

Conservation implications of small Indian mongoose (*Herpestes auropunctatus*) predation in a hotspot within a hotspot: the Hellshire Hills, Jamaica

Delano S. Lewis · Rick van Veen · Byron S. Wilson

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Abstract This study documents impacts of the small Indian mongoose (*Herpestes auropunctatus*) on a threatened endemic fauna occurring in a biodiversity hotspot within a hotspot, the Hellshire Hills, Jamaica. We analyzed the stomach contents of 217 mongooses and supplemented this information with behavioural observations. The mongoose's diet consists primarily of invertebrates and lizards, but bird feathers, mammal hair, and a small number of seeds were also recorded. Invertebrates and lizards accounted for 93% of identified prey items. Of special concern were the remains of threatened species such as the recently re-discovered blue-tailed galliwasp (*Celestus duquesneyi*), indicating that the mongoose may represent a considerable threat to this poorly known taxon. Dietary analyses did not reveal remains of the Critically Endangered Jamaican iguana (*Cyclura collei*), yet field observations confirmed that the mongoose is a potent predator of hatchling iguanas. Ignoring issues

of sample size, this suggests that the analysis of stomach contents alone may mask important demographic impacts attributable to the mongoose (or other predator species). In other words, rare and endangered species may not be detected in diet samples, but the impact of predation may be of demographic significance for effected prey taxa. This study supports previous arguments concerning the negative impact of the mongoose on endemic insular species, and underscores the utility of employing field observations of mongoose foraging behaviour to provide important insights into the conservation implications of predation by non-native predators.

Keywords Extinction · *Herpestes auropunctatus (javanicus)* · Invasive Alien Species (IAS) · Jamaican Iguana · Mongoose · Predation

Introduction

The negative influence of invasive alien species (IAS) is second only to habitat loss as a source of endangerment and extinction among insular native biotas (Whittaker and Fernandez-Palacios 2007; Vitusek 1988). Many non-native species are restricted to degraded areas, but others have been able to invade natural habitats where they prey on, or compete with, native species. They can also introduce diseases to naturally occurring populations, so the potential loss of endemic biodiversity to IAS is of major concern.

D. S. Lewis · R. van Veen · B. S. Wilson (✉)
Department of Life Sciences, University of the West
Indies, Mona, Kingston 7, Jamaica
e-mail: byron.wilson@uwimona.edu.jm

D. S. Lewis · R. van Veen · B. S. Wilson
Jamaican Iguana Recovery Group, Kingston, Jamaica

Present Address:

D. S. Lewis
The McGuire Center for Lepidoptera and Biodiversity,
Florida Museum of Natural History, 34th Street & Hull
Road, PO Box 112710, Gainesville, FL 32611-2710, USA

These introduced species represent all major taxonomic groups, but impacts from non-native mammalian predators on insular faunas have been especially dramatic and well documented (e.g., Atkinson 1985; Coblenz and Coblenz 1985; Iverson 1978; Johnstone 1985; Tobin 1994; Tolson 2000; Urich 1931; Watari et al. 2008; Whittaker 1978; Wiewandt 1977). Indeed, island endemic species have proven to be extremely vulnerable to introduced predators, due in part to their long isolation from such “unnatural” predation, and a corresponding lack of evolved anti-predator adaptations (Honegger 1980; Lodge 1993; Yamada 2001).

The small Indian mongoose, *Herpestes auropunctatus* (formerly *H. javanicus*—see Patou et al. (2009) and Veron et al. (2007) for recent taxonomic clarification), is one of the most notorious of introduced predators, and is ranked among the world’s 100 worst invasive species (Lowe et al. 2000). Hereafter referred to simply as the mongoose, *H. auroreatus* is an opportunistic diurnal forager that will take a variety of animal (and some plant) species (Table 1), but appears to have impacted island reptiles and ground nesting birds most dramatically (Case and Bolger 1991). The mongoose was introduced to the island of Jamaica from Calcutta on 13 February 1872 for the control of rats on sugar cane plantations (Espeut 1882; Horst et al. 2001). In the original introduction, nine animals were released (four male and five females, one of which was believed to be pregnant) on the Spring Garden Estate in the Parish of Portland. The population expanded rapidly, and Jamaica soon served as a source for the introduction of the mongoose to other Caribbean and Hawaiian islands (Espeut 1882; Hoagland et al. 1989; Simberloff et al. 2000). This seemingly innocent introduction would prove to be extremely detrimental to the endemic faunas of Jamaica and other islands (Case and Bolger 1991; Henderson and Powell 2009; Powell and Henderson 2005; Schwartz and Henderson 1991).

On Jamaica alone, the extinction of six endemic vertebrates and the decline of various other species have been attributed to the introduction of the mongoose; however, little scientific evidence of this impact is available (Henderson 1992; Vogel et al. 1996). For example one lizard (Giant Galliwasp, *Celectus occiduus*) and one snake (Black Racer, *Alsophis ater*) both disappeared about the time of the mongoose introduction, as did three bird taxa

(Jamaican Petrel, *Pterodroma hasitata caribbaea*; Jamaican Uniform Crane, *Amaurolimnas concolor concolor*; Jamaican Poorwill, *Siphonorhis americanus*), and the one of the island’s two native land mammals (the Jamaican rice rat, *Oryzomys antillarum*) (Haynes et al. 1989; Raffaele et al. 1998). Other disappearances may also be attributable to the mongoose, but in no case is definitive evidence available. On the other hand, documented impacts on other islands have been incontrovertible. For example, on the Fijian islands of Viti Levu and Vanua Levu the mongoose was the principal agent in the extinction of seven species of ground nesting birds (Smith and Remington 1996; Watling 1982), and in Hawaii the mongoose eliminated honeycreepers by preying on their eggs and reducing their food base (Smith and Remington 1996). In the Caribbean, and in addition to several extinctions, a number of ground-inhabiting reptiles have been extirpated from main islands and persist only on small predator-free offshore cays (e.g., *Liophis cursor* from Martinique, *L. ornatus* from St. Lucia, and *Alsophis antiquae* from Antigua) (Corke 1992; Henderson 1992). Evidence of mongoose impacts on the native fauna of Amani Island (Japan) has been particularly compelling because the introduction was recent (1979); hence, these studies were contemporary rather than historical (Yamada 2001, 2002; Yamada and Sugimara 2004). Overall, the mongoose’s reputation as one of the most harmful introduced predators appears to be well founded (Barun et al. 2008; Case and Bolger 1991; Hays and Conant 2007; Lowe et al. 2000; Watari et al. 2008).

Of course, the mongoose has also contributed to the catastrophic decline or near extinction of other species on Jamaica. Thought extinct for much of the twentieth century, the Jamaican iguana was “re-discovered” in 1990, in the remote interior of the Hellshire Hills. The remnant population appeared to be heavily skewed toward older individuals, and mongoose predation on eggs and hatchlings was considered to be the leading cause of apparent low recruitment (Vogel 1994; Vogel et al. 1996). Based on the results of a Population and Habitat Viability Analysis (PHVA) conducted in 1993, a decision was made to reduce mongoose density within a core iguana conservation zone containing the two known communal nesting areas. This conservation concern was the impetus for the present study.

Table 1 Diet of *Herpestes auro punctatus* in previously reported studies

Study site		Mammal	Bird	Reptile	Amphibians	Invertebrates	Fish	Plant ^a
Africa	1					X		
Fiji	2	X				X		
Hawaii	3	X						
	4	X	X			X		X
	5	X						
Jamaica	6	X						
	7	X	X	X	X	X	X	X
	8	X						
	9	X	X	X		X		X
Korcula	10	X				X		X
Mauritius	11	X	X	X	X	X		X
Puerto Rico	12	X		X	X	X		
	13	X		X		X		X
	14	X				X		X
Puerto Rico and St. Croix	15			X	X	X		
Trinidad	16	X	X	X	X	X		
U.S. Virgin Islands	17			X				
West Indies	18	X	X	X	X			

¹ Eisner and Davis (1967) and Eisner (1968), ² Gorman (1975), ³ Pemberton (1925), ⁴ Baldwin et al. (1952), ⁵ Kami (1964), ⁶ Duerden (1896), ⁷ Hill (1897), ⁸ Cockerell (1901), ⁹ Current Study, ¹⁰ Cavallini and Serafini (1995), ¹¹ Roy et al. (2002), ¹² Pimentel (1955), ¹³ Vilella and Zwank (1993), ¹⁴ Vilella (1998), ¹⁵ Walcott (1953), ¹⁶ Williams (1918), ¹⁷ Nellis and Small (1983), ¹⁸ Myers (1931); X Present

^a Category include carrion and refuse

The specific objectives of this study were to describe the diet of the mongoose in an undisturbed dry forest ecosystem, and assess impacts on rare and threatened endemic species. Few previous studies have focused on mongoose diet in critically important wildlife areas, and instead have described the species' diet in moderately to highly modified habitats of correspondingly diminished conservation value (e.g., Gorman 1975; and see other references in Hays and Conant 2007). Finally, we address the question of whether the mongoose's reputation as a driver of past extinctions is warranted, and more importantly, whether the mongoose is likely to be the driver of future extinctions.

Materials and methods

Study area

This study was conducted in the central, least disturbed section of the Hellshire Hills dry limestone

forest (Vogel et al. 1996; Wilson and Vogel 2000). The area is characterised by two depressions formed by hydrological erosion along a north–south slip or collapse feature. These are among the most extreme of this landform feature in the Hellshire Hills and tend to contain the deepest soils. The larger depression contains one of the two known communal nesting sites of the Jamaican iguana; the other main nesting site is southwest of the depression's western slope. As a consequence, this small (1 km²) area of remnant forest is of major conservation importance, certainly for the iguana.

The Hellshire forest supports a rich Jamaican herpetofauna, including the Critically Endangered cave frog (*Eleutherodactylus cavernicola*), 12 species of lizards (notably the recently re-discovered Jamaican iguana and blue-tailed galliwasp), and four endemic snake species (Vogel et al. 1996; Wilson and Vogel 2000). The area is also an Important Bird Area (IBA), and is listed by the Alliance for Zero Extinction as one of ~600 sites worldwide that is

facing an imminent extinction (see Ricketts et al. 2005). By virtue of being located in a global biodiversity hotspot (Myers et al. 2000), the Hellshire Hills represent a hotspot within a hotspot.

Data collection

Trapping was conducted from May to June 1997, and resumed February 1998 until December 2000. In 1997 and 1998 traps were generally open and operational for 3 days a week, and were checked daily. Since May 1999 traps remained open throughout the year and were baited (salted herring) and checked regularly (every 1–3 days). Our trap loop consisted of 41 trapping stations using up to 50 standard (Havahart or Duke Single Door) mesh live traps. Captured mongooses were sacrificed (cervical dislocation), sexed, weighed, and stomach and intestinal samples were collected.

Stomachs and intestines of 217 mongooses were preserved in 70% alcohol. Seven stomachs that contained only bait were excluded from the analysis. One stomach contained a baby mongoose that was born in the trap and eaten by the mother under duress; this sample was also excluded from analysis. Food items were analyzed after being removed from the stomachs, sieved (to remove excess liquid), and dried in small plastic containers for 24 h at 77°C.

Incomplete prey remains were identified with the use of a stereoscopic dissecting microscope. A reference collection of prey types was used to classify partial prey items and to estimate their size. The majority of prey types had been previously collected in the area using pitfall traps (Wilson and Vogel 2000). Prey items were then placed into the following major taxonomic groups: mammals, birds, lizards, invertebrates, and plants. Mammals were classified to species based on comparison to reference hair samples; however, only crude estimates of their sizes (volumes) could be made using the average weight of individuals in the species, and approximating this to volume. Birds could not be identified (only small or finely chewed feathers were found); therefore, no estimate of their sizes was made. An estimate of their numbers was based simply on the number of stomachs containing feathers. Lizards were classified to species (*Anolis* were classified only to genus), and invertebrates to order or sub-order.

The snout-vent lengths (SVL) of lizards were estimated from remains, and their sizes calculated using the formula: $\text{Mass} = 0.000026 \times (\text{SVL})^3$ —based on a regression equation of mass vs. SVL in a sample of Jamaican lizards. The constant (X^3) was derived from the gradient of \log_{10} mass versus \log_{10} SVL regressions, which were approximately the same for all lizard taxa examined. Invertebrates were treated as cylinders since their basic body form is roughly cylindrical. Length and diameter were estimated, and size was calculated based on the equation for the volume of a cylinder. Plant material (seeds) could not be classified, so an estimate of their numbers was based simply on the number of stomachs containing seeds. No estimates of volumes were made for plants.

Behavioural observations

Behavioural observations were obtained while conducting related field work in the area, especially a radio-telemetry study focused on the ecology of hatchling Jamaican iguanas during 2004–2005 (van Veen et al., in preparation).

Results

Stomach content analyses

244 mongooses were captured between 3 May 1997 and 31 December 2000, and stomachs were collected from 217 individuals. Food items (consisting of incomplete prey remains) from 94 of the 217 stomachs analysed were classified into 327 prey items. Empty stomachs, or stomachs containing only bait (totalling 123 or 57%), were not included in the analysis. The number of prey individuals per stomach averaged 3.5 ± 0.2 and ranged from 1 to 17. The average prey volume was $2.97 \pm 0.51 \text{ cm}^3$ (excluding birds and plants) and ranged from 0.04 cm^3 (a coleopteran) to 90 cm^3 (a rat). The average volume of prey per stomach was $9.96 \pm 1.76 \text{ cm}^3$ and ranged from 0.13 to 99.91 cm^3 . Multiple prey individuals were present in 82% of the stomachs, with five stomachs containing more than six individual prey items. Mongoose mass and the total number of prey were significantly correlated (Spearman Rank Correlation; $P = 0.02$, $r_s = 0.14$); there was no correlation

between mongoose mass and total volume of prey, sex and total number of prey, or sex and total volume of prey (Spearman Rank Correlations; $P = 0.19$, $P = 0.35$, and $P = 0.66$, respectively).

Of the 327 prey individuals, lizards represented 45%, invertebrates 48%, birds 4%, mammals 2%, and plants 1%. The 146 lizards consisted of *Anolis* spp. (42%), *Celestus cruscus* (33%), *Mabuya sloanii* (14%), and *Celestus duquesneyi* (11%). Invertebrate prey consisted primarily of orthopterans (62%). The remaining invertebrates were coleopterans (15%), hymenopterans (11%), scorpions (8%), centipedes (3%), and lepidopterans (1%). Lizards accounted for 50% of the prey composition by volume; mammals accounted for 33%; the remaining 17% were invertebrates. Among lizards, *C. cruscus* accounted for 34% by volume, *Anolis* spp. 25%, *M. bistrriata* 21%, and *C. duquesneyi* 20%. Orthopterans, coleopterans, and scorpions represented the largest volumes for invertebrates (37, 32, and 21%, respectively), with the remaining invertebrates accounting for only 10% (hymenopterans 6%, centipedes 3%, and lepidopterans 1%) (Table 2).

Behavioural observations of mongoose foraging

Notable mongoose foraging observations include the following:

1. On one occasion between 1245 and 1315 h a mongoose was flushed from within the home range of a hatchling iguana that was being closely monitored with radio-telemetry. The mongoose took refuge in the forest, but returned ~20 min later and began methodically investigating known retreat hides of the iguana (hollows in low branches). The mongoose investigated all hides known to the investigator, and ultimately focused its attention on an unknown retreat site; on examination, this hitherto unknown retreat site contained the transmitterd iguana.
2. In another instance, a transmitterd hatchling iguana was tracked to the mouth of a mongoose, which then ran a short distance and disappeared into a hole in the limestone substrate.
3. Mongooses (or their tracks) have been noted entering active iguana nests, so they clearly represent a predator of eggs as well as hatchling and juvenile iguanas.

Table 2 Proportions of mongoose prey categories by numbers and volume (cm³)

Prey categories	Numbers	%	Volumes	%
Mammals				
Rats	3	0.9	270	29.2
Mice	2	0.6	40	4.3
Lizards				
<i>Anolis</i> sp.	62	19.0	114.8	12.4
<i>Celestus cruscus</i>	48	14.7	155.5	16.8
<i>Celestus duquesneyi</i>	16	4.9	94.1	10.2
<i>Mabuya sloanii</i>	20	6.1	95.8	10.3
Invertebrates				
Centipedes	5	1.5	4.9	0.5
Coleoptera	24	7.3	49.6	5.4
Hymenoptera	18	5.5	10.1	1.1
Lepidoptera	2	0.6	0.9	0.1
Orthoptera	99	30.3	57.9	6.3
Scorpions	13	4.0	32.2	3.5
Birds	12	3.7	NE	NE
Plants	3	0.9	NE	NE
Total	327	100.0	925.8	100.0

4. A mongoose was observed foraging on the common *Anolis lineatopus* in coastal vegetation around 2–2.5 m high. Over a roughly 4-min period the mongoose attacked four individual *A. lineatopus*, capturing and consuming two of them. This observation not only illustrates the predatory prowess of the mongoose, but also confirms that they will forage above ground, in the vertical matrix that constitutes the preferred habitat of hatchling and juvenile iguanas.
5. Direct observations of mongooses raiding sea turtle nests along the coast bordering the iguana forest further attest to the voracity of the mongoose as a predator of reptile eggs.

Discussion

Our analysis of stomach contents confirms that the mongoose is a voracious predator of lizards and invertebrates that also forages opportunistically on birds, rodents, and vegetation (fruit) (Table 2). In addition to preying on common Jamaican species such as *Anolis* lizards, the mongoose also preys on

relatively rare and threatened species, such as the skink (*Mabuya sloanii*), and the recently re-discovered Blue-tailed Galliwasp (*Celestus duquesneyi*) (Wilson and Vogel 2000). However, several notable taxa were absent from these stomach samples, including the Jamaican iguana, and the four endemic snake species that occur in the area. Of special conservation interest are field observations confirming the importance of the mongoose as a predator of species that were not detected in the dietary analyses—particularly the endemic and Critically Endangered iguana.

Failure to find iguana remains in our sample of mongoose stomachs was perhaps unsurprising: the iguana is exceedingly rare, the availability of hatchlings is seasonal, and even at >200 mongooses examined for prey remains, our sample size was ultimately not sufficient for detecting the presence of such a rare prey species. On the other hand, field observations indicate that the mongoose is an exceptionally potent predator of young iguanas. The mongoose apparently remembers the location of iguanas it encounters; thus, even if an initial attack is avoided, a detected iguana is likely to be subjected to repeated, systematic hunting effort in the future. The loss of hatchling iguanas to the mongoose was further demonstrated in a complementary study of hatchling ecology, which indicated that mortality of young iguanas due to mongoose predation was extraordinarily high (Wilson and van Veen 2005).

Four endemic snake species occur in the Hellshire Hills, but incidental encounter rates and pitfall trapping results suggest that none of them are common (Wilson and Vogel 2000). Hence, like the iguana, snakes are likely consumed by the mongoose, but their representation in the mongoose's diet is low. Nevertheless, as for the iguana, the demographic consequences of mongoose predation for snake populations may be substantial, and may help explain the apparent rarity of these taxa.

This study supports previous arguments concerning the threat of the mongoose to endemic wildlife on Jamaica and elsewhere, and in particular, provides graphic evidence confirming the extreme vulnerability of young iguanas to this unnatural source of heavy mortality. Because the mongoose is common in the Hellshire Hills, it likely represents the most important mammalian predator in this Caribbean dry forest hotspot (see Myers et al. 2000; Ricketts et al.

2005). Given the precarious status of the iguana, and the presence of other threatened endemic species, this study underscores the importance of maintaining a mongoose control programme in a core conservation zone. Fortunately, the mongoose is easily trapped (Coblentz and Coblentz 1985; Nellis and Everard 1983; Roy et al. 2002; Yamada 2002), and abundance can be reduced dramatically with continuous trapping. For example, our initial trapping effort (1997) resulted in the removal of 7 mongooses per 100 trap days, but subsequent (1998) trapping efforts resulted in the removal of only 0.25 mongooses per 100 trap days—a difference exceeding an order of magnitude. Moreover, observations of mongooses are rare in the trapping area yet remain common outside of it; in addition, a heavy male bias among trapped animals suggests that we are trapping primarily dispersing males, which is consistent with post-trapping recolonization (Roy et al. 2002). Most encouragingly, recent results indicate that the remnant iguana breeding population in Hellshire has more than doubled since mongoose control was initiated (Wilson and van Veen 2008). And, while other conservation activities (e.g., “headstarting” and release) have doubtless contributed to demographic recovery of the iguana, the benefits of mongoose control appear clear: new recruits from the wild population in the mongoose-controlled area can only be explained by enhanced survival among younger age classes. Demonstration of the efficacy of mongoose control has important conservation implications, because it points to the potential utility of this management activity in other areas containing vulnerable or threatened native species (e.g., Coblentz and Coblentz 1985).

The ‘mongoose problem’ re-visited

Despite much published evidence that it has been a major contributor to the decline and extirpation of insular fauna, the mongoose has had its defenders. For example, Corke (1992) noted that among-island correlations between mongoose presence and the extinction or extirpation of Lessen Antillean snakes were confounded by other contributing factors, such as island size, and human population density. Corke (1992) concluded that the evidence implicating the mongoose in historical extinctions was equivocal, and that purported impacts could just as easily be

explained by other IAS or by persecution. Corke (1992) also argued that if the mongoose was responsible for historical extinctions, then prey species that survived the original onslaught were no longer at risk. Hays and Conant (2007) also considered the historical case against the mongoose to be equivocal, and argued that the impacts of this IAS had been exaggerated. They also highlighted the difficulty of attributing extinctions to a single IAS predator when more than one such species is present. However, rhetorically sound such arguments may be, they are potentially damaging if they diminish legitimate concern over mongoose impacts on globally threatened species.

First, the evidence against the mongoose is considerable, and continues to grow (see references above). And though the mongoose may not have been responsible for every extinction or extirpation it is accused of precipitating, a likely contributory role appears clear in a large number of examples. The argument that species that have co-existed with the mongoose in the past are no longer at risk of extinction is weak. As population size and suitable habitat contract due to other anthropogenic assaults, such species become increasingly vulnerable to extinction by any cause. Thus, in spite of over a century of previous co-existence with a particular prey species, the mongoose could still ultimately deliver the final blow to its persistence. We are of the opinion that this is precisely the predicament in which we now find the Jamaican iguana, and perhaps the Blue-tailed galliwasp as well.

Conclusions and recommendations

Our results indicate that the mongoose continues to represent a threat to the persistence of endangered endemic species in a remote insular hotspot. Related work has demonstrated significant demographic recovery of one Critically Endangered species (the iguana), due at least in part to an on-going mongoose control programme. Accordingly, we argue that such removal trapping programmes may be crucially important in averting future extinctions. Such control programmes should be encouraged—and funded. If funding agencies were to advertise their willingness to fund control activities (many do not), this might

encourage researchers and other conservationists to engage in this critical intervention. Such activities can be integrated into existing conservation and management programmes for a comparatively small additional investment. If support is available for sustained conservation efforts, incorporation of a continuous trapping programme can be extremely cost effective; indeed, if population size is critically low, the cost of control activities can be more than cost effective (Engeman et al. 2003b). Arguments that removal trapping is ineffective because of re-colonization (e.g., Hays and Conant 2007) are vacant; recolonization will of course occur, which is precisely why trapping programmes must necessarily be continuous. The question is not whether trapping can be effective, but whether the associated costs are justified by the conservation value.

Given the documented efficacy of predator control in recovering threatened species (e.g., Basse et al. 2003; Engeman et al. 2003a; Harding et al. 2001; Innes et al. 1999; Moorhouse et al. 2003; Pierce and Westbrooke 2003), such efforts have been relatively uncommon. To be sure, predator control is not a pleasant activity, nor is it uncomplicated (Courchamp et al. 2003). So, in spite of the demonstrated utility of control efforts, many studies continue to monitor threatened prey species without directly addressing the source of endangerment. Put simply, measuring an animal or inserting a PIT tag, or documenting population parameters, will not enhance survival prospects or population viability: removing the source of endangerment will. We recommend the incorporation of control efforts into endangered species programmes when predation by IAS has been identified as a major source of population loss. But we caution that such activities can be problematic (Courchamp et al. 2003), and should only be implemented within the context of an adaptive management approach. For example, our work in the Hellshire Hills has paid rich conservation dividends with no discernable negative outcomes (e.g., increased rodent densities); this is because insights gained from continuous monitoring efforts have guided programme expansion, and suggest that further expansion would be of significant conservation value. Unfortunately, larger-scale control or eradication will likely await the availability of a mongoose-specific chemical control agent (see Roy et al. 2002).

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