ARTICLE

Sexual dimorphism and condition dependence in the anal pad of the small Indian mongoose (*Herpestes auropunctatus*)

M.A. Owen and D.C. Lahti

Abstract: Secondary sexual traits tend to be sexually dimorphic, and theory predicts that such traits should also be condition-dependent in a sex-specific manner. We investigate these phenomena in a field study of the small Indian mongoose (*Herpestes auropunctatus* (Hodgson, 1836); formerly *Herpestes javanicus* (É. Geoffroy Saint-Hillaire, 1818)), in the first attempt at understanding secondary sexual traits and sexual selection in this species. Small Indian mongooses are solitary and nonterritorial, and they likely depend on chemical (scent) rather than visual or acoustic signals for communication. Additionally, they possess a fleshy projection around their anus, the anal pad, thought to aid in scent-marking. Our results revealed strong male-biased sexual dimorphism in mass, skull and body lengths, canine diameters, and anal pad area. After controlling for the influence of body length, males were 31% heavier and possessed anal pads that were 68% larger than females'. Additionally, anal pad size was positively related to body size in males but not in females and was condition-dependent in males but not in females. Taken together, our findings provide indirect evidence that the anal pad might have evolved, at least in part, via sexual selection.

Key words: small Indian mongoose, *Herpestes auropunctatus*, invasive species, sexual dimorphism, sexual selection.

Résumé : Les caractères sexuels secondaires ont tendance à présenter un dimorphisme sexuel, et la théorie prédit également une variation selon le sexe de la dépendance de ces caractères sur l'état d'embonpoint. Nous examinons ces phénomènes dans le cadre d'une étude de terrain de la petite mangouste indienne (*Herpestes auropunctatus* (Hodgson, 1836); anciennement *Herpestes javanicus* (É. Geoffroy Saint-Hillaire, 1818)), dans la première étude visant à comprendre les caractères sexuels secondaires et la sélection sexuelle chez cette espèce. Les petites mangoustes indiennes sont des animaux solitaires et non territoriaux, et elles ont probablement recours à des signaux chimiques (odeur) plutôt que visuels ou acoustiques pour communiquer. Elles présentent en outre une projection charnue autour de l'anus, le coussin anal, qui aiderait au marquage olfactif. Nos résultats révèlent un dimorphisme sexuel marqué et biaisé vers les mâles de la masse, des longueurs du crâne et du corps, du diamètre des canines et de la superficie du coussin anal. Après correction pour tenir compte de l'influence de la longueur du corps, les mâles étaient 31 % plus lourds et présentaient des coussins anaux 68 % plus grands que les femelles. En outre, la taille des coussins était positivement corrélée à la taille du corps chez les mâles, mais non chez les femelles, et dépendait de l'embonpoint chez les mâles, mais non chez les femelles. Dans l'ensemble, nos résultats indiquent de manière indirecte que le coussin anal pourrait avoir évolué, du moins en partie, par sélection sexuelle. [Traduit par la Rédaction]

Mots-clés : petite mangouste indienne, *Herpestes auropunctatus*, espèce envahissante, dimorphisme sexuel, sélection sexuelle.

Introduction

Sexual selection favors the evolution of traits that aid in competing for and acquiring mates (Darwin 1871). This process often results in substantial trait sexual dimorphism, e.g., secondary sexual traits that are only possessed by one sex or that are larger in one sex than in the other. According to sexual selection theory, such traits are also predicted to be costly or otherwise impossible for individuals in poorer condition to exhibit, thus functioning as honest indicators in a mate choice or competition context (Johnstone 1995; Searcy and Nowicki 2005). Therefore, the expression of sexually selected traits should correlate positively with individual condition (Maynard Smith 1991; Bonduriansky 2007; Emlen et al. 2012). Furthermore, the degree of condition dependence should correlate with sexual dimorphism, because the trait value in one sex (usually females) is expected to remain at the trait optimum, whereas sexual selection should displace the trait from it in the other sex (Bonduriansky 2007). In light of these considerations, we might predict that a putative sexually selected trait should be both sexually dimorphic and condition-dependent.

We test these predictions in the small Indian mongoose (*Herpestes auropunctatus* (Hodgson, 1836); formerly *Herpestes javanicus* (É. Geoffroy Saint-Hillaire, 1818)) (Veron et al. 2007; Patou et al. 2009), a diurnal carnivore best known for its status as one of the 100 worst invasive species on earth (Lowe et al. 2000). This South Asian native was introduced to the Caribbean and Hawaiian islands in the late 1800s to control agricultural pests, but quickly multiplied out of control (Thulin et al. 2006; Hays and Conant 2007). This species appears to be an extreme dietary generalist (Gorman 1975; Hays and Conant 2007) with a solitary social system (Nellis 1989; Hays and Conant 2003), and demonstrates high degrees of both inter- and intra-sexual home-range overlap, suggesting a lack of territoriality (Gorman 1979; Roy et al. 2002). Nothing is known of mate choice or competition in the small Indian mongoose, but semicaptive studies indicate that they are promiscuous and that males provide no parental care (Nellis and Everard 1983; Schneider and Kappeler 2014). In such mating systems, sexual selection generally favors males with larger bodies or elaborate weapons (Andersson 1994). These traits often function in resource or territory defense or in competition for access to fe-

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males (Haley et al. 1994; Kruuk et al. 2002; Plavcan and Ruff 2008; Stankowich 2012). Alternatively, although understudied, females may also prefer such traits (Charlton et al. 2007; Clutton-Brock and McAuliffe 2009). Studies of wild populations and museum specimens suggest that male small Indian mongooses are indeed larger than females (Nellis and Everard 1983; Simberloff et al. 2000), indicating that either males do compete for females or that females prefer larger males. However, because these animals are not territorial, the ways in which males are competing for females or how females are choosing males are unknown. One possibility is that males advertise themselves to other males or to females by marking objects in their home range.

Traditionally, scent-marking in mammals was thought to be a territory identification tool, but the challenge to the universality of this function is now several decades old (Johnson 1975). More recent evidence has revealed the importance of scent marks in the advertisement of individual status, quality, and condition (Rich and Hurst 1998; Gosling and Roberts 2001). Females can mark to advertise their sexual receptivity status, and males use marks both for intrasexual competition and intersexual advertisement (Johansson and Jones 2007). In meadow voles (*Microtus pennsylvanicus* (Ord, 1815)), for instance, males attend more to a mark placed by a female in postpartum estrus than one placed by a female not in postpartum estrus (Ferkin et al. 2004). Male house mice (*Mus musculus* L., 1758) infected with *Salmonella* Lignieres, 1900 reduce the frequency of marking compared with uninfected males, and infection reduces the attractiveness of a male's mark to females (Zala et al. 2004).

No studies have characterized the marking behavior of the small Indian mongoose, but scent communication is likely of particular importance due to its solitary nature: interactions with conspecifics might be rare, resulting in the limited utility of visual and auditory communication. Individual small Indian mongooses can distinguish each other by scent alone (Gorman 1976), and their marks can be detected for up to 14 days (Gorman et al. 1974). The small Indian mongoose possesses a pair of anal glands, like other members of its family (Herpestidae) and many other mammals (Thiessen and Rice 1976; Burger 2005). Both sexes possess these glands, as well as a fleshy hairless pad around the anus, the anal pad. The anal glands produce a secretion containing saturated carboxylic acids formed by bacterial action on sebum and apocrine products; this secretion is applied to a surface with the aid of the anal pad (Gorman et al. 1974; Nellis and Everard 1983; Nellis 1989). The possible reproductive relevance of this marking system has not been studied in the genus *Herpestes* Illiger, 1811, except for the discovery that the male secretion of the Egyptian mongoose (*Herpestes ichneumon* (L., 1758)) contains one chemical not found in the secretion of females (Hefetz et al. 1984). In the more distantly related banded mongoose (*Mungos mungo* (Gmelin, 1788)), marking and subsequent over-marking with the anal glands are associated with mate-guarding by males earlier in life, and mate-guarding is positively related to reproductive success (Jordan et al. 2011). Furthermore, in many mammals, anal glands are larger in males than in females (e.g., European badger, *Meles meles* (L., 1758): Kruuk et al. 1984; Japanese vole, *Microtus montebelli* (Milne-Edwards, 1872): Umeda et al. 1993; Eurasian beaver, *Castor fiber* L., 1758: Rosell and Schulte 2004), and this dimorphism appears to be associated with more frequent marking by males than females.

If the scent-marking system of the small Indian mongoose is used in sexual advertising, we might predict that males mark more frequently than females and that females differentiate males based on these marks. However, their solitary nature and apparent lack of territoriality pose challenges to direct behavioral observation. Therefore, as a proxy, we investigated the scent-marking apparatus of the small Indian mongoose in an introduced population in Hilo, Hawai'i, in the first attempt to understand secondary sexual traits and sexual selection in this species. Spe-

cifically, we predicted that both anal glands and pads will be larger in males than in females. Moreover, since Nellis and Everard (1983) and Simberloff et al. (2000) have already demonstrated sexual size dimorphism in the small Indian mongoose, we must distinguish possible sexual selection on body size from that on the marking system. Therefore, we predicted that anal gland and pad sizes remain larger in males than females after controlling for body size. We also predicted that both the anal glands and pads will be condition-dependent in males but not in females.

Materials and methods

Trapping site and methods

In June 2012, small Indian mongooses were trapped for removal within the rainforest and high grasslands surrounding the Keaukaha Military Reservation in Hilo, Hawai'i. A total of 25 small (43 cm × 18 cm × 18 cm) and medium-sized (61 cm × 18 cm × 18 cm) Havahart® traps were used. Each trap was baited with fresh sardines and water in separate containers, and was covered with lengths of cardboard to reduce animal stress. Traps were set at dawn and checked the following morning. Traps were placed approximately 10–20 m apart, along dirt paths at the treeline in the forest and under shade and high brush within grasslands. Unsuccessful traps for each day were rebaited, and some were moved to another location. Successful traps were not reset that day, but were set the following day during that morning's trap check. Catch locations and location conditions were noted and used to determine subsequent trap placement so as to maximize capture rate. The mean daily trap success rate was 48%. On two occasions, a feral cat was caught and taken to a local animal shelter.

Morphological measurements

Mongooses were collected for removal by the United States Department of Agriculture Animal and Plant Health Inspection Service (USDA–APHIS). Upon arrival at the field station, individuals were sacrificed using a custom-built CO_2 chamber and each was placed in its own plastic bag until processing. Mass, body (including and excluding tail), tail, and skull (condylobasal) lengths, and the diameter of all four canines were measured for each mongoose within 12 h of sacrifice. Canine diameters were measured to test for intersexual differences in fluctuating asymmetry, as this has been suggested to be an indication of sexual selection in carnivores (Badyaev 1998; Pertoldi et al. 2003). Mass was measured using a digital scale to 0.001 g. Body and tail lengths were measured with a tape measure to 0.1 mm. Skull lengths and canine diameters were measured at their widest axes using digital calipers to 0.01 mm. Measurements recorded with digital calipers were taken three times and mean values were used in analyses. To determine anal pad area, photographs of each mongoose's anal pad were taken with a ruler inset in the photograph. After isolating the area of hairless skin of each photograph, the analysis feature of Photoshop CS5 (Adobe Systems Incorporated, San Jose, California, USA) was used to calculate anal pad area to 0.01 mm². Only the area of hairless skin was included in this measurement; the gap of the anus itself was excluded.

Because of time constraints resulting from the high number of animals requiring processing each day, anal glands from only 75% of the mongooses were removed and examined. The anal glands are located immediately anterior to the anus and attach to the opening of the anus via a connective duct. Anal gland volume was calculated in similar fashion to the area of the anal pad, but two photographs of each gland were taken to obtain lengths in all three axes, where the first photograph was used for the x and y axes and the second was used for the z axis.

Data analysis

Analyses were performed using SYSTAT version 10 (SPSS Inc., Chicago, Illinois, USA). Prior to analyses, a Levene's test of unequal variance was performed on all variables to test for homogeneity of

Table 1. Uncorrected trait values and degrees of sexual size dimorphism (SSD) in the small Indian mongoose (*Herpestes auropunctatus*; formerly *Herpestes javanicus*).

	Male		Female			
	N	Mean ± SD	N	Mean ± SD	t	SSD (M:F)
Mass (g)	34	618.67±68.02	23	430.58±62.88	−10.55***	1.44
Skull length (mm)	34	67.83±1.86	23	63.10±2.12	−8.90***	1.07
Body length (mm)	34	343.03±17.68	23	309.17±14.21	−7.66***	1.11
Tail length (mm)	33	248.55±11.72	23	231.44±15.08	−4.78***	1.07
Total body length (body + tail; mm)[a]	33	590.55±23.06	23	546.29±15.40	−8.45***	1.08
Anal pad area (mm²)[a]	34	142.23±29.82	23	77.85±17.07	−10.33***	1.83
Canine diameter (mm)						
RT[a]	30	3.05±0.19	20	2.72±0.11	−7.78***	1.12
RB	32	2.79±0.20	21	2.46±0.27	−5.18***	1.13
LT	32	3.02±0.20	20	2.73±0.16	−5.59***	1.11
LB	29	2.89±0.21	22	2.63±0.27	−3.88***	1.10

Note: M, male; F, female; R, right; L, left; T, top; B, bottom. ***, $P < 0.001$.

[a]Trait with unequal variance.

variance between the sexes. Analyses included two-tailed Student's t test and Welch's t test (depending on homogeneity of variance) to determine differences between sexes in morphological traits, and two-tailed paired t tests to determine within-sex differences in canine diameter. Linear regressions and simple correlation analyses were used to test for relationships among morphological characters within a sex and to determine the relationship between morphological features and anal pad area and volume. The residuals of an ordinary least-squares (OLS) regression of total body length and mass were used as a metric of condition. This is a widely used proxy for condition that assumes that individuals with higher energetic reserves are in better condition (Schulte-Hostedde et al. 2005; Edelman 2011; White et al. 2012). That is, individuals that are heavier for a given body length are assumed to be in better condition than those that weigh less for the same body length. Condition dependence of anal gland volume, anal pad area, and canine diameters was assessed by regressing the residuals of the total body length and mass regression against the measured values for each trait. Additionally, since several variables were correlated, a principal components analysis (PCA) was performed to reduce the number of variables. Degrees of sexual size dimorphism (SSD) were calculated as the mean male trait value divided by the mean female trait value.

Ethical note

The work performed in this study conforms to the legal requirements of the USDA. Mongoose capture and euthanasia were performed by the USDA–APHIS, i.e., the animals were not collected for research purposes. Disposal was approved by USDA–APHIS WS SOP #AC 005.00. We were granted access to the animals posthumously.

Results

During 8 days of trapping, 25 female and 34 male mongooses were caught. Three females were pregnant with well-developed fetuses. Excluding the pregnant females did not qualitatively affect the outcome of analyses, so they were included. Two juveniles were caught and were excluded from the analysis.

As predicted, mongooses were sexually dimorphic in all traits measured: males were heavier, had longer bodies, tails, and skulls, a longer total body length, larger canine diameters, and larger anal pads than females, with degrees of SSD being greatest for mass (1.44) and anal pad area (1.83) (all $t_{[48−55]} < −3.80$, all $P < 0.001$; Table 1). After controlling for total body length, males were still heavier ($t_{[54]} = −8.24$, $P < 0.001$) and had larger anal pads ($t_{[55]} = −8.17$, $P < 0.001$) than females, with degrees of SSD of 1.31 and 1.68, respectively; however, they did not differ in any other trait (Table 2). After controlling for mass, males were still larger than females in anal pad area ($t_{[55]} = −3.60$, $P = 0.001$), but females were proportionally larger in all other morphological

traits (all $t_{[48−55]} > 6.00$, all $P < 0.001$). In both sexes, skull length positively predicted both total body length (male: $F_{[1,3]} = 4.73$, $R^2 = 0.13$, $P = 0.037$; female: $F_{[1,19]} = 4.81$, $R^2 = 0.20$, $P = 0.041$) and mass (males: $F_{[1,31]} = 19.78$, $R^2 = 0.39$, $P < 0.001$; females: $F_{[1,21]} = 8.26$, $R^2 = 0.28$, $P = 0.009$). Total body length positively predicted mass in males ($F_{[1,31]} = 12.27$, $R^2 = 0.28$, $P = 0.001$) but not in females ($F_{[1,16]} = 0.160$, $R^2 = 0.1$, $P = 0.695$). Additionally, mass was positively related to anal pad area in males (Pearson's $r = 0.36$, $P = 0.037$, $N = 34$) but not in females ($r = 0.05$, $P = 0.814$, $N = 23$).

Anal pad area was condition-dependent in males ($F_{[1,31]} = 5.83$, $R^2 = 0.16$, $P = 0.022$) but not in females ($F_{[1,18]} = 1.84$, $R^2 = 0.01$, $P = 0.657$) (Fig. 1). For males, the bottom right canine showed a positive relationship with condition ($F_{[1,29]} = 4.65$, $R^2 = 0.14$, $P = 0.039$), but none of the other canines showed any relationship (all $F_{[1,25−28]} < 3.81$, $R^2 < 0.12$, $P > 0.06$). For females, there was no relationship between any canine diameter and condition (all $F_{[1,14−16]} < 0.59$, $R^2 < 0.04$, $P > 0.453$).

Because of the numerous correlations found between traits, a PCA was performed to reduce the number of variables. All measured traits with the exception of anal gland volume (explained below) and anal pad area were included in the PCA. PC1 loaded highly across all traits and explained over 60% of the variance (Table 3), and thus it can be considered a general measure of body size. PC2 loaded positively on major body traits (mass, body length, tail length, and skull length) and negatively on teeth diameters, and explained less than 17% of the variance (Table 3). Because of a large number of mongooses with at least one missing tooth ($N = 16$) and one male missing a tail, the sample available for analyses with the PCs was greatly reduced. Nevertheless, PC1 (body size) positively predicted anal pad area in males but not in females (males: $F_{[1,23]} = 5.20$, $R^2 = 0.18$, $P = 0.032$; females: $F_{[1,13]} = 0.40$, $R^2 = 0.03$, $P = 0.536$; Fig. 2), whereas PC2 (teeth) was not significantly related to anal pad area in either sex (males: $F_{[1,23]} = 0.168$, $R^2 = 0.01$, $P = 0.686$; females: $F_{[1,13]} = 0.313$, $R^2 = 0.02$, $P = 0.585$).

No comparison between male and female anal glands could be performed because a majority of the males possessed abnormal glands. Normal, healthy anal glands are filled with a brown paste formed from dead epidermal cells mixed with sebaceous and apocrine gland secretions (Gorman et al. 1974). All measured female anal glands were normal, but 88% of the males had at least one gland that was misshapen, visibly swollen, and filled with pus. Among the 25 males whose glands were measured, 18 possessed two abnormal anal glands, 4 possessed one abnormal and one normal anal gland, and 3 possessed two normal anal glands. The abnormal glands appeared characteristic of the common ailment of dogs and house cats termed anal sac disease (Washabau and Brockman 1995; Hedlund and Fossum 2007). In these pets, anal sac (gland) disease is a result of inflammation, infection (sacculitis), or an accumulation of anal sac contents (impaction) resulting from

Table 2. Trait values and degrees of sexual size dimorphism (SSD) in the small Indian mongoose (*Herpestes auropunctatus*; formerly *Herpestes javanicus*) after correcting for total body length.

	Male		Female			
	N	Mean ± SD	N	Mean ± SD	t	SSD (M:F)
Mass (g)	33	1.046±0.103	23	0.798±0.121	−8.24***	1.31
Skull length (mm)	33	0.115±0.005	23	0.117±0.004	1.58	0.98
Body length (mm)	33	0.579±0.014	23	0.572±0.016	−1.70	1.01
Tail length (mm)	33	0.421±0.014	23	0.428±0.016	1.70	0.98
Anal pad area (mm²)	33	0.242±0.051	23	0.144±0.031	−8.17***	1.68
Canine diameter (mm)						
RT	31	0.005±0.001	22	0.005±0.001	−1.27	1.00
RB	31	0.005±0.001	21	0.005±0.001	−1.41	1.00
LT	32	0.005±0.001	21	0.005±0.001	−0.85	1.00
LB	28	0.005±0.001	22	0.005±0.001	−0.30	1.00

Note: M, male; F, female; R, right; L, left; T, top; B, bottom. ***, $P < 0.001$.

Fig. 1. Linear regression demonstrating condition dependence of male but not female anal pad area in the small Indian mongoose (*Herpestes auropunctatus*; formerly *Herpestes javanicus*). Condition is represented as the residuals from a regression of mass on total body length.
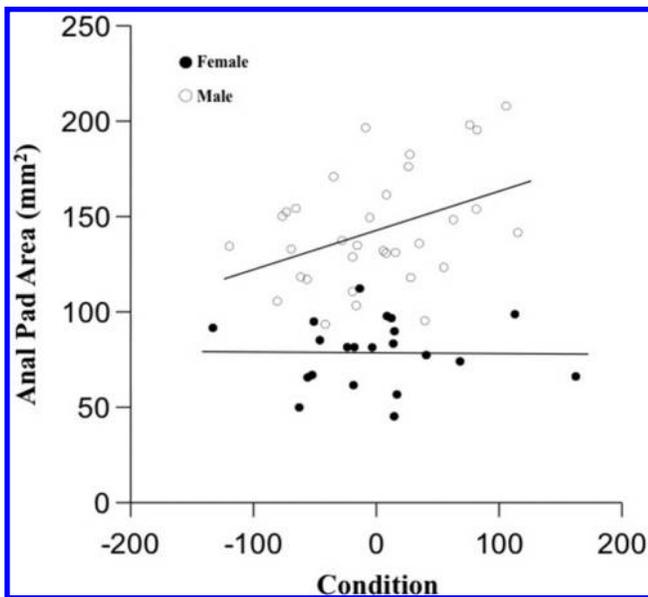
an obstruction of the duct connecting the gland to the exterior of the body. As a result of the heterogeneity in male anal gland contents, anal gland volume could not be used as a correlate with other morphological traits for males. Among females, however, the collective volume of both anal glands was not correlated with any trait except for a weakly positive relationship with total body length (Pearson's $r = 0.39$, $P = 0.096$, $N = 23$). Anal gland volume also was not related to condition in females ($F_{[1,13]} = 0.724$, $R^2 = 0.05$, $P = 0.410$). To determine whether the diseased anal glands influenced the size of male anal pads, the anal pads of males that possessed at least one normal anal gland ($N = 7$) were compared with those of males that possessed only diseased anal glands ($N = 18$). Although the sample sizes were small, the health of the anal gland was not related to anal pad area ($t_{[23]} = -1.24$, $P = 0.227$). That is, the infected, swollen glands did not appear to be influencing anal pad area.

Both sexes exhibited asymmetry between left and right canines. In both sexes, the upper two canines did not differ in diameter (males: paired *t* test, $t_{[29]} = -0.015$, $P = 0.988$; females: paired *t* test, $t_{[17]} = -0.586$, $P = 0.566$); however, the bottom left canine possessed a significantly wider diameter in both sexes than the bottom right

canine (males: paired *t* test, $t_{[27]} = -4.02$, $P < 0.001$; females: paired *t* test, $t_{[18]} = -5.56$, $P < 0.001$).

Discussion

The Hawaiian population of the small Indian mongoose is highly sexually dimorphic in size, corroborating earlier findings from other areas of introduction (Nellis and Everard 1983; Simberloff et al. 2000), and in several morphological traits. Males are larger than females in mass, body and tail lengths, skull size, canine diameter, and anal pad area. Only the anal pad and mass remained larger in males after controlling for body length, with males being nearly one-third more massive and possessing anal pads more than two-thirds larger than females. Moreover, anal pad size is predicted by body size (PC1) in males but not in females, and is condition-dependent in males but not in females. Together, these findings suggest that sexual selection has played a role in the evolutionary history of the anal pad. The scent-marking system of the small Indian mongoose appears to function in communication for mate acquisition, either between males or from males to females or both.

The overall larger size of males than females is common in mammals, usually owing to male competition for mates or territories, sometimes augmented by female choice of larger males (Darwin 1871; Clutton-Brock and McAuliffe 2009). Hyperallometry in the male anal pad, indicating male-specific or at least male-biased function, requires a more specific explanation. Previous studies have speculated that the anal pad aids in spreading scent from the anal glands (Gorman et al. 1974; Nellis and Everard 1983; Nellis 1989). This explanation is plausible considering the proximity of the fleshy projection to the scent-producing glands. Less clear is why these animals would need an external tool to aid in marking when many other mammals mark without one, and why it is markedly larger in males than in females even after controlling for body length. To our knowledge, this study is the first to investigate the anal pad in any mongoose species. Perhaps individuals with larger anal pads have an advantage in the maintenance of their own marks or in the propensity or efficiency of over-marking rivals. Over-marking, defined as placing a mark on or near a previously placed mark, functions mainly as a form of intrasexual competition and intersexual communication (Ferkin and Pierce 2007). Most studies have found that the top or most recent mark has the most influence on the response to the marks, suggesting a "masking effect" (Johnston et al. 1994, 1997*a*, 1997*b*; Ferkin and Pierce 2007). Over-marking is also suggested to be a signal of quality because of the time and energy required to monitor and update marks (Rich and Hurst 1999; Fisher et al. 2003). A male that can more effectively saturate an area might signal to conspecifics his quality or competitive ability. Although much research has investigated the acts of scent-marking and over-marking and the behavioral consequences of these acts, few studies have investigated the relative amount or surface-area coverage

Table 3. Eigenvalues and eigenvectors of the two principal components (PCs) that cumulatively accounted for 77% of the variation in the morphological traits of the small Indian mongoose (*Herpestes auropunctatus*; formerly *Herpestes javanicus*).

			Eigenvector of morphological trait							
PC	Eigenvalue	Variation explained (%)	Mass	Skull length	Body length	Tail length	RT canine length	RB canine length	LT canine length	LB canine length
PC1	4.81	60	0.39	0.40	0.37	0.25	0.38	0.32	0.39	0.30
PC2	1.33	17	0.17	0.23	0.23	0.47	−0.15	−0.46	−0.12	−0.56

Note: R, right; L, left; T, top; B, bottom.

Fig. 2. Linear regression of anal pad area against principal component 1 (PC1; body size) in male and female small Indian mongooses (*Herpestes auropunctatus*; formerly *Herpestes javanicus*).
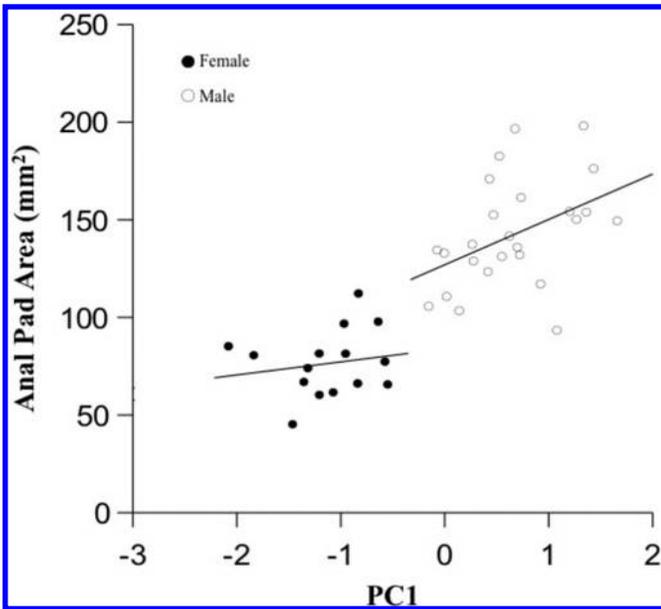
of scent that is actually placed on an object. The coverage of the mark or the investment of scent in it might influence responses and therefore functionality. A small mark over-marking a large mark might fail to be perceived as the top or more recent mark. Such effects are likely to be influenced by a number of factors including the status of the individual (Hobbs and Ferkin 2012) and the amount of time between marks. Perhaps, then, male small Indian mongooses with larger anal pads are able to more effectively over-mark and to reduce the likelihood of being effectively over-marked. If this hypothesis does indeed explain the existence of an anal pad and the male hyperallometry, we predict that these features will mainly be seen in species where over-marking is a consistent possibility. The high degree of home-range overlap and lack of territoriality in the small Indian mongoose, for instance, probably render over-marking more frequent because of the high probability of encountering conspecific marks than in a strictly territorial species for which neighbors are known and intrusions uncommon.

The epidemic anal gland disease in the males (but not females) in the study population might compromise the current function of anal scent marks. Veterinary literature describes anal sac (gland) disease as a secondary result of inflammation, infection, or obstruction of gland ducts (Washabau and Brockman 1995; Hedlund and Fossum 2007), but few cases have been documented from wild animals (but see Hamir 1998). The causes of this disease are unknown in the small Indian mongoose, but diet generally plays a role in dogs and cats (Vanduijkeren 1995). This disease could interfere with small Indian mongoose marking, either in terms of the delivery of the scent or the chemical messages en-

coded therein, which can include relatedness (Ferkin 1990), genetic similarity (Penn and Potts 1999), and condition (Zala et al. 2004). Unfortunately, however, no further information is known about the infection, as the contents of the anal glands were only visually inspected in the present study. One possibility is that the anal pad originally evolved as a sexually selected trait in the small Indian mongoose's ancestral range in South Asia, but that—either as a result of relaxed sexual selection or dietary changed following introduction (or both)—its functionality has been compromised by this disease in the Hawaiian population. This hypothesis could be tested in future research by comparing morphology or behavior between introduced and native populations, and by assessing the impact of different food types on anal gland function.

Acknowledgements

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