CHARACTER DISPLACEMENT AND RELEASE IN THE SMALL INDIAN MONGOOSE, *HERPESTES JAVANICUS*

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Abstract. In western parts of its native range, the small Indian mongoose (*Herpestes javanicus*) is sympatric with one or both of two slightly larger congeners. In the eastern part of its range, these species are absent. The small Indian mongoose was introduced, about a century ago, to the West Indies, the Hawaiian islands, Mauritius, the Fijian islands, and Okinawa. All introductions except possibly that to Mauritius were from the region of Calcutta and Bangladesh, where it is sympatric with both congeners. No other mongoose is present on any of these islands. In each instance, the introduced population derived from a small propagule. We examined size variation in the maximum diameter of the upper canine tooth (the prey-killing organ) and skull length. In the eastern (allopatric) part of its native range, males of the small Indian mongoose are much larger in both traits than in the western (sympatric) regions, approaching the size of the smaller of its absent two congeners, *Herpestes edwardsii.* Females from the allopatric part of the range are also larger than those of the source region. The species is more sexually dimorphic in the region of allopatry. On all islands to which it has been introduced, in 100–200 generations the small Indian mongoose has increased in male size and in sexual dimorphism; changes in female size have been slight and inconsistent. In general, sizes of island individuals are approximately intermediate in size between those in the region of origin (where they are sympatric and small) and those in the region of allopatry. Sexual dimorphism is greatest for canine diameter. Thus, *H. javanicus* shows variation consistent with ecological release from competition with its congeners. There is no evidence on whether this variation is genetic, nor on what dietary items might be partitioned between species and between sexes. However, morphological variation is consistently smaller for both traits and both sexes on the islands of introduction than in any part of the native range, consistent with idea of a genetic bottleneck imposed by the small propagule size. Neither of the two congeneric mongooses shows morphological variation consistent with ecological release from competition with *H. javanicus* in the southern part of their ranges, where the latter species is absent.

Key words: biological introduction; character displacement; character release; geographic variation; Herpestes; *island population; mongoose; sexual size dimorphism.*

Do you think a snake-killer kills musk-rats?
—R. Kipling, *Rikki-tikki-tavi*

INTRODUCTION

The role of interspecific competition in producing geographic variation in morphology was suggested by Brown and Wilson (1956). They hypothesized that two species with partially overlapping geographic ranges might evolve under the selective pressure of competition to have accentuated differences in the region of sympatry. Despite the initial popularity of this concept of ''character displacement,'' the phenomenon and its dual, ''character release'' (Grant 1972) in areas of al-

lopatry from a competitor, were widely seen for many years as uncommon at best, and alternative explanations for geographic variation are often available (Grant 1972). Nevertheless, recent research has provided strong evidence that character displacement and release occur in some situations (Schluter and McPhail 1992, Dayan and Simberloff 1996, 1998). It has also pointed to changes in sexual size dimorphism that may similarly be related to release from, or imposition of, competition.

Taper and Case (1992*a, b*) review the recent theoretical literature on character displacement and conclude that several approaches have debilitating assumptions, particularly revolving around biased predictions associated with asymmetric competition, and also an inability to accommodate intraspecific phenotypic variation. As competition between species of different size is quite likely to be asymmetric (see *Discussion*) and many species have substantial phenotypic

variation, these are serious shortcomings. Taper and Case (1992*a, b*) advocate an approach based on a model by Slatkin (1980) and developed by Taper and Case (1985). Although their models succeed in showing circumstances under which character displacement should evolve (indeed, for a wide range of parameter sets, they predict it will arise), the "biggest barrier to making the models predictive for specific situations is the large number of parameters in these models that are nearly impossible to measure" (Taper and Case 1992*b*:101). Our goal is thus not to test these models, as we lack much crucial quantitative information; we enumerate the key lacunae in the *Discussion.* Rather, we aim to show that a remarkable pattern of geographic variation in a widely introduced species is consistent with an hypothesis of evolutionary character displacement.

It is surprising that nonindigenous species have played a minor role in studies of character displacement and release (e.g., Robinson and Wilson 1994, Dayan and Simberloff 1998). After all, deliberate introductions often remove species from contact with potential competitors in their native range and/or place them in contact with new potential competitors. Further, as dates of introduction are often known, the interest in the possibility of rapid phenotypic change, whether or not genetic (e.g., Losos et al. 1997), suggests that introduced species would be well worth study in this context. We examined variation in size and sexual size dimorphism in the small Indian mongoose (*Herpestes javanicus*) in its native range and on several islands to which it has been introduced.

Small Asian Mongooses

The small Indian mongoose, *Herpestes javanicus* (Herpestidae), has a native range from Pakistan and northern India to southern China and the Malay Peninsula, as well as Hainan and Java; in the west it extends to Iran and Iraq (Corbet and Hill 1992). Populations formerly ascribed to *H. auropunctatus* are now subsumed in *H. javanicus* (Corbet and Hill 1992, Wilson and Reeder 1993). In addition, *H. javanicus* has been widely introduced for biological control, primarily for rats and snakes: Jamaica (Espeut 1882) and numerous other of the West Indies (Hoagland et al. 1989), the Hawaiian islands (Bryan 1938), Mauritius (Cheke 1987), Fiji (Gorman 1975), Okinawa (Ogura et al., *unpublished manuscript*), Amami-Oshima (Ishii 1998), Ngazidja in the Comoro islands (Louette 1987), and Adriatic islands (Tvrtkovic and Kryštufek 1990). There are erroneous reports that the Indian grey mongoose, *H. edwardsii,* was introduced to Mauritius (e.g., Lever 1985, Wilson and Reeder 1993), Fiji (Ryan 1988), Okinawa (Takashima 1954, Wilson and Reeder 1993), and the Adriatic (Van den Brink 1972), but no evidence supports these claims. In only two locations of *H. javanicus* introduction are there native or introduced herpestids, viverrids, or mustelids. The stone marten (*Martes foina*) is native on the Adriatic islands (Tvrtkovic

and Kryštufek 1990), and the small Indian civet (*Viverricula indica*) has been introduced to Ngazidja (Louette 1987). By contrast, in large parts of its Asian native range, *H. javanicus* is sympatric with either or both of two slightly larger mongooses, *H. edwardsii* and the ruddy mongoose, *H. smithii,* as well as several substantially larger congeneric species and many other carnivores. In the eastern parts of its range, its two similar congeners are absent (Corbet and Hill 1992).

The small Indian mongoose, the gray mongoose, and the ruddy mongoose are all solitary carnivores (the ruddy mongoose also lives in pairs), occupy a wide variety of habitats, and eat many kinds of prey, as well as some vegetable matter (Macdonald 1984, Corbet and Hill 1992, Creel and Macdonald 1995). The small Indian mongoose and the Indian grey mongoose are mainly diurnal, while the ruddy mongoose is mainly nocturnal (Rood 1986). The possible ecological significance of the different activity time of the ruddy mongoose has not been studied. The ecological similarities of these three species and their differing native and introduced ranges suggest the following questions:

1) In its introduced range, in the absence of its two slightly larger congeners, as well as of other morphologically similar potential competitors, does the small Indian mongoose increase in size?

2) As are most other small carnivores, the small Indian mongoose is sexually dimorphic, with the male substantially greater than the female. Does this dimorphism increase in its introduced range?

3) In the eastern part of its native range, where its two similar congeners are missing, is the small Indian mongoose larger, and is it more sexually dimorphic?

4) In parts of their native ranges in which the small Indian mongoose is absent, is either of the other two species smaller?

History of the Introductions

An early introduction of *H. javanicus* to the West Indies (Trinidad) from India in 1870 apparently failed (Hoagland et al. 1989). In 1872, four males and five females arrived in Jamaica from Calcutta (Espeut 1882, Hoagland et al. 1989), where they were released on Espeut's Spring Garden Estate and, within a few months, establishment and reproduction were obvious. Other Jamaican planters obtained a few individuals from India but it is not believed that these reproduced (Hoagland et al. 1989). Mongooses were then trapped on the Spring Garden Estate and sold to other Jamaican planters, and Espeut and other planters then sent mongooses to Cuba, Puerto Rico, Grenada, Barbados, and Santa Cruz (Trinidad) (Espeut 1882). Numerous other introductions were made among islands in the West Indies, mostly from Jamaica (references in Hoagland et al. 1989), including that of four to eight individuals from Jamaica to St. Croix in 1882–1884.

In 1883, 72 live mongooses from Jamaica were released by the Hilo Planters' Association at Hilo, on the

island of Hawaii (Bryan 1938). These flourished, and they were perceived to be so good at killing rats that a large number of additional small Indian mongooses were imported from the West Indies to Hamakua (Hawaii) in 1885. The offspring of these early populations were subsequently taken to Maui, Molokai, and Oahu, where they established (Bryan 1938).

Mongooses of uncertain species were introduced to Mauritius in the mid-nineteenth century but did not survive (Cheke 1987). In 1900, 16 males and three females of *H. javanicus* were released and rapidly established themselves (Carié 1916, Cheke 1987). The origin of this propagule is an unknown location in India (Macmillan 1914, Haltenorth and Diller 1980).

The small Indian mongoose population in the Fiji Islands was established by an independent introduction of a single founding pair from the Calcutta region in 1883 (M. Gorman, *personal communication*) after an attempted introduction in 1870 failed.

The Okinawan population arises from an introduction in 1910 of six males, six females, and 1–5 individuals of unknown sex, all from an area that is now Bangladesh. The Adriatic island populations all derive from seven males and four females, probably from western India, introduced in 1910 (Tvrtkovic and Kryštufek 1990). This population will not be discussed further. Nor will those of Amami-Oshima and Ngazidja, both initiated within the last fifty years.

In sum, a series of large populations, all started about a century ago directly or ultimately by small propagules, are now prospering independently. Thus, if any morphological change of the sort suggested in questions 1–4 above has occurred, the question arises, (5) how long did it take? And, given that the small propagule sizes could have led to bottlenecks in each location of introduction except perhaps the Hawaiian islands, (6) how does phenotypic variation differ between populations in the native range and those in the areas of introduction?

MATERIALS AND METHODS

With digital calipers (precision 0.01 mm) we measured collections of *Herpestes javanicus* from throughout Asia as well as recent collections from St. Croix and Jamaica in the West Indies, Oahu and Hawaii in the Hawaiian islands, Viti Levu in Fiji, Mauritius, and Okinawa. We also measured very small older collections from Oahu and Jamaica. Finally, we measured collections of *H. edwardsii* and *H. smithii* from their native ranges in Asia. For adult specimens, where possible we measured the maximum diameters of the upper canine teeth ($C^{sup}L$) and the condylobasal skull length (CBL), as in Dayan et al. (1989) and Dayan and Simberloff (1994). We did not include unsexed adults and did not measure skull length of subadult individuals with unfused cranial sutures. Worn or cracked teeth were not measured. In many instances, teeth were miss-

ing and/or the skull was broken; thus sample sizes for the different traits differ.

We measured skull length because it is often taken as a measure of size, particularly within genera or families (Ralls and Harvey 1985, Gittleman and Van Valkenburgh 1997). For assemblages of mustelids (in one instance including a herpestid), there is strong evidence suggesting that the upper canine tooth is a weapon 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). Similar use of upper canines in prey capture by mongooses (Zannier 1965, Ewer 1973) suggests the possibility that canine diameters will also be selected in this group.

For the dental measurements, we used either the mean of right and left canine where both were measured, or the single measurement where only one was measured.

With few exceptions, the various areas of sympatry and allopatry of these three mongooses in their native ranges are delineated by geographic features. Thus we divided Asia into seven regions as follows (Fig. 1):

I) Sri Lanka, inhabited by *H. smithii* and *H. edwardsii*.

II) Southern Indian peninsula, dominated by highlands, south of the Satpura Range in the west and the valley of the Godvari River in the east. Inhabited by *H. smithii* and *H. edwardsii*.

III) Central India, largely lowlands, including the valley of the Indus River, the western reaches of the Ganges River, and extending northward to the Vale of Kashmir. This region is inhabited by all three species.

IV) Iraq, Iran, Afghanistan, and northern Pakistan (northwest of the valley of the Indus River), inhabited by *H. edwardsii* and *H. javanicus.*

V) From the foot of the Himalayas northward: Kashmir and Jammu, montane Himchal Pradesh and Uttar Pradesh, Nepal, Tibet, Sikkim, Bhutan, and western montane Assam. This region is inhabited by both *H. javanicus* and *H. edwardsii,* though we have specimens only of the former species.

VI) A lowland region including and surrounding Calcutta: West Bengal, part of Bihar, Bhangla Desh, and extreme southwestern Assam, extending east to the Irrawaddy River and its valley. All three species are present. This is the only region not marked in any way by either geography or species composition, and we delineated it because so many of the founding propagules of the introduced populations could be traced to this region rather than region III, with which it is continuous and shares the same species set.

VII) Areas east of the Irrawaddy River and its valley: eastern Assam, Myanmmar, Thailand, the Malay Peninsula, the Indochina Peninsula, and China. Only *H. javanicus* is present.

For coordinates of the tag locations of Asian specimens, and elevations of those locations where possi-
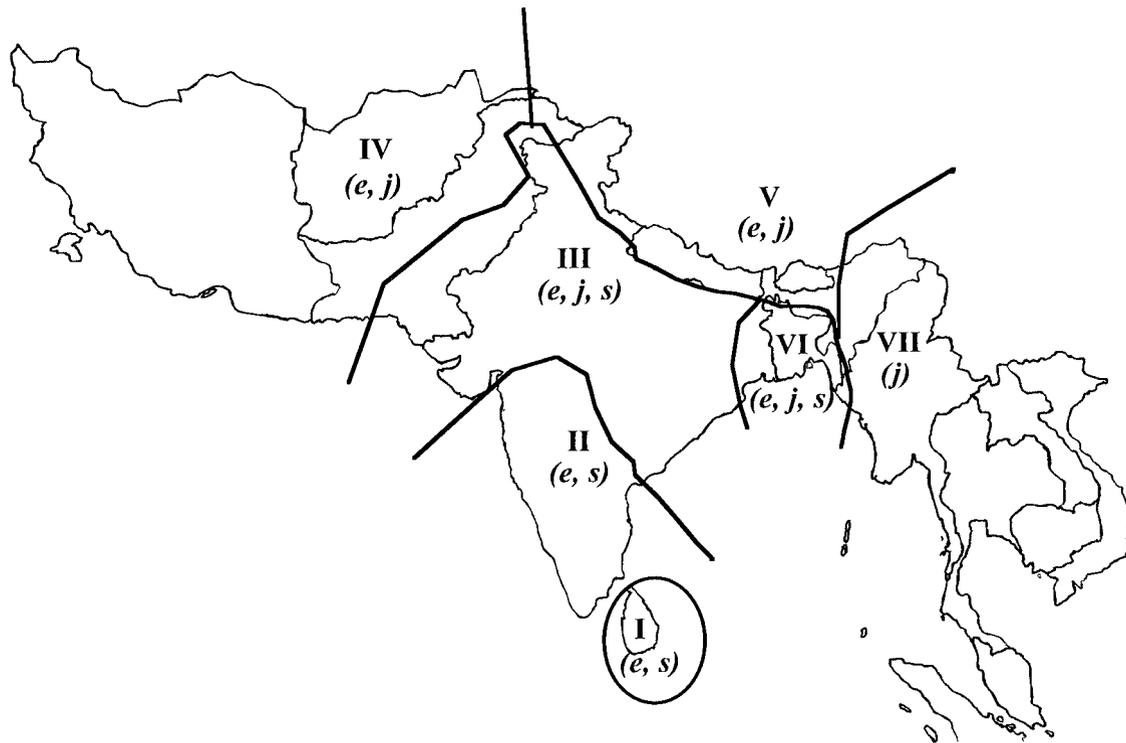
FIG. 1. Native geographic ranges of *Herpestes edwardsii* (*e*), *H. javanicus* (*j*), and *H. smithii* (*s*).

ble, we used a variety of maps, atlases, and gazetteers. For many Asian specimens of *H. javanicus* and *H. edwardsii,* tag data included elevation. Thus, for the Asian specimens of these two species only, lumping elevations in classes of 300 m, we conducted Spearman's rank correlation tests between elevation and the various size measures. For the island populations, such data were generally unavailable.

Finally, to ascertain whether differences in degree of morphological variation between islands and continental regions were solely due to the fact that mainland regions are much larger, we sought restricted sections of continental regions, roughly the size of the islands, for which we had substantial samples. We found sufficient collections of both sexes from a small region of the Vale of Kashmir (S-I, part of Asia III), males from a region of Vietnam including Quang Tri and Quang Nam (S-II, part of Asia VII), and females from part of the continental Chinese island of Hainan (S-III, part of Asia VII).

RESULTS

For specimens from the Asian range of *H. javanicus* and from areas of introduction collected after 1965, the data for upper canine diameter and condylobasal skull length are listed in Table 1. The sample for region IV consisted of but one male and one female, and this region is thus omitted from subsequent figures. There is nothing notable about these two individuals, although the male is larger than the means for Asia III

and V. The measurable sample for region VI (the source area of most introductions) unfortunately comprised just two individuals of each sex. Fig. 2 depicts the sizes and sexual size dimorphism for each location for canine diameter, while Fig. 3 depicts sizes for skull length.

One-way ANOVA shows one pattern for canine diameters of the Asian *H. javanicus* (Fig. 2). For male canine diameter, the ANOVA is significant at $P < 0.001$ ($F_{4,51} = 22.005$). By a Tukey multiple-comparison test at $P < 0.05$, individuals of region VII exceed those of all other regions (except IV, which contains only one individual), and the others are indistinguishable. The result for male skull length (Fig. 3) is identical. In particular, for both traits, individuals from region VI are smaller than those of region VII and do not differ from those of adjacent region III. Similarly, for female canine diameter, the ANOVA is significant at $P < 0.001$ ($F_{4,45} = 8.954$), but a Tukey test suggests not many differences. Individuals from region VII exceed those from regions III and VI, but not those of regions IV and V (the small sample sizes in the latter regions would almost surely have defeated efforts to find significance). For female skull length (Fig. 3), the ANOVA is again significant at $P < 0.001$ ($F_{4,42} = 6.393$), and a Tukey test shows that individuals from region VII exceed those of region III. They barely miss significantly exceeding those of region VI, even though the latter are smaller than those of region III; again, there are only two females from region VI, so significance would have been difficult to achieve.

DANIEL SIMBERLOFF ET AL.

TABLE 1. Means, coefficients of variation (CV), and standard errors (SE) for *Herpestes javanicus* upper canine diameters ($C^{sup}L$) and condylobasal skull length (CBL) from regions within its native range (defined in text) and recent specimens from several areas of introduction.

Location	Sex	$C^{sup}L$ (mm)				CBL (mm)			
		N	Mean	CV	SE	N	Mean	CV	SE
Asia III	m	21	2.87	7.21	0.05	19	60.98	5.23	0.73
	f	20	2.68	7.92	0.05	18	59.51	7.86	1.10
Asia IV	m	1	3.05			1	65.98		
	f	1	2.65			1	58.06		
Asia V	m	7	2.81	6.59	0.07	5	62.24	4.24	1.18
	f	3	2.74	8.02	0.13	3	62.85	8.68	3.15
Asia VI	m	2	2.65	4.55	0.09	2	61.94	2.61	1.15
	f	2	2.39	10.06	0.17	2	58.04	11.76	4.83
Asia VII	m	25	3.55	9.68	0.07	28	73.10	6.47	0.89
	f	24	3.13	10.59	0.07	23	66.85	7.48	1.04
S-I	m	9	2.89	7.55	0.07	7	63.29	4.43	1.06
	f	8	2.84	8.53	0.09	7	64.37	3.94	2.53
S-II	m	11	3.77	5.96	0.07	15	75.03	3.73	0.72
S-III	f	8	2.99	5.00	0.05	8	64.28	3.55	0.81
St. Croix	m	18	3.26	4.85	0.04	19	65.73	2.80	0.42
	f	24	2.89	4.40	0.03	29	61.09	2.09	0.24
Hawaii	m	40	3.11	5.02	0.03	44	65.67	2.84	0.28
	f	27	2.70	5.66	0.03	31	60.52	2.95	0.32
Oahu	m	45	3.09	3.93	0.02	46	66.54	2.61	0.26
	f	41	2.73	4.23	0.02	42	61.97	2.41	0.23
Mauritius	m	41	3.15	3.40	0.02	43	65.48	2.41	0.24
	f	16	2.77	4.60	0.03	15	60.51	2.34	0.37
Viti Levu	m	39	3.14	6.02	0.03	38	65.48	3.54	0.38
	f	14	2.86	6.66	0.05	15	61.37	4.36	0.69
Okinawa	m	10	3.14	4.31	0.04	10	65.49	2.54	0.53
	f	10	2.81	2.74	0.02	11	59.98	1.85	0.34

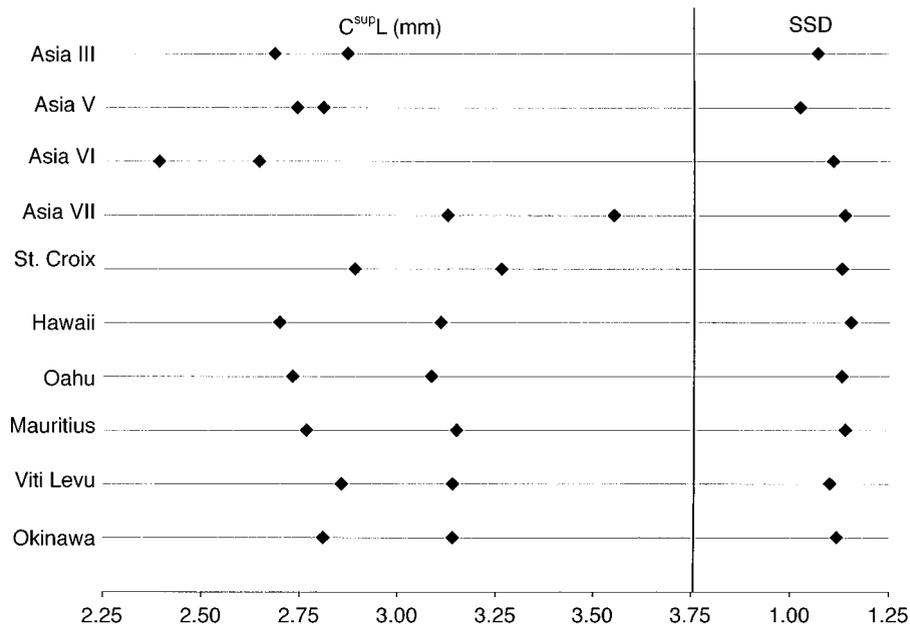*Note:* Coefficients of variation are percentages.

FIG. 2. Maximum diameter (mm) of upper canine ($C^{sup}L$) and sexual size dimorphism (SSD) for this trait for *Herpestes javanicus* in its native and introduced range. For $C^{sup}L$, symbols on the left represent mean female size; symbols on the right represent mean male size.
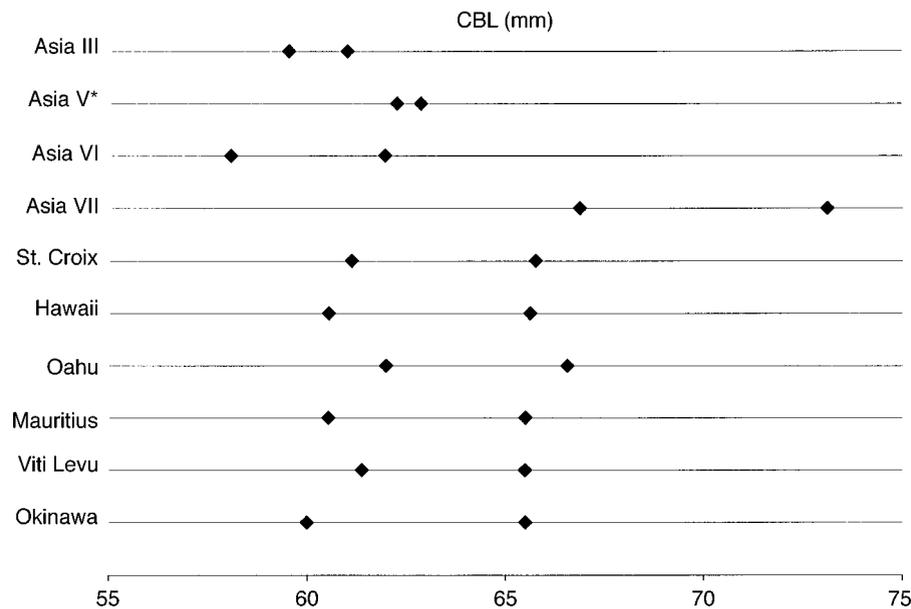
FIG. 3. Condylobasal skull length (CBL, in mm) for *Herpestes javanicus* in its native and introduced range. Symbols on the left represent mean female size; symbols on the right represent mean male size.

Thus, the pattern for both sexes appears to be that individuals from region VII are usually larger than those of the other regions, but there are not consistent differences among the other regions. In particular, both males and females of source region VI do not differ from their counterparts in region III. They are certainly no larger than those from any other Asian region.

This latter fact is important in light of comparisons of the areas of introduction with Asian regions. An ANOVA of the areas of introduction and the Asian areas in which *H. javanicus* is native shows that, for most comparisons, individuals of region VII are larger than those from the areas of introduction, which in turn are larger than those from the rest of Asia. For male canine diameters, the ANOVA is significant at $P < 0.001$ ($F_{10, 238} = 22.532$), and, as seen in Fig. 2 and confirmed by Tukey's test, individuals from region VII are significantly larger than those of all the introduced populations, which in turn exceed those from the rest of Asia (except for region IV with its lone individual). For male skull length, the pattern is similar but not so clean (Fig. 3). The ANOVA is significant at $P < 0.001$ ($F_{10, 243} = 33.307$). Again excepting region IV with its single individual (in this case larger than those of many island populations), a Tukey test shows that individuals of region VII are larger than those of all the introduced populations as well as the rest of Asia. The introduced island populations do not differ from one another. Individuals from all island populations are significantly larger than those from region III, but (except for Oahu individuals) not those from regions V and VI.

Female canine diameter differs among populations (Fig. 2) similarly to that of males ($F_{10, 171} = 11.522$, $P < 0.001$). By a Tukey test, individuals of region VII are greater than those from all introduced populations and the rest of Asia. The differences, both positive and negative, of individuals from Asia V and the introduced populations are not significant. The increments for individuals from St. Croix and Viti Levu over individuals from Asia VI are significant. Those for the other islands are not, nor are the differences between the islands of introduction and Asia III and Asia V. For female skull length, the ANOVA is significant ($F_{10, 179} = 7.860$, $P < 0.001$). Individuals from Asia VII are greater by a Tukey test than those for all islands of introduction and all other Asian regions except for V. Though individuals in our samples from Asia V and all the islands of introduction were larger than those of Asia III and VI, the differences are not significant.

In sum, for both sexes and both traits, individuals from the native region of allopatry, VII, are larger than those of all islands of introduction and also all other parts of the native range (except for female skull length in region V). For males, for canine diameter, individuals from all islands of introduction are larger than the two individuals from source region VI as well as from region III, which is physically similar to and continuous with region VI. For skull length, the males from the introduced island populations are significantly larger than those from region III, but not than the two individuals from region VI (however, skull sizes do not differ between regions III and VI). For females, canine diameters of the individuals in our introduced samples are larger than those from regions III and VI, but only those from St. Croix and Viti Levu significantly exceed those from Asia VI, and only those from St. Croix are larger than those from Asia III. Again, individuals from Asia III and VI do not differ. Skulls of individual fe-

TABLE 2. Sexual dimorphism in *Herpestes javanicus* in its native and introduced ranges. Data are ratios of mean size of male to mean size of female.

Location	C^{sup}L	CBL
Asia III	1.071	1.025
Asia IV	1.151	1.136
Asia V	1.026	0.990
Asia VI	1.109	1.067
Asia VII	1.134	1.093
St. Croix	1.128	1.076
Hawaii	1.152	1.084
Oahu	1.132	1.074
Mauritius	1.137	1.082
Viti Levu	1.098	1.067
Okinawa	1.117	1.092

males in all our introduced samples were larger than those from Asia III and VI, but not significantly so; individuals from Asia III and VI do not differ.

Degree of sexual dimorphism, as indicated by the ratio of mean male size to mean female size, is listed in Table 2 and depicted in Fig. 2 for canine diameters. It should be recalled that the sample size for Asia IV consists of just one individual of each sex, while that for Asia VI consists of just two individuals of each sex, so the contribution of these locations to any pattern should be treated with extreme caution. Certain patterns are very clear. First, for all five Asian regions and all six islands of introduction, sexual dimorphism is greatest for upper canine diameter. Second, within Asia, sexual dimorphism in upper canine diameter is greatest for the region of allopatry with the similar congeners, region VII, except for the ratio for Asia IV, which rests on just one male and one female. Third, for all the islands except Viti Levu and Okinawa, upper canine sexual dimorphism is similar to that for Asia VII, the allopatric area. For Viti Levu, it is smaller than those of Asia IV, VI, and VI, greater than those of Asia III and V. For Okinawa, it is smaller than those of Asia IV but greater than those of Asia II, V, and VI.

For Oahu, we found four specimens (two of each sex) collected between 1905 and 1923, while for Jamaica, we found six males and three females collected between 1896 and 1919. The mean canine diameters for these collections are shown in Table 3. The old Jamaican specimens are significantly smaller than the recent descendent collection from St. Croix (males: $t = -2.58$, df = 22, $P < 0.02$; females: $t = -1.95$, df = 25, $P < 0.06$). The old Oahu specimens are virtually the same size as the recent collection from Oahu. For skull lengths, neither descendent population differs significantly from its progenitor population.

It is apparent from Table 1 that the coefficients of variation for the introduced island populations are, in general, less than those from the native Asian populations. The pairwise comparisons are generally not statistically significant, but the pattern is clear. For example, for either canine diameter or skull length, a Mann-Whitney U test (both sexes together) shows the

island coefficients of variation to be less than the mainland ones at $P < 0.001$ (two-tailed). For the three small continental regions, the coefficients of variation are generally somewhat less than those of the regions of which they are constituents, but they are still greater than the great majority of the island values.

Combining contiguous Asian regions III, V, and VI together, and with elevation represented by classes 300 m in breadth, we found by Spearman's rank correlations that *Herpestes javanicus* skull length in both sexes is significantly positively correlated with elevation (males: $r_s = 0.49$, $n = 26$, $P < 0.02$; females: $r_s = 0.54$, $n = 19$, $P < 0.02$), but there is no such correlation for upper canine diameter. For *H. edwardsii* in regions II, III, and VI together, there is a significant correlation of skull length with elevation for females ($r_s = 0.50$, $n = 35$, $P < 0.006$), but not for males; again there is no such correlation for canine diameter.

Measurement statistics for *H. edwardsii* and *H. smithii* are given in Table 4. For *H. edwardsii,* as observed by Corbet and Hill (1992), variation is remarkably slight. The individuals in region VI are smallest, just as for *H. javanicus,* but none of the differences are significant at $P < 0.05$ by ANOVA for either trait and sex (male canines, $F_{3,37} = 1.236$; male skulls, $F_{3,41} = 1.722$; female canines, $F_{3,32} = 0.682$; female skulls, $F_{3,33} = 2.720$). The only ANOVA that even approaches significance is that for female skulls ($P = 0.060$); a Tukey test shows the only significant difference (at $P < 0.05$) for this trait to be that between regions II and IV. Nor are there any apparent differences among the regions for *H. smithii,* although the sample sizes are too small for an ANOVA to be informative. The single female from region VI is the second smallest of 7 for canine diameter and skull length, but obviously no statistical tests are possible. In particular, neither species in regions I and II, where *H. javanicus* is absent, is smaller than in the regions where it is present.

DISCUSSION

Schluter and McPhail (1992), surveying the literature on character displacement, found an extensive list of criteria. They saw the key ones as: (1) The pattern should not be due to chance. (2) The phenotypic differences should have a genetic basis. (3) The differences should arise evolutionarily, rather than by selective survival of invaders of different sizes. (4) Morphological differences should reflect differences in

TABLE 3. Mean sizes and standard errors (SE) of specimens from Jamaica and Oahu collected soon after introduction.

Location	Sex	N	C^{sup}L (mm)		CBL	
			Mean	SE	Mean	SE
Jamaica	m	6	3.07	0.06	65.57	0.93
	f	3	2.74	0.02	61.32	0.57
Oahu	m	2	3.05	0.19	65.31	0.61
	f	2	2.77	0.01	60.48	0.29

TABLE 4. Mean sizes, coefficients of variation (CV), and standard errors (SE) for *Herpestes edwardsii* and *H. smithii* in regions (defined in text) of Asia within their native ranges.

Location	Species	Sex	$C^{sup}L$ (mm)				CBL (mm)			
			N	Mean	CV	SE	N	Mean	CV	SE
Asia I	*smithii*	m	4	4.26	6.27	0.13	4	84.64	6.44	2.73
	smithii	f	4	4.08	5.27	0.11	4	80.13	2.33	0.93
	edwardsii	m								
	edwardsii	f	1	3.40			1	72.32		
Asia II	*smithii*	m	8	4.35	6.21	0.10	9	84.48	3.66	1.03
	smithii	f	1	4.32			1	82.61		
	edwardsii	m	20	3.94	7.06	0.06	20	79.91	3.37	0.60
	edwardsii	f	6	3.42	5.03	0.07	6	75.15	1.43	0.44
Asia III	*smithii*	m	1	4.50			1	86.39		
	smithii	f	1	4.40			1	84.71		
	edwardsii	m	27	3.93	7.67	0.06	29	79.04	3.98	0.58
	edwardsii	f	27	3.43	8.80	0.06	28	73.86	3.70	0.52
Asia IV	*edwardsii*	m	5	3.95	8.10	0.14	4	74.31	1.38	0.51
	edwardsii	f	7	3.50	7.76	0.10	7	71.48	4.02	1.09
Asia VI	*smithii*	m								
	smithii	f	1	3.92			1	79.69		
	edwardsii	m	6	3.82	6.08	0.10	6	77.76	2.98	0.95
	edwardsii	f	4	3.29	3.93	0.07	4	72.24	3.45	1.25

food use. (5) Sites of sympatry and allopatry should not differ in food or other environmental feature in a way that would account for the pattern. (6) Similar phenotypes should actually compete for limited food. The criteria for ecological release would be analogous. For *Herpestes javanicus,* we view the evidence as strong only for (1) and (3), suggestive for (2) and (5), and almost wholly lacking for (4) and (6).

With respect to criterion 1, the pattern is unlikely to be due to chance. The standard errors for regional and island populations are low, and the ANOVAs are generally significant, as are the male differences between most pairs of sites and many of the female ones. From the regions for which there are adequate sample sizes, it is evident that there is rather little variation in the entire western part of its range, but, abruptly, *H. javanicus* become much larger in region VII, exactly where the two congeneric species are not found. Further, *H. javanicus* from the region adjacent to VII, region VI (the origin of most or all of the island populations), are certainly no larger than those from the rest of the western part of their range; those in our samples are smaller (though insignificantly so). They do not differ in any trait in either sex from those of adjacent and topographically similar region III. The measured *H. javanicus* individuals of region V are not statistically different from those from regions III and VI; *H. edwardsii* is present in at least the southern part of this region, though we found no specimens. Both Pocock (1937) and Corbet and Hill (1992) describe the range of *H. edwardsii* as including Nepal, and the CBLs of the single specimen of each sex that Pocock (1937) reported from this region are very similar to those we found for regions III and VI.

The comparison of the islands of introduction to Asia shows some striking patterns. For both sexes and both traits, individuals from the allopatric region VII of Asia are larger than those of all introduced populations. For males, canines of the island populations are significantly greater than those of the source region, VI, and the adjacent region III. For skull length the comparison with Asia VI barely misses significance, and the sample for Asia VI consists of only two individuals. For females, although the individuals in our island samples were, on average, larger than those from Asia III and VI for both traits, these differences were usually not significant.

These differences apparently arose rather rapidly. *H. javanicus* probably has two litters per year in all these areas of introduction (Pearson and Baldwin 1953, Nellis and Everard 1983). However, though males may become sexually mature at four months, even males that mature in the year they are born will not find sexually mature females of their own age until the next spring (Pearson and Baldwin 1953). Thus, depending on whether males mate with older females or not, the changes we document have probably occurred in at most 100–200 generations. Although there are very few early Oahu specimens, collected after the population had been established for no more than 20 years (and its ancestral population in Jamaica not much longer than that), those few are already identical in size to the recent Oahu specimens. For the old Jamaican specimens, collected ~25 years after establishment, the skull lengths are virtually identical to those of recent St. Croix specimens derived from Jamaica, while the canine diameters are approximately midway between those of the native region (VI) of the ancestral founding population and the those of the current St. Croix population (Table 3).

Thus, *H. javanicus* is bigger in the section of its native range where its two similar congeners are absent, and the males have rapidly increased in size on all the islands of introduction, where these two congeners are

absent and there are no other small carnivorous mammals. The females in our island samples are also larger, but not significantly so; perhaps a larger sample from the source region would have shown significance, but even the differences for both traits for females from Asia III, with a substantial sample size, are not significant. If female size has increased at all, it has increased less than male size has.

Our observations are certainly consistent with the hypothesis that *H. javanicus* has undergone character release (Grant 1972) where it is allopatric from *H. edwardsii* and *H. smithii*; that is, morphological change resulting from the lifting of competitively induced selection. This hypothesis is also consistent with the observation that sexual dimorphism is increased in the native area of allopatry and on the islands of introduction, because male size his increased more than female size.

With respect to criterion 2, we have no evidence that these morphological differences are genetically based, and it would not be shocking if some fraction of them are nongenetic (cf. James 1983). However, the fact that very similar changes have occurred on islands scattered in three oceans suggests that at least part of the change results from natural selection. Although we have not attempted to characterize differences in the physical environment among locations, surely there must be some, yet the morphology of specimens from all the locations of introductions is quite consistently and unidirectionally different from that in the region from which they arose. Further, the fact that the morphology of West Indies populations appears to have changed between 0 and 25 years after introduction, then changed further between 25 and 100 years after introduction, is consistent with a genetic interpretation.

Criterion 3, that differences should not arise by size-selective survival of invading species, is not applicable to our study. On the islands of introduction, no other mongooses (indeed, any small carnivorous mammals) were introduced, so size-selective extinction surely did not occur. With respect to the size differences between Asia VII and other native regions, there is no firm hypothesis about where the three small *Herpestes* species evolved. A selective extinction hypothesis for Asia VII would require invasion of this region by *H. edwardsii* and/or *H. smithii,* followed by subsequent extinction caused by competition from larger species. Of course we cannot prove that this did not happen, but there is no evidence that it did. Although the precise range limits are not known, the next largest herpestid, *H. urva* (the crab-eating mongoose) is possibly found only in region VII but not region VI (Corbet and Hill 1992). It is a much larger species (males: mean canine diameter = 5.31, SE = 0.16, n = 5; mean skull length = 92.65, SE = 2.13, n = 5; females: mean canine diameter = 5.06, SE = 0.11, n = 9; mean skull length = 91.62, SE = 1.58, n = 6). Its diet is largely fishes, crabs, frogs, and other aquatic prey (Corbet and Hill

1992). It would seem unlikely to compete strongly with *H. edwardsii* or *H. smithii*. Other species, more distantly related to these mongooses but with more similar diets, may also be found only in region VII but not west of it (again, exact range limits are uncertain): the spotted linsang (*Prionodon pardicolor*) and the masked palm civet (*Paguma larvata*). On the other hand, the small Indian civet (*Viverricula indica*) is found both east and west of the boundary between regions VI and VII. As there are no data to begin to address dietary overlap and food limitation for any of these species, it seems fruitless to hypothesize further on this point.

Criterion 4 is that morphological differences reflect differences in food use. No published data on *H. javanicus* address this point, either within populations or between populations, although an intriguing observation from a study in progress, discussed below, suggests that at least sexual size differences are correlated with diet. Neither is there any published evidence on criterion 6, food limitation.

Finally, there is also no evidence on criterion 5, the requirement that morphological differences between different populations not be explicable in terms of resource or other environmental differences between sites. The large regions we demarcated for Asia all have diverse habitats. So do at least some of the islands. All are more or less mountainous, for example. *Herpestes javanicus* occupies a great range of habitats—in both the West Indies (Pimentel 1955, Nellis and Everard 1983) and the Hawaiian islands (Baldwin et al. 1952) it is found in grasslands, crops, and forests of various kinds, coastal areas, and even settled suburbs. In Asia it ranges from sea level to over 2100 m, while it reaches the highest areas of Molokai, Oahu, and Maui, and the limit of vegetation (~3000 m) on Hawaii (Baldwin et al. 1952). The fact that the rank correlations for skull length and elevation in Asia are significant for both sexes suggests that environmental variation does affect morphology, but they are not significant for upper canine diameter, which shows the same pattern of decreased island variation that skull length does. One would expect the local diet to select for canine diameter size and variation, but there are simply insufficient dietary data to pursue this line of inquiry. It is difficult to imagine an environmental difference that would characterize all the islands of introduction, plus Asia VII, but not the other regions of Asia, that would explain these size differences.

Other hypotheses suggest themselves for the differences between island and continental populations, although some turn out, upon close examination, not to be mutually exclusive of character release. Foster (1963, 1964) proposed an "island rule" for sizes of island mammals, generalized by Van Valen (1973) to the observation that small species get larger on islands, while large species get smaller. There are at least ten published explanations for the island rule (Dayan and Simberloff 1998) and many exceptions. The key fac-

TABLE 5. Major dietary items in various populations of *H. javanicus*.

Item	Location	Reference
Crabs	Hawaiian Islands	Hinton and Dunn (1967)
	Fiji	Gorman (1975, 1979)
	St. Croix	Nellis and Everard (1983)
	Mauritius	Carié (1916)
Brachiopods	Fiji	Gorman (1975)
Scolopendroid centipedes	St. Croix	Nellis and Everard (1983)
Insects	Hawaii	Baldwin et al. (1952)
	Viti Levu	Gorman (1975, 1979)
	Trinidad	Williams (1918)
	St. Croix	Nellis and Everard (1983)
	Puerto Rico	Pimentel (1955)
Arthropods	Korcula (Aegean)	Cavallini and Serafini (1995)
Starfish	Puerto Rico	Pimentel (1955)
Fish	Hawaiian Islands	Hinton and Dunn (1967)
Bufo marinus	Fiji	Gorman (1975)
	St. Croix	Nellis and Everard (1983)
	Puerto Rico	Pimentel (1955)
Amphibians	Mauritius	Carié (1916)
Anolis lizards	Puerto Rico	Pimentel (1955)
Reptiles	Fiji	Gorman (1975)
	Mauritius	Carié (1916)
Birds	Hawaii	Baldwin et al. (1952)
	Fiji	Gorman (1975)
	Maritius	Carié (1916)
	Korcula (Aegean)	Cavallini and Serafini (1995)
Shrews	Mauritius	Carié (1916)
Tenrecs	Mauritius	Carié (1916)
Rodents	Hawaii	Baldwin et al. (1952)
	Fiji	Gorman (1975)
Mammals	Korcula (Aegean)	Cavallini and Serafini (1995)
Fruit and seeds	Hawaiian Islands	Baldwin et al. (1952), Hinton and Dunn (1967)
	Trinidad	Williams (1918)
	St. Croix	Nellis and Everard (1983)
	Mauritius	Carié (1916)
	Korcula (Aegean)	Cavallini and Serafini (1995)

tors, alone or in combination, in most explanations are decreased numbers of competing species, more limited resources, and decreased predation on islands. In particular, fewer competitors should lead to competitive character release, thus increased size, for small species (Lomolino 1985), but decreased predation on islands should also lead to increased size, at least for small mammals that escape predation by seeking refuges (Van Valen 1973, Heaney 1978). The fact that *H. javanicus* has an enormous dietary breadth (Table 5) may seem difficult to reconcile with the hypothesis that resources are more limiting on islands than in its native range, as does the fact that it has gotten bigger on the islands. The small Indian mongoose probably does escape from predators by seeking refuge, although this behavior has not been documented. Most study of the species has been on the islands, where it has no predators except perhaps feral dogs and cats, but Baldwin et al. (1952) describe in detail the requirement for retreats such as cracks, interstices among boulders, root

masses, and tangled underbrush. It is also noteworthy that, in the eastern part of its native range, *H. javanicus* is even larger than on the islands in spite of the presence of predators such as jackals, dholes, raccoon-dogs, bears, martens, civets, and several cats regionally present in various combinations (Corbet and Hill 1992). We discuss further the hypothesis of release from competition below.

Case (1978), Damuth (1993), and Brown (1995) see size of mammals on islands as evolving to maximize the energy that individuals can garner from the environment. Thus, Case (1978) believes that nonterritorial species should not increase in size on islands (because increased resources will simply be absorbed by increased densities). There is no direct evidence that *H. javanicus* is territorial, in spite of extensive study of their agonistic behavior and movements in some areas of introduction. Baldwin et al. (1952) go so far as to say they are not territorial, although the presence of prominent anal scent glands (Baldwin et al. 1952) and

characteristic marking behavior suggests adaptation to territoriality (Hinton and Dunn 1967). Brown (1995) and Damuth (1993) both argue from physiological models that there is an optimal body size at which species control most energy, and that species alone on islands should tend toward that optimum, but they see different optima (100 g for Brown [1995], 1 kg for Damuth [1993]). Female *H. javanicus* average ~0.5 kg, and males ~0.8 kg (e.g., Baldwin et al. 1952), so this literature does not give a clear prediction, although it certainly suggests that absence of potential competitors should affect body size. Some explanations invoking release from competition to explain the island rule are explicit that the sizes of the species reaching an island and of those that do not are not the sole factors selecting for change is size of the island individuals (e.g., Case 1978, Lomolino 1985); thus one would not automatically expect character release—evolution of an island species' size in the direction of its ''missing'' mainland competitor. Without a good indication of food availability and use on islands and the continent, it is probably unlikely that any strong prediction about direction of evolution is possible.

Herpestes javanicus is highly sexually dimorphic in size, with males typically weighing 50% more than females (Baldwin et al. 1952). As in mustelids (Dayan et al. 1989; Dayan and Simberloff 1994), this dimorphism is greater for the maximum diameter of the upper canine teeth than for condylobasal skull length, which is often taken as a measure of size in carnivores (Gittleman and Van Valkenburgh 1997). Generally, carnivore species are more dimorphic for canine measurements than for skull length (Gittleman and Van Valkenburgh 1997). What is special about the diameter of the upper canines?

The study of mongoose prey-killing techniques points to a highly efficient killing bite used on vertebrate prey, even in the least predaceous species (Ewer 1973). Ewer (1973) suggests that mongooses must originally have been more predaceous and that, while adaptations to insectivory have led to changes in dentition away from the strictly carnivorous pattern, the stylized killing bite has not been lost (Ewer 1973). Killing prey with a perfectly aimed bite at the back of the skull or with a neck bite has been observed in several mongoose species (Zannier 1965, Ewer 1973). Specifically, *H. javanicus,* a swift and aggressive carnivore (Nellis et al. 1984, Nellis 1989), manifests efficient, stereotyped kill behavior with vertebrate prey: a well-aimed bite drives the long, slender, and slightly recurved canines into the brain or vertebral column of rodents, birds, and snakes (Nellis 1989). Nellis and Everard (1983) and S. Roy (*personal communication*) describe highly accurate death bites to the base of the skull of mammalian and avian prey. As in mustelids (cf. Dayan et al. 1989, Dayan and Simberloff 1994), the upper canines act as a dagger to drive apart the vertebrae, and

the diameter of the canines determines what size prey will be efficiently killed by this technique.

For mustelids, an alternative hypothesis for the enhanced sexual size dimorphism of the upper canines is their possible use in threat displays, including those that may generate sexual selection (Dayan et al. 1989, Whitehead and Walde 1993). This seems unlikely in mustelids because upper canines in mustelids, even when prominent, are not known to be widely used in displays, and in some species canine display is unknown (references in Dayan and Simberloff [1994]). Similarly, the literature does not suggest this hypothesis for *Herpestes.* The threat behavior of *H. javanicus* has not been thoroughly documented, although detailed accounts of their mating behavior (Nellis and Everard 1983) and response to attacks (Baldwin et al. 1952, Nellis and Everard 1983) make no mention of canine display. S. Roy (*personal communication*) has observed fighting males baring their teeth and charging at one another, open mouthed. In the slender mongoose, *H. sanguineus,* threat behavior entails a slight opening of the mouth with vertically retracted lips, the gape resembling a snarl and giving the snout a wrinkled appearance (Baker 1981). Although Baker (1982) stressed the communicative role of the pink color of the mouth and did not refer to canine display in such interactions, the above description suggests that canine display might play a role. The social structure of *H. javanicus* is not known to vary among regions; it is polygamous (Rood 1986), although it has been closely studied only in the West Indies and Fijian islands. Thus it is difficult to interpret the changes in size and sexual size dimorphism of the canines in light of a possible behavioral role. Moreover, similar nonrandom morphological patterns in canine size have been found in other carnivore assemblages in spite of interfamilial and intergeneric differences in social structure and differing emphasis on the use, or lack thereof, of canines in threat behavior (references in Dayan and Simberloff 1998).

Mongooses eat small vertebrates, arthropods, and plant food (Ewer 1973, Rood 1986), and *H. javanicus, H. edwardsii,* and *H. smithii* are no exceptions. There have been no quantitative studies on *H. edwardsii* diets, but it eats a wide variety of vertebrate and invertebrate prey (Corbet and Hill 1992) and often eats carrion (Hinton and Dunn 1967). There are also no quantitative studies of the diet of *H. smithii,* although there is no reason to think it is other than a generalized carnivore.

The diet of *H. javanicus* is known largely from studies in the areas of introduction, particularly the Hawaiian islands, Viti Levu, the West Indies, and Mauritius. In its native range it is known to prey on a wide variety of vertebrates and invertebrates (Corbet and Hill 1992), and even on bovid droppings, perhaps for the insects on them (Haque 1989). On the islands of introduction it is an omnivorous carnivore with a remarkably broad potential diet, and with major differ-

ences in populations even within the same island. For example, in four different populations studied in the Hawaiian islands, the diet was dominated, respectively, by crabs and fishes, bananas and papayas, rodents, and insects (Pemberton 1925, Baldwin et al. 1952, Kami 1964, Hinton and Dunn 1967). In various populations, an astonishing variety of foods were reported by researchers to be substantial parts of the diet (Table 5).

In sum, three points stand out in the accumulated information on the diet of *H. javanicus*. First, this species can eat almost anything. Second, there is great geographic variation, sometimes quite local, in the diet. And third, no published account addresses possible dietary differences between the sexes. With respect to our finding of apparent character release of *H. javanicus* in the absence of *H. edwardsii* and *H. smithii,* these findings (and absence of a search for sexual differences) are problematic. As far as we know, *H. edwardsii* and *H. smithii* also have very broad diets, and, if the character release of *H. javanicus* is driven by release from competition with one or both of them for food, it would be interesting to learn what foods are limiting in their areas of sympatry. Of course, the absence of Asian data allows the hypothesis that, in its native range, *H. javanicus* is forced by competition to use a greater portion of smaller prey, particularly invertebrates, and release from that competition on the islands allows greater use of vertebrates, especially mammals and birds.

It is interesting, in light of the increased sexual dimorphism particularly for canines in all the areas of introduction, that a current study of *H. javanicus* diets in Mauritius (S. Roy, *personal communication*), apparently the first to look at sex differences, finds that females on average eat more insects and fewer rats than males do. Dayan and Simberloff (1994) cite numerous references for European mustelid species showing dietary differences between the sexes. They also present data for British Isles mustelids showing more pronounced sexual dimorphism for upper canine diameters than for skull length, as well as increased sexual dimorphism in Ireland of the pine marten (*Martes martes*) and especially the stoat (*Mustela erminea*) in the absence of the polecat (*Mustela putorius*) and the weasel (*Mustela nivalis*), with which they are sympatric in Great Britain. Thus an analogous hypothesis of competitive character displacement and release for *Herpestes javanicus* is at least plausible.

Following the finding for mustelids of higher coefficients of variation for Irish mustelids than for their conspecific populations in Great Britain (Dayan and Simberloff 1994), one might have expected to see a similar pattern for the island populations here, in line with the niche-variation hypothesis (Van Valen 1965). Alternatively, one could have predicted lower variation on the island (at least if the traits are genetically determined) because the small propagule sizes might have imposed a genetic bottleneck and there has been little

time for genetic variation to increase. The clear pattern of lower coefficients of variation for all measurements for island populations rather than continental ones is consistent with the latter hypothesis. With such small propagules as founders of all the island populations except perhaps those in Hawaii and Okinawa, and only 100–200 generations at most since introduction, one might have expected limited genetic variation, and this might perhaps have limited phenotypic variation. Another possibility is that the lower island coefficients of variation are an artifact arising from the fact that each of our seven regions of Asia is huge, whereas the islands are very small. Although some of the regions were delineated specifically to encompass a certain range of elevations, all of them surely include enormous habitat variation. However, the three samples from restricted continental areas (males and females from the Vale of Kashmir, males from a region of Vietnam, females from a part of the continental island of Hainan) also show generally greater coefficients of variation than do the island populations, and these small regions are unlikely to contain greater habitat variation that the islands do. Further, as noted above, at least some of the islands have a great diversity of habitats, though neither we nor any other authors have characterized this feature quantitatively for this system.

Several authors have suggested that ecological release in the absence of competitors is more likely to be accomplished by increased sexual dimorphism than by the increased intrasexual variation envisioned by Van Valen (1965) in the niche-variation hypothesis (references in Dayan and Simberloff [1994]). In fact, as we observe above, we know so little about the trophic niche of *H. javanicus* in its native range that it is impossible to say if it has expanded in its introduced range. If it has, perhaps the increased sexual dimorphism we have documented is associated with the expansion.

Finally, one might have expected at least *Herpestes edwardsii,* and perhaps *H. smithii,* to have manifested character release in the opposite direction in the Asian regions (I and II) where they are allopatric to *H. javanicus.* They do not. In fact, both *H. edwardsii* and *H. smithii* show remarkably little variation over their entire ranges, and no decrease in the areas of allopatry analogous to the striking increase of *H. javanicus* in region VII. If there is competition for food in the region of sympatry, there is no a priori reason to believe that it weighs equally on both species. McNab (1971) and Taper and Case (1992a) reason that, for predator guilds in general, larger individuals and species have an advantage because they can use a greater range of food particle sizes. Rummel and Roughgarden (1985) present additional arguments that competition should generally be asymmetric and favor larger species. Malmquist (1985), studying character displacement between the pygmy shrew (*Sorex minutus*) and common shrew (*S. araneus*), found the smaller pygmy shrew to in-

crease in size where it is allopatric on islands relative to where it is sympatric on the mainland, but found no corresponding tendency for the common shrew to be smaller on islands where it is allopatric. Such diminution as a form of character release is certainly possible. For example, the Irish stoat (*Mustela erminea*) is much smaller than conspecific individuals from Great Britain, with increased sexual dimorphism generated by the particularly dramatic decrease in the size of the females (Dayan and Simberloff 1994). This may be due to the absence from Ireland of the smaller least weasel (*M. nivalis*); the female Irish stoat is about the size of a male British least weasel. Or it may be due to the depauperate prey spectrum on Ireland, leading the female stoat to specialize on shrews (Sleeman 1992). Why *H. edwardsii* is not reduced in the absence of its smaller congener will remain a mystery until there are more data on diet and food availability.

CONCLUSION

On the whole, our results are compatible with a hypothesis of character release in *H. javanicus* induced by release from competition with one or more slightly larger mongooses and rapidly achieved on islands to which it was introduced. The increase in sexual size dimorphism, particularly pronounced in the killing organ (the upper canine tooth), is also compatible with the hypothesis of character release, and with intraspecific partitioning of food. More data on the relationship of diet to morphology and on the degree to which food is limiting are crucial to test this hypothesis further.

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