Decline in Population Density and Group Size of Mona Monkeys in Grenada

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Abstract: Mona monkeys (*Cercopithecus mona*) were introduced from West-Central Africa to the Caribbean island of Grenada about 250 years ago. Little is known, however, about the recent trends in size and conservation status of this non-native primate population. We estimated the population density and abundance of mona monkeys in and around the forested areas located in central Grenada (including the Grand Etang National Park). We used repeat line transect distance sampling, a standard method for census surveys of forest-dwelling primates. The estimated group density, individual density, average mixed-sex and all-male group sizes, and total population size throughout the rain forest habitat on the island were 0.7 group/km², 6.0 individuals/km², 10.3 ± 3.0 individuals/mixed-sex group, 2.1 ± 0.3 individuals/all-male group, and 289 individuals, respectively. The comparison of these values with those obtained from a previous study conducted 20 years ago, in the same area and with the same method, showed a marked population decline. This decrease may be explained by the ecological devastation of Hurricane Ivan in 2004, combined with persistent over-hunting. We discuss the theoretical implications of this study for evolutionary processes and biodiversity patterns.

Key Words: distance sampling, population density, hurricane, hunting pressure, bushmeat, pet trade, introduced primates, *Cercopithecus mona*

Introduction

Accurate and updated information on the status and trends of primate populations is a prerequisite for successful conservation programs (Plumptre and Cox 2006). Evidently, most conservation efforts consist in preserving the diversity of species and subspecies in their native habitats (Dobson and Lyles 1989). However, knowledge of non-native primate populations, i.e., those introduced outside the species' native range as a direct or indirect consequence of human action (Heinsohn 2003), can also have major implications for conservation issues and further our understanding of evolutionary patterns and processes (Schlaepfer *et al.* 2011).

Research on differences in the ecology, demography, life history, behavior, genetics, and health status between native and non-native primate populations provides valuable information with regard to habitat disturbance (González-Martínez 2004), phenotypic plasticity (Corlett 2004), genetic diversity (Aarnink *et al.* 2014), phylogenetic inertia (Sol *et al.* 2008), biogeographic history (Denham 1987), hybridization/speciation (Oliveira and Grelle 2012), pathogen transmission (Hamilton *et al.* 2014), and conservation strategies (Hernandez-Pacheco *et al.* 2016). Therefore, even though a major tenet of conservation management holds that non-native animals are ecologically harmful, recent research suggests some introduced primate species can have beneficial impacts, and at least, a heuristic value.

This is particularly true for relatively small, inbred primate populations, historically introduced to island ecosystems. Examples include: green monkey species, *Chlorocebus sabaeus*, introduced to the West Indian islands of Anguilla, Barbados, Nevis, Saint Kitts, and Saint Martin (Denham 1987); long-tailed macaques, *Macaca fascicularis*, introduced to the island of Mauritius (Sussman and Tattersall 1986), and across (east of) Wallace's Line into Papua and the Lesser Sundas (Heinsohn 2001); East Javan langurs, *Trachypithecus auratus*, into Lombok (Heinsohn 2001); and rhesus macaques, *Macaca mulatta*, and patas monkeys, *Erythrocebus patas*, introduced to Puerto Rico (González-Martínez 2004). After a founder event, such as the arrival of a few members from an original population onto an island, the founding population experiences a bottleneck (i.e., a loss in genetic diversity due to a reduction in population size and geographic isolation for several generations) and is more vulnerable to genetic drift (Nei *et al.* 1975). This is why island ecosystems are excellent models for research on evolutionary processes and biodiversity patterns (Vitousek *et al.* 1995).

Mona monkeys (*Cercopithecus mona*) were introduced to the Caribbean island of Grenada from West-Central Africa during the slave trade. Although we lack direct historical information about their exact date of introduction, the most likely scenario based on trade patterns covers a range of dates between the late 1600s and 1807, most probably in the mid-1700s (Glenn 1996; Glenn and Bensen 2013). A recent genetic study, using a mitochondrial DNA analysis, showed that the total founding population of mona monkeys introduced to Grenada was extremely small, and originated from the island of São Tomé, Gulf of Guinea, rather than directly from mainland Africa (Horsburgh *et al.* 2002). This complex history of introduction makes the Grenadian mona monkeys good candidates for the study of ecological flexibility in fragmented habitats and speciation processes (Glenn and Bensen 2013).

Even though mona monkeys are still the only nonhuman primates on Grenada island today, the insular population trend is unknown. Two first surveys were conducted in 1987 and 1989 (Lippold 1989), but the information was not systematically collected, as it was based on opportunistic sightings in different locations, and possibly not reliable, as some population estimates were drawn from interviews with hunters (cf. Glenn 1996). The only reliable evaluation of the mona monkey population density in Grenada comes from a five-month survey conducted in 1994 and 1995 that used the repeat line-transect distance sampling technique; this study found that the population density estimate averaged 42.1 ± 35.7 individuals/km², and the extrapolated island-wide population estimate was 2,021 individuals based on the cover of available forested areas (Glenn 1998). However, assessing population trends requires at least two data points (ideally more) obtained several years apart and using the same methodology (e.g., Leca *et al.* 2013).

An updated demographic assessment is necessary for three reasons. First, unlike most other non-native insular primates that are considered invasive (Sussman and Tattersall 1986; Denham 1987; González-Martínez 2004), local biological and socio-economic effects of the mona monkeys in Grenada have not been quantified and are largely unknown. Even though the monkeys occasionally raid crops, particularly in the agricultural areas along the forest edge (Glenn 1996), no cost-benefit analysis is available. In light of the aforementioned valuable scientific information derived from small, inbred, insular populations, the conservation status of the mona monkeys of Grenada should be monitored regularly.

Second, although the mona monkeys of Grenada have few food competitors and no animal predators, they face the major anthropogenic threat of persistent and considerable hunting. For decades, the monkeys have been extensively hunted for bushmeat, served at local restaurants and food fairs (Lippold 1989; Glenn 1998). Recently, adult monkeys have also been hunted for the purpose of capturing live youngsters to sell them as pets (Michael Sanderson, pers. comm.). However, there is a disagreement on whether such intense hunting rates are sustainable (Bensen and Glenn 1997) or represent a risk for the future of this non-native primate in Grenada (Lippold 1989). Third, this monkey population recently faced a natural disaster that might have led to another bottleneck effect: the devastation of most of the forested habitat on the island by Hurricane Ivan in 2004 (Glenn and Bensen 2008). A post-Ivan demographic evaluation of their population is needed, in order to assess whether a management program should be put into practice for the survival of these introduced monkeys (Levy 2005).

Figure 1. Adult male mona monkey, *Cercopithecus mona*, in the Grand Etang National Park (photo by N. Gunst).

This study aimed to evaluate possible demographic changes in the population of mona monkeys (Fig. 1) in and around the forested areas located in central Grenada (including the Grand Etang National Park). The demographic parameters estimated include group and individual densities, group size, and total population size. We discussed our results from the perspective of the threats faced by the mona monkeys in Grenada, and suggested management plans for the protection of this primate population.

Methods

Study species

The mona monkey is a forest-dwelling arboreal guenon, originally ranging in West-Central Africa (i.e., Benin, Cameroon, Ghana, Nigeria, and Togo), inhabiting a variety of forested habitats, and exhibiting an omnivorous diet (Matsuda Goodwin 2007; Glenn *et al.* 2013). It forms one-male multi-female groups, multimale-multifemale groups, and all-male groups (Glenn, 1996; Matsuda Goodwin 2007). Solitary males also occur (Glenn 1996, 1997; Matsuda Goodwin 2007).

Data collection

This study was conducted over two months in March and April 2014, and in two types of habitats in central Grenada:

(1) forested areas, including the Grand Etang National Park and Forest Reserve, covering approximately 1,540 ha of montane tropical rain forest between 340 and 710 m above sea level, and (2) cultivated areas along the forest edge, between 220 and 410 m above sea level (Table 1, Fig. 2; cf. Glenn 1996 for further information about habitat types in central Grenada).

On a daily basis (except on rainy days) between 6:30 am and 4:30 pm, NG and JBL used the repeat line-transect distance sampling technique, with records of the perpendicular distances from the transect line to the estimated center of the group of the study subjects (Buckland *et al.* 1993). Successive walks on the same transect were separated by at least 48 hours. Observers walked on the transects at a constant speed of 1.5 km/h, looking ahead and sideways to detect the monkeys, and occasionally using binoculars to determine group sizes.

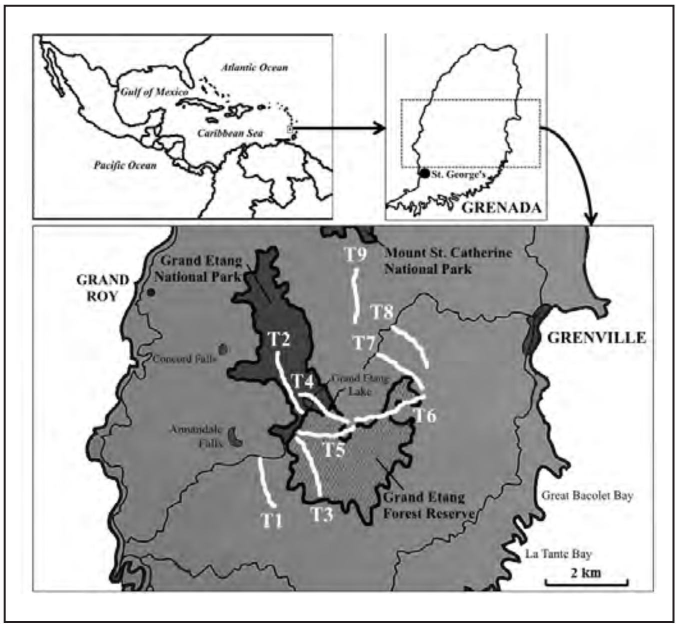

Figure 2. The study site in Grenada showing the location of the nine survey transects.

We used a pen and paper and a Garmin GPSmap 60CSx to record, for each encounter, the following data: (1) time, (2) GPS coordinates of the detection point on the transect, (3) the perpendicular distance, estimated by eye, from the transect line to the position on the ground directly under the center of the group of individuals, and (4) the number of individuals detected during each encounter (referred to as group size). We used the term "group" to refer to a cluster/aggregation of mona monkeys at a given moment in time, and that were located within a maximum of 300 m of each other (cf. Matsuda Goodwin 2007). During our transect walks, we also recorded the presence and location of anthropogenic activities or artefacts (e.g., possible hunting activity as inferred by fresh dog footprints and recently discarded empty shell cases). We sampled a total of nine transects throughout the study area (covering 10.3 km²; Table 1, Fig. 2) and the distance surveyed was 173.3 km.

We recorded perpendicular distance data by categorizing them into 13 distance intervals, namely 0−5 m, 5−10 m, 10−15 m, 15−20 m, 20−25 m, 25−30 m, 30−40 m, 40−50 m, 50−60 m, 60−70 m, 70−80 m, 80−90 m, and 90−100 m. To ensure that perpendicular distances would be estimated accurately, observers were trained on evaluating distances by eye prior to the onset of the study (cf. Leca *et al.* 2013). Data collection started only after they reached 95% accuracy. We recorded a total of 46 encounters during the transect walks. An encounter was defined as the visual detection from the transect of at least one individual monkey. This research adhered to the legal requirements of the Republic of Grenada.

Data analysis

The perpendicular distances that we measured were used to estimate a detection function (i.e. the probability that a monkey is detected, as a decreasing function of its distance from the line), which in turn, allows for the calculation of the density of monkeys (or groups of monkeys) in the study area (Buckland *et al.* 1993). In order to provide estimates of density and abundance of mona monkeys in the study area,

Table 1. The nine transects surveyed, with the two main habitats encountered, number of times (N) walked, transect length (km), and total distance sampled (km). [a] Lower montane forest (between 340 and 400 m elevation); [b] Upper montane forest (between 500 and 710 m elevation); [c] between 220 and 410 m elevation.

Transect	Transect name	Main habitat	N walked	Length km	Total walked km
T1	Black Forest	Montane forest[a]	11	1.0	11.0
T2	Mount QuaQua	Montane forest[b]	17	1.5	25.5
T3	Après-Toute	Montane forest[b]	18	1.0	18.0
T4	Shoreline	Montane forest[b]	19	1.5	28.5
T5	Cross Trail	Montane forest[b]	20	1.3	26.0
T6	Seven Falls (down)	Montane forest[b]	19	1.1	20.9
T7	Seven Falls (up)	Cultivated area[c]	18	1.0	18.0
T8	Gangadee	Cultivated area[c]	11	1.0	11.0
T9	Spring Garden	Cultivated area[c]	12	1.2	14.4
Total	-		145	-	173.3

we used the computer software program Distance 6.0 (Buckland *et al.* 1993). Our sample of encounters reached the size required by this program, i.e. at least 40 encounters for fitting the detection function (cf. Buckland *et al.* 1993).

We examined the distribution of distances and found that no data were collected beyond 50 m. Therefore, no extra adjustment terms—sometimes required to fit a long tail to the detection function (Leca *et al.* 2013)—were necessary, and we did not truncate our distance data prior to analysis (Buckland *et al.* 1993). To estimate the mean group size, we averaged the number of individuals detected (i.e., seen not heard) during our 46 encounters. The encounter rate was defined as the number of groups detected per unit length of transect, i.e. per kilometer walked. After testing different detection function models, we selected the one that best fit our data set, based on well-established criteria (cf. Buckland *et al.* 1993): the half-normal key with cosine adjustments.

Results

Estimates of group and individual densities, group size, and estimated total population size

We plotted the detection function, superimposed on the histogram showing the detection probability as a decreasing function of the distance from the transect line to the monkeys detected (Fig. 3). The result of our chi-square goodness-of-fit test ($\chi^2 = 1.94$, df = 5, p = 0.858) showed that the model selected fit our data well (cf. Buckland *et al.* 1993).

The detection function allowed for the calculation of the main estimated values for our study of the population density and abundance of mona monkeys in and around the forested areas located in central Grenada. In the 10.3 km² of study area, we found, on average, 0.7 ± 0.1 group/km² and 6.0 ± 1.5 individuals/km². The estimated number of individuals in the study area was 62 ± 13. Based on the assumption that the population density of mona monkeys was constant across all rain forested areas in Grenada (covering approximately 48 km²; cf. Glenn 1998), the projected island-wide total population estimate was 289 individuals. Of the 46 encounters during the transect walks, we recorded 30 mixed-sex groups (mean group size: 10.3 ± 3.0 individuals/group, range: 5−15), nine all-male groups (2.1 ± 0.3 individuals/group, range: 2−3), and 7 solitary males.

Spatial distribution of mona monkeys in and around the forested areas of central Grenada

Table 2 shows the group abundance and size in the different transects sampled. This preliminary assessment of the spatial distribution of mona monkeys in the study area showed statistically significant local differences in the mean numbers of encounters per km walked (Chi-square goodness-of-fit test: $\chi^2 = 78.67$, df = 8, p < 0.001) and individuals detected per km walked ($\chi^2 = 658.02$, df = 8, p < 0.001). With regards to the mean number of encounters/km, the lowest values were

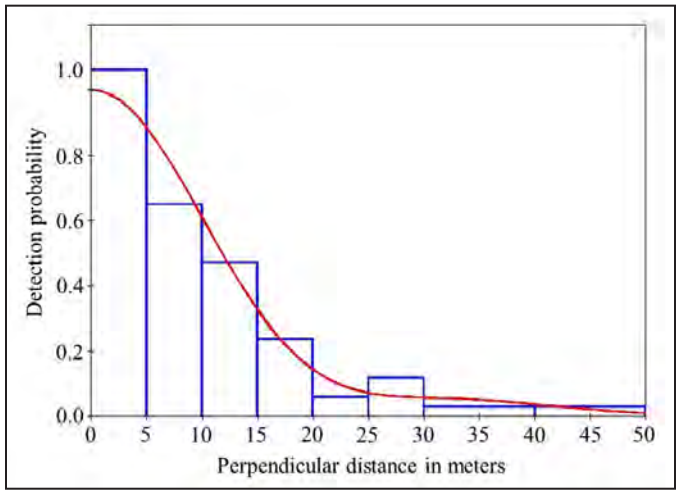

Figure 3. Histogram showing the detection probability as a function of the perpendicular distance from the transect line (interval distances), as generated by the analytical program Distance 6.0. The curve represents the detection function obtained with the detection function model that best fit the data.

Table 2. Cumulative and mean numbers of encounters and individuals detected in the different transects sampled ([a] encounters include groups and solitary individuals).

Transect	Total number of encounters[a] (cumulated over visits)	Mean number of encounters[a] per km	Total number of individuals detected (cumulated over visits)	Mean number of individuals detected per km	Mean ± SD (min-max) number of individuals detected per encounter[a]
T1	3	0.27	33	3.00	11.0 ± 1.7 (10-13)
T2	5	0.20	9	0.35	1.8 ± 0.4 (1-2)
T3	5	0.28	37	2.06	7.4 ± 3.6 (2-11)
T4	10	0.35	68	2.39	6.8 ± 5.5 (1-15)
T5	5	0.19	30	1.15	6.0 ± 4.8 (1-11)
T6	8	0.38	67	3.21	8.4 ± 2.7 (3-11)
T7	2	0.11	2	0.11	1.0 ± 0.0 (1-1)
T8	3	0.27	37	3.36	12.3 ± 0.6 (12-13)
T9	5	0.35	53	3.68	10.6 ± 6.2 (2-15)
Total	46	0.27	336	1.94	7.3 ± 4.8 (1-15)

found on transects T7, T5, and T2, and the highest values on T4, T9, and T6 (Table 2). With regards to the mean number of individuals detected/km, the lowest values were found on transects T7, T2, and T5, and the highest values on T6, T8, and T9 (Table 2).

We also found significant local differences in the estimated mean group sizes across transects ($\chi^2 = 16.55$, df = 8, p = 0.035). The smallest group sizes were recorded on T7 and T2, and the highest group sizes were recorded on T9, T1, and T8 (Table 2).

Effect of potential anthropogenic disturbance on the encounter rate

During our transect walks in the forested areas, we recorded 20 spots or artefacts of potential anthropogenic disturbance (e.g., indirect evidence of hunting activity as inferred by fresh dog footprints and recently discarded empty shell cases; four spots/artefacts on T3, five on T4, five on T5 and six on T6). The occurrence of such signs of anthropogenic disturbance significantly decreased the encounter rate on the same day (Mann-Whitney U test: z = -3.32, p = 0.001). We never encountered mona monkeys on a trail where we found indirect evidence of recent hunting activity.

It is also noteworthy that the temporary presence of the military in the Grand Etang National Park, including soldiers setting up camp around the T2 and T4 transects for about 10 days during the study period, resulted in a lower encounter rate in this area during this particular sub-period (mean number of encounters/km during the military presence: 0.15, versus 0.31 before the military presence, and 0.38 after the military presence). However, the difference in the encounter rate across these three sub-periods was not statistically significant (Kruskal-Wallis test: $\chi^2 = 4.3$, df = 2, p = 0.114).

Discussion

With regards to the demography of the mona monkeys in central Grenada, all the estimated values provided by the current study were markedly lower than those found 20 years before by Glenn (1998): (1) the estimated group density was 0.7 group/km² in 2014 versus 2.3 groups/km² in 1995, that is a 70% decrease; (2) the estimated individual density was 6.0 individuals/km² in 2014 versus 42.1 individuals/km² in 1995, that is a 86% decrease; and (3) the projected island-wide total population estimate was 289 individuals in 2014 versus 2,021 individuals in 1995, that is a 86% decrease. Moreover, the estimated mixed-sex group size was 10.3 individuals/group in 2014 versus 18.0 individuals/group in 1995 (Glenn 1997), that is a 43% decrease. Overall, the direct comparison of our current data with findings obtained 20 years before in the same area and with the same sampling method leads to the conclusion that there has been a marked decrease in the group and individual densities, group size, and overall abundance of the mona monkey population between these two points in time.

The decrease in group size of non-habituated mona monkeys over the past 20 years, also confirmed by long-term forestry staff (Kester Charles, pers. comm.) is particularly alarming. The current average size of mixed-sex groups is also lower than that estimated at Lama Forest, Benin (13.3 individuals/group: Matsuda Goodwin 2007). In guenons (including mona monkeys), there may be a minimum group size—defined as the minimum number of individuals in a group necessary for continued functioning of the group—below which the entire population may be at risk of extinction (Young and Isbell 1994).

Despite the claim by the forestry staff that the recent decrease in primate encounters and group size was not seasonal (Kester Charles, pers. comm.), we cannot definitely rule out any seasonal effect. Indeed, our survey was conducted during the dry season, with relatively low fruit availability in the montane forest areas (Glenn 1996). It could be argued that several groups of monkeys had moved from the Grand Etang National Park to lower elevations to find more abundant food patches. However, our results on the spatial distribution of mona monkeys did not show a clear pattern of higher densities in cultivated areas than in the montane forest (Table 2).

On September 4, 2004, Hurricane Ivan devastated most of the island of Grenada, including the forested areas of the Grand Etang National Park and Forest Reserve that were completely flattened (Levy 2005; Glenn and Bensen 2008). Even though no demographic study has been conducted in the immediate aftermath of Hurricane Ivan, it is likely that the majority of the mona monkey population was wiped out during the storm (Glenn cited in Levy 2005). In the weeks following this natural disaster, there were many reports of hungry mona monkeys being driven into the streets of mountain villages and sometimes accidentally run over by cars or shot to prevent them from stealing food (Levy 2005). The combination of massive die-offs following Hurricane Ivan and the forced movement of the surviving monkeys into unfamiliar and dangerous areas may have put severe restrictions on the viability of the mona monkey population in Grenada.

Previous studies have shown that local habitat devastation associated with powerful tropical cyclones generally lead to population reduction, decrease in group size, social disorganization, and behavioral changes in ranging and foraging activities in nonhuman primates (Dittus 1985; Pavelka *et al.* 2003). Even though these dramatic effects are generally temporary (Pavelka *et al.* 2003), any concomitant hunting pressure could put primate populations at increased risk of extinction (Young and Isbell 1994).

Even though a two-year hunting moratorium was decided by the Wild Game and Conservation Association of Grenada in the aftermath of Hurricane Ivan, its implementation and effect were impossible to assess due to the lack of systematic wildlife monitoring on the island (Michael Sanderson, pers. comm.). According to the Forestry Department, the mona monkey hunting season is typically open from October through December and only outside the Grand Etang National Park. Former and current hunters, however, harvest mona monkeys throughout the year, and there are no guards to monitor the protected areas in Grenada (Glenn 1997). Although we did not record any direct evidence of hunting, we recorded a series of indirect indications for a persistent hunting pressure, including in the protected areas of the Grand Etang National Park and Forest Reserve: (1) fresh dog footprints and recently discarded empty shell cases in the protected forested areas, (2) accounts from several interviewed hunters, who often team up and mainly use shotguns to kill monkeys of all age and sex classes, and occasionally use dogs to retrieve dead individuals, and (3) the recent account of the killing by a hunter of a free-ranging but resident male mona monkey around Annandale Falls (Row Murrell, pers. comm.). Moreover, our results showed that hunting artefacts were associated with a decrease in the mona monkey encounter rate. In line with the considerable hunting pressure on the mona monkeys in the mid-1990s (Glenn 1997), two of the hunters we interviewed confirmed that the harvest rate was substantial and were concerned about the viability of the monkey population in Grenada in the near future. However, with few hunters interviewed, much caution is required when discussing a trend in hunting over time.

In Grenada, there is no subsistence hunting of mona monkeys, nor any organized monkey meat market. However, monkey meat is considered a delicacy by some Grenadian people and often consumed in abundance during special celebrations in a few local restaurants and at regular “wild meat fairs” in Black Bay Beach, West Grenada (Kester Charles, pers. comm.). Inextricably linked to the bushmeat trade is the sale of orphaned mona monkeys as pets, which has recently become a major concern in Grenada (Michael Sanderson, pers. comm.). Many wealthy residents and foreign students acquire young monkey pets (sold for up to US$1,100 and advertised via flyers in touristic areas; N. Gunst, pers. obs.), which is legally allowed on the island. As part of the exotic pet trade, mona monkeys are also exported from Grenada upon the agreement of the Forestry Department (Anthony Jeremiah, pers. comm.). Such a frequent demand for young monkey pets had led several local hunters to specialize in killing adult members of a group in order to catch a live infant (Michael Sanderson, personal communication).

Overall, the current population decrease is probably the consequence of the ecological devastation of Hurricane Ivan in 2004, combined with persistent over-hunting. To better monitor the population dynamics of the mona monkeys in Grenada, we urge for the replication of the same study design in the same area, at least every five years. Although this primate species is able to cope with a certain degree of habitat disturbance and appears to be resilient to hunting (Linder and Oates 2011), it is not clear whether this primate population can sustain such a dramatic decline. Introduced free-ranging animals can be grouped into three categories, depending on whether their local biological and socio-economic effects are deemed mainly negative, positive, or neutral/unknown (Schlaepfer *et al.* 2011). Until a quantitative cost-benefit analysis is conducted on the mona monkeys of Grenada, they should be grouped into the third category before contemplating any population management plan. Considering the wealth of scientific information derived from small inbred insular populations, “it may not be a lost cause to conserve very small populations of forest primate species in habitat fragments” (Glenn and Bensen 2013; p. 413).

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Literature Cited

Aarnink, A., B. Jacquelin, A. Dauba, S. Hébrard, E. Moureaux, M. Müller-Trutwin and A. Blancher. 2014. MHC polymorphism in Caribbean African green monkeys. *Immunogenet.* 66: 353–360.

Bensen, K. J. and M. E. Glenn. 1997. Population size, hunting rates, and sustainability of mona monkeys (*Cercopithecus mona*) on the Caribbean island of Grenada. *Am. J. Primatol.* 42: 93–94.

Buckland, S. T., D. R. Anderson, K. P. Burnham and J. L. Laake. 1993. *Distance Sampling: Estimating Abundance of Biological Populations*. Chapman and Hall, London.

Corlett, R. 2004. Macaques as seed predators and dispersal agents in Hong Kong. *Porcupine* 30: 8–10.

Denham, W. W. 1987. *West Indian Green Monkeys: Problems, Historical Biogeography*. Karger, New York.

Dittus, W. 1985. The influence of leaf-monkeys on their feeding trees in a cyclone disturbed environment. *Biotropica* 17: 100–106.

Dobson, A. P. and A. M. Lyles. 1989. The population dynamics and conservation of primate populations. *Conserv. Biol.* 3: 362–380.

Glenn, M. E. 1996. The Natural History and Ecology of the Mona Monkey (*Cercopithecus mona* Schreber, 1774) on the Island of Grenada, West Indies. PhD Dissertation, Northwestern University, Evanston, IL.

Glenn, M. E. 1997. Group size and group composition of the mona monkey (*Cercopithecus mona*) on the island of Grenada, West Indies. *Am. J. Primatol.* 43: 167–173.

Glenn, M. E. 1998. Population density of *Cercopithecus mona* on the Caribbean island of Grenada. *Folia Primatol.* 69: 167–171.

Glenn, M. E. and K. J. Bensen. 2008. Forest structure and tree species composition of the Grand Etang Forest on Grenada, West Indies, pre-Hurricane Ivan. *Caribb. J. Sci.* 44: 395–401.

Glenn, M. E. and K. J. Bensen. 2013. The mona monkeys of Grenada, São Tomé and Príncipe: Long-term persistence of a guenon in permanent fragments and implications for the survival of forest primates in protected areas. In: *Primates in Fragments: Complexity and Resilience*, L. K. Marsh and C. A. Chapman (eds.), pp. 413–422. Springer, New York, USA.

Glenn, M. E., K. J. Bensen, and R. Matsuda Goodwin. 2013. *Cercopithecus mona*, Mona monkeys. In: *Mammals of Africa, Volume 2: Primates*, T. M. Butynski, J. Kingdon and J. Kalina (eds.), pp. 322–324. Bloomsbury Publishing, London, UK.

González-Martínez, J. 2004. The introduced free-ranging rhesus and patas monkey populations of southwestern Puerto Rico. *Puerto Rico Health Sci. J.* 23: 39–46.

Hamilton, C. M., F. Katzer, A. Beierschmitt, E. Soto, E. A. Innes and P. J. Kelly. 2014. First report of *Toxoplasma gondii* seroprevalence in wild-caught Caribbean African green monkeys. *Parasite Vector* 7: 571.

Heinsohn, T. E. 2001. Human influences on vertebrate zoogeography: animal translocation and biological invasions across and to the east of Wallace's Line. In: *Faunal and Floral Migrations and Evolution in SE Asia-Australasia*, I. Metcalfe, J. M. B. Smith, M. Morwood and I. Davidson (eds.), pp.153−170. A. A. Balkema Publisheres, Lisse, The Netherlands.

Heinsohn, T. E. 2003. Animal translocation: long-term human influences on the vertebrate zoogeography of Australasia (natural dispersal versus ethnophoresy). *Aust. Zool.* 32: 351–376.

Hernandez-Pacheco, R., D. L. Delgado, R. G. Rawlins, M. J. Kessler, A. V. Ruiz-Lambides, E. Maldonado and A. M. Sabat. 2016. Managing the Cayo Santiago rhesus macaque population: the role of density. *Am. J. Primatol*. 78: 167–181.

Horsburgh, K. A., E. Matisso-Smith, M. E. Glenn and K. J. Bensen. 2002. A genetic study of a translocated guenon: Cercopithecus mona on Grenada. In: *The Guenons: Diversity and Adaptation in African Monkeys,* M. E. Glenn and M. Cords (eds.), pp.99–109. Plenum Publishers, New York.

Leca, J.-B., N. Gunst, A. Rompis, G. Soma, I. G. A. Arta Putra and I. N. Wandia. 2013. Population density and abundance of ebony leaf monkeys (*Trachypithecus auratus*) in West Bali National Park, Indonesia. *Primate Conserv.* 26: 133–144.

Levy, S. 2005. Primate research: die hard. *Nature* 434: 268–269.

Linder, J. M. and J. F. Oates. 2011. Differential impact of bushmeat hunting on monkey species and implications for primate conservation in Korup National Park, Cameroon. *Biol. Conserv.* 144: 738–745.

Lippold, L. K. 1989. Mona monkeys of Grenada. *Primate Conserv.* 10: 22–23.

Matsuda Goodwin, R. 2007. Behavior and Ecology of the Mona Monkey in the Seasonally Dry Lama Forest, Republic of Bénin. PhD Dissertation, University of New York, New York.

Nei, M., T. Maruyama and R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29: 1–10.

Oliveira, L. C. and C. E. V. Grelle. 2012. Introduced primate species of an Atlantic Forest region in Brazil: present and future implications for the native fauna. *Trop. Conserv. Sci.* 5: 112–120.

Pavelka, M. S. M., O. T. Brusselers, D. Nowak and A. M. Behie. 2003. Population reduction and social disorganization in *Alouatta pigra* following a hurricane. *Int. J. Primatol.* 24: 1037–1055.

Plumptre, A. J. and D. Cox. 2006. Counting primates for conservation: primate surveys in Uganda. *Primates* 47: 65–73.

Schlaepfer, M. A., D. F. Sax and J. D. Olden. 2011. The potential conservation value of non-native species. *Conserv. Biol.* 25: 428–437.

Sol, D., M. Vilà and I. Kühn. 2008. The comparative analysis of historical alien introductions. *Biol. Invasions* 10: 1119–1129.

Sussman, R. W. and Tattersall, I. 1986. Distribution, attendance, and putative ecological strategy of *Macaca fascicularis* on the island of Mauritius, southwestern Indian Ocean. *Folia Primatol.* 46: 28–43.

Vitousek, P. M., L. L. Loope and H. Adsersen. 1995. *Islands: Biological Diversity and Ecosystem Function*. Springer, Berlin.

Young, T. P. and J. L. Isbell. 1994. Minimum group size and other conservation lessons exemplified by a declining primate population. *Biol. Conserv.* 68: 129–134.

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