Hawaii. *Journal of Mammalogy*, **33**, 335–356.

Barun, A., Budinski, I. & Simberloff, D. (2008) A ticking time-bomb? The small Indian mongoose in Europe. *Aliens*, **26**, 14–16.

Barun, A., Simberloff, D. & Budinski, I. (2010) Impact of the small Indian mongoose (*Herpestes auropunctatus*) on native amphibians and reptiles of the Adriatic islands, Croatia. *Animal Conservation*, **13**, 549–555.

Barun, A., Hanson, C.C., Campbell, K.J. & Simberloff, D. (2011) A review of small Indian mongoose management and eradications on islands. *Island invasives: eradication and management* (ed. by C.R. Veitch, M. N Clout and D.R. Towns), pp. 17–25. International Union for Conservation of Nature (IUCN), Gland, Switzerland.

Bourke, P., Magnan, P. & Rodríguez, M.A. (1999) Phenotypic responses of lacustrine brook charr in relation to the intensity of interspecific competition. *Evolutionary Ecology*, **13**, 19–31.

Brown, W.L. & Wilson, E.O. (1956) Character displacement. *Systematic Zoology*, **5**, 49–64.

Carié, P. (1916) *L'acclimatation à l'Île Maurice*. Société Nationale d'Acclimatation de France, Paris, France.

Carvalho, J.C. & Gomes, P. (2004) Feeding resource partitioning among four sympatric carnivores in the Peneda-Geres National Park (Portugal). *Journal of Zoology*, **263**, 275–283.

Cavallini, P. & Serafini, P. (1995) Winter diet of the small Indian mongoose, *Herpestes auropunctatus,* on an Adriatic island. *Journal of Mammalogy*, **76**, 569–574.

Ćirović, D., Raković, M., Milenković, M. & Paunović, M. (2010) Small Indian mongoose *Herpestes auropunctatus* (Herpestidae, Carnivora): an invasive species in Montenegro. *Biological Invasions*, **13**, 393–399.

Clevenger, A.P. (1994) Feeding ecology of Eurasian pine martens and stone martens in Europe. *Martens, sables, and fishers: biology and conservation* (ed. by S.W. Buskirk, A.S. Harestad, M.G. Raphael and R.A. Powell), pp. 326–340. Comstock Publishing Associates, Ithaca, NY.

Davies, J.T., Meiri, S., Barraclough, T.G. & Gittleman, J.L. (2007) Species co-existence and character divergence across carnivores. *Ecology Letters*, **10**, 146–152.

Dayan, T. & Simberloff, D. (1994) Character displacement, sexual dimorphism, and morphological variation among British and Irish mustelids. *Ecology*, **75**, 1063–1073.

Dayan, T. & Simberloff, D. (2005) Ecological and community-wide character displacement: the next generation. *Ecology Letters*, **8**, 875–894.

Dayan, T., Simberloff, D., Tchernov, E. & Yom-Tov, Y. (1989) Inter- and intraspecific character displacement in mustelids. *Ecology*, **70**, 1526–1539.

Delibes, M. (1978) Feeding habits of the stone marten, *Martes foina* (Erxleben, 1777), in northern Burgos, Spain. *Zeitschrift für Säugetierkunde*, **43**, 282–288.

Dhondt, A.A. (2012) *Interspecific competition in birds*. Oxford University Press, New York.

Ewer, R.G. (1973) *The carnivores*. Cornell University Press, Ithaca, NY.

Foster, J.B. (1964) Evolution of mammals on islands. *Nature*, **202**, 234–235.

van der Geer, A.A., Lyras, G.A., Lomolino, M.V., Palombo, M.R. & Sax, D.F. (2013) Body size evolution of palaeo-insular mammals: temporal variations and interspecific interactions. *Journal of Biogeography*, **40**, 1440–1450.

Gittleman, J.L. & Van Valkenburgh, B. (1997) Sexual dimorphism in the canines and skulls of carnivores: effects of size, phylogeny, and behavioural ecology. *Journal of Zoology*, **242**, 97–117.

Goldberg, E.E. & Lande, R. (2006) Ecological and reproductive character displacement on an environmental gradient. *Evolution*, **60**, 1344–1357.

Grant, P.R. (1965) The adaptive significance of some size trends in island birds. *Evolution*, **19**, 355–367.

Grant, P.R. (1972) Convergent and divergent character displacement. *Biological Journal of the Linnaean Society*, **4**, 39–68.

Gray, S.M. & Robinson, B.W. (2002) Experimental evidence that competition between stickleback species favours adaptive character displacement. *Ecology Letters*, **5**, 264–272.

Hays, W.S.T. & Conant, S. (2007) Biology and impacts of Pacific island invasive species. A worldwide review of effects of the small Indian mongoose, *Herpestes javanicus* (Carnivora: Herpestidae). *Pacific Science*, **61**, 3–16.

Hays, W.S.T. & Simberloff, D. (2006) A morphometric trend linked to male sociality in the small Indian mongoose. *Acta Theriologica*, **51**, 303–310.

Hinton, H.E. & Dunn, A.M.S. (1967) *Mongooses: their natural history and behavior*. University of California Press, Berkeley, CA.

Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.

Kryštufek, B. & Kletečki, I. (2007) Biogeography of small terrestrial vertebrates on the Adriatic landbridge islands. *Folia Zoologica*, **56**, 225–234.

Kurtén, B. (1968) *Pleistocene mammals of Europe*. Weidenfeld and Nicolson, London.

Lanszki, J. (2003) Feeding habits of stone martens in a Hungarian village and its surroundings. *Folia Zoologica*, **52**, 367–377.

Lewin, R. (1983) Santa Rosalia was a goat. *Science*, **221**, 636–639.

Lomolino, M.V. (1985) Body size of mammals on islands: the island rule re-examined. *The American Naturalist*, **125**, 310–316.

Lomolino, M.V. (2005) Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography*, **32**, 1683–1699.

Lomolino, M.V., Sax, D.F., Palombo, M.R. & van der Geer, A.A. (2012) Of mice and mammoths: evaluations of causal explanations for body size evolution in insular mammals. *Journal of Biogeography*, **39**, 842–854.

Lomolino, M.F., van der Geer, A.A., Lyras, G.A., Palombo, M.R., Sax, D.F. & Rozzi, R. (2013) Of mice and mammoths: generality and antiquity of the island rule. *Journal of Biogeography*, **40**, 1427–1439.

Losos, J.B. (2000) Ecological character displacement and the study of adaptation. *Proceedings of the National Academy of Sciences USA*, **97**, 5693–5695.

Masseti, M. (1995) Quaternary biogeography of the Mustelidae family on the Mediterranean islands. *Hystrix (n.s.)*, **7**, 17–34.

Meiri, S., Dayan, T. & Simberloff, D. (2004a) Body size of insular canivores: little support for the island rule. *The American Naturalist*, **163**, 469–479.

Meiri, S., Dayan, T. & Simberloff, D. (2004b) Carnivores, biases and Bergmann's rule. *Biological Journal of the Linnaean Society*, **81**, 579–588.

Meiri, S., Dayan, T. & Simberloff, D. (2005a) Variability and correlations in carnivore crania and dentition. *Functional Ecology*, **19**, 337–343.

Meiri, S., Dayan, T. & Simberloff, D. (2005b) Area, isolation and body size evolution in insular carnivores. *Ecology Letters*, **8**, 1211–1217.

Meiri, S., Dayan, T. & Simberloff, D. (2006) The generality of the island rule reexamined. *Journal of Biogeography*, **33**, 1571–1577.

Meiri, S., Dayan, T. & Simberloff, D. (2007) Guild composition and mustelid morphology – character displacement but no character release. *Journal of Biogeography*, **34**, 2148–2158.

Meiri, S., Cooper, N. & Purvis, P. (2008) The island rule: made to be broken? *Proceedings of the Royal Society B: Biological Sciences*, **275**, 141–148.

Meiri, S., Simberloff, D. & Dayan, T. (2011) Community-wide character displacement in the presence of clines: a test of Holarctic weasel guilds. *Journal of Animal Ecology*, **80**, 824–834.

Nellis, D.W. & Everard, C.O.R. (1983) The biology of the mongoose in the Caribbean. *Studies on the Fauna of Curaçao and other Caribbean Islands*, **1**, 1–162.

Padial, J.M., Ávila, E. & Gil-Sánchez, J.M. (2002) Feeding habits and overlap among red fox (*Vulpes vulpes*) and stone marten (*Martes foina*) in two Mediterranean mountain habitats. *Mammalian Biology*, **67**, 137–146.

Palombo, M.R. (2009) Body size structure of the Pleistocene mammalian communities from Mediterranean islands. *Integrative Zoology*, **4**, 341–356.

Patou, M.L., McLenachan, P.A., Morley, C.G., Couloux, A., Jennings, A.P. & Veron, G. (2009) Molecular phylogeny of the Herpestidae (Mammalia, Carnivora) with a special emphasis on the Asian *Herpestes*. *Molecular Phylogenetics and Evolution*, **53**, 69–80.

Pritchard, J. & Schluter, D. (2001) Declining competition during character displacement: summoning the ghost of competition past. *Evolutionary Ecology Research*, **3**, 209–220.

Raia, P. & Meiri, S. (2006) The island rule in large mammals: paleontology meets ecology. *Evolution*, **60**, 1731–1742.

Ralls, K. & Harvey, P.H. (1985) Geographic variation in size and sexual dimorphism of North American weasels. *Biological Journal of the Linnean Society*, **25**, 119–167.

Rana, S.A., Smith, S.M. & Siddiqui, M.J.I. (2005) Scat analysis of small Indian mongoose (*Herpestes auropunctatus*) feeding on fauna of some high and relatively low input crop fields. *International Journal of Agriculture and Biology*, **7**, 777–780.

Reig, S. (1992) Geographical variation in pine marten (*Martes martes*) and beech marten (*M. foina*) in Europe. *Journal of Mammalogy*, **73**, 744–769.

Robinson, B.W. & Parsons, K.J. (2002) Changing times, spaces and faces: tests and implications of adaptive morphological plasticity in the fishes of northern postglacial lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1819–1833.

Schluter, D. (1994) Experimental evidence that competition promotes divergence in adaptive radiation. *Science*, **266**, 798–801.

Schluter, D. (2000) Ecological character displacement in adaptive radiation. *The American Naturalist*, **156**, 4–16.

Schoener, T.W. (1969) Size patterns in West Indian *Anolis* lizards: I. Size and species diversity. *Systematic Zoology*, **18**, 386–401.

Sidorovich, V., Kruuk, H. & Macdonald, D.W. (1999) Body size, and interactions between European and American mink (*Mustela lutreola* and *M. vison*) in Eastern Europe. *Journal of Zoology*, **248**, 521–527.

Simberloff, D. & Dayan, T. (1998) Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Review*, **28**, 99–124.

Simberloff, D., Dayan, T., Jones, C. & Ogura, G. (2000) Character displacement and release in the small Indian mongoose, *Herpestes javanicus*. *Ecology*, **81**, 2086–2099.

Sondaar, P.Y. (1977) Insularity and its effects on mammal evolution. *Major patterns in vertebrate evolution* (ed. by M.K. Hecht, P.C. Goody and B.M. Hecht), pp. 671–707. Plenum Press, New York.

Strauss, S.Y., Lau, J.A. & Carroll, S.P. (2006) Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters*, **9**, 357–374.

Trinajstic, I., Rauš, Đ., Vukelic, J. & Medvedovic, J. (1992) Vegetation map of forest communities of Croatia. *Forests of Croatia* (ed. by D. Rauš), p. 319. Graficki zavod Hrvatske, Zagreb.

Tvrtković, N. & Kryštufek, B. (1990) Small Indian mongoose *Herpestes auropunctatus* (Hodgson, 1836) on the Adriatic Islands of Yugoslavia. *Bonner Zoologische Beitrage*, **41**, 3–8.

Van Valen, L.M. (1973) Pattern and the balance of nature. *Evolutionary Theory*, **1**, 31–49.

Veron, G.M.L., Patou, M.L., Pothet, G., Simberloff, D. & Jennings, A.P. (2007) Systematic status and biogeography of the Javan and small Indian mongooses (Herpestidae, Carnivora). *Zoologica Scripta*, **36**, 1–10.

Virgós, E. & Casanovas, J.G. (1998) Distribution patterns of the stone marten (*Martes foina*) in Mediterranean mountains of central Spain. *Zeitschrift für Säugetierkunde*, **63**, 193–199.

Virgós, E., Recio, M.R. & Cortés, Y. (2000) Stone marten (*Martes foina*) use of different landscape types in the

mountains of central Spain. *Zeitschrift für Saügetierkunde*, **65**, 375–379.

Wasserzug, R.J., Yang, H., Sepkoski, J.J., Jr & Raup, D.M. (1979) The evolution of body size on islands: a computer simulation. *The American Naturalist*, **114**, 287–295.

Williams, C.B. (1918) The food of the mongoose in Trinidad. *Bulletin of the Department of Agriculture of Trinidad and Tobago*, **17**, 167–186.

Yom-Tov, Y., Yom-Tov, S. & Moller, H. (1999) Competition, coexistence, and adaptation amongst rodent invaders to Pacific and New Zealand islands. *Journal of Biogeography*, **26**, 947–958.

Zhou, Y.B., Newman, C., Xu, W.T., Buesching, C.D., Zalewski, A., Kaneko, Y., Macdonald, D.W. & Xie, Z.Q. (2010) Biogeographical variation in the diet of Holarctic martens (genus *Martes*, Mammalia: Carnivora: Mustelidae): adaptive foraging in generalists. *Journal of Biogeography*, **38**, 137–147.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of species of terrestrial mammals on Adriatic islands.
Appendix S2 Mongoose (*Herpestes auropunctatus*) $C^{sup}L$ and CBL summary data.
Appendix S3 Stone marten (*Martes foina*) $C^{sup}L$ and CBL summary data.

BIOSKETCHES

Arijana Barun is an ecologist who has conducted research for over 10 years on many aspects of impacts, management and evolution of introduced vertebrate predators. She has worked on islands in the United States, Caribbean, Croatia and New Zealand and has published in *Molecular Ecology, Biological Invasions, Animal Conservation, Neobiota, Copeia, Aliens*, and *The Encyclopedia of Biological Invasions*. She is currently a postdoctoral fellow at Lincoln University developing new toxins, lures and delivery methods for animal pest control in New Zealand.

Daniel Simberloff has published several hundred papers on ecology, evolution, biogeography, conservation biology, and especially in the last two decades, on invasion biology. From 1974 to 1991, he was the Founding Associate Editor of the *Journal of Biogeography*. He is the Nancy Gore Hunger Professor of Environmental Studies at the University of Tennessee. The International Biogeography Society honoured him with the Alfred Russel Wallace Award in January 2015, and his Wallace Award lecture was drawn from this paper.

Author contributions: A.B. and D.S. conceived the ideas; all authors collected the skulls; D.S. and S.M. measured skulls, A.B. analysed the data; and A.B. and D.S. led the writing.

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