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NEWS AND PERSPECTIVES

Possible shift in macaque trophic level following a century of biodiversity loss in Singapore

Luke Gibson

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Abstract Biodiversity loss in tropical forests is a major problem in conservation biology, and nowhere is this more dire than in Southeast Asia. Deforestation and the associated loss of species may trigger shifts in habitat and feeding preferences of persisting species. In this study, I compared the habitat use and diet of long-tailed macaque (*Macaca fascicularis*) populations in Singapore from two time periods: museum specimens originally collected between 1893 and 1944, and living macaques sampled in 2009. I collected hair and used stable carbon and nitrogen isotope analysis to identify temporal changes in dietary source and trophic position, respectively. δ^{13}C ratios were virtually identical, suggesting that macaques foraged in similar habitats during both time periods. However, δ^{15}N ratios decreased considerably over time, suggesting that macaques today feed at a lower trophic level than previously. This decline in trophic level may be because of the disappearance or decline of other species that compete with macaques for fruit. This study highlights the effect of biodiversity loss on persisting species in degraded habitats of Southeast Asia, and improves our understanding of how species will adapt to further human-driven changes in tropical forest habitats.

Keywords Deforestation · Extinctions · Frugivory · *Macaca fascicularis* · Stable isotopes · Trophic decline · Urbanization

L. Gibson (✉)
Department of Biological Sciences,
National University of Singapore, 14 Science Drive 4,
Singapore 117543, Republic of Singapore
e-mail: lggibson@nus.edu.sg

Introduction

Tropical forests harbor a large portion of the world's biodiversity, and their continued destruction remains a major challenge in conservation biology. The fragmentation of forests and their conversion to agricultural or urban developments has caused great losses in diversity and several regional extinctions (Whitmore 1992), and this problem is nowhere more rampant than in Southeast Asia, where rates of forest destruction and biodiversity loss are the highest among tropical regions (Sodhi and Brook 2006; Sodhi et al. 2010). Biodiversity loss in Southeast Asia and elsewhere often triggers changes in population abundance and animal behavior. The loss of predators, prey species, or competitors may cause a species to shift its behavior, habitat preferences, or feeding preferences (Crooks and Soule 1999; Ripple and Beschta 2004). Such shifts in behavior are perturbations in the ecosystem triggered by human disturbance.

Changes in animal behavior or foraging patterns may be documented independently by making temporal comparisons of persisting species before and after biodiversity loss. Although limited by historical surveys to serve as a baseline comparison, the use of museum specimens may provide a reference collection for studies that utilize animal tissues. Becker and Beissinger (2006) and Norris et al. (2007) sampled feathers from marbled murrelet museum specimens and from living marbled murrelets to examine changes in diet over time, and found that nitrogen isotope ratios declined substantially in the past century, reflecting a decrease in trophic level that paralleled the collapse of a fishery. In this way, museums provide an invaluable reference source with which to compare current populations and identify temporal shifts in behavior.

As in the marbled murrelet study above, stable isotope analysis has increasingly been used to describe the diet of a species or population, utilizing natural differences in the ratios of heavy to light isotopes, particularly for carbon (^{13}C:^{12}C) and nitrogen (^{15}N:^{14}N; Hoefs 2004; reviewed by Kelly 2000; Crawford et al. 2008). Nitrogen isotope ratios, expressed as $\delta^{15}N$, become enriched by 2–4‰ with each trophic transfer, and may thereby reveal an organism's trophic level (DeNiro and Epstein 1981; Post 2002; Fry 2006). Differences in nitrogen isotope values may also reflect differences in habitat disturbance. In Borneo, rats and mice had higher $\delta^{15}N$ values in degraded forests than in primary forests, possibly because of increased arthropod abundance that enriched the diet of the generalist rodents (Nakagawa et al. 2007). In these ways, nitrogen isotope ratios may be used to gauge an animal's trophic level or the level of disturbance in its habitat. Alternatively, carbon isotope ratios, expressed as $\delta^{13}C$, vary between C_3, C_4, and crassulacean acid metabolism (CAM) plants, and may thereby be used to differentiate between habitat types (DeNiro and Epstein 1978). Schoeninger et al. (1997) sampled hair from multiple Neotropical primate species and found that $\delta^{13}C$ values clustered into groups depending on forest type. In these ways, stable isotopes may be used to measure changes in habitat use and trophic level.

In this study, I used stable isotope analysis to compare the diet of long-tailed macaques (*Macaca fascicularis*) between two time periods in Singapore (1°20′N, 103°50′E), using museum specimens collected between 1893 and 1944 to represent a baseline control and sampling live macaques in 2009 to serve as a contemporary comparison. Following extensive cultivation and urbanization beginning in the early nineteenth century, Singapore lost over 95% of its primary forest, which was accompanied by the extinction of an estimated 34–59% of all birds, and an estimated 42–78% of all mammals, including all large terrestrial mammals (Corlett 1992; Castelletta et al. 2000; Brook et al. 2003; Lane et al. 2006). The long-tailed macaque is one of two remaining primates on the island, with a current estimated population of between 1218 and 1454 individuals (Sha et al. 2009). Approximately 70% of the population inhabits Nature Reserves in the interior of the island, mostly along forest perimeters bordering residential and recreational areas and roads, where there is substantial interaction with humans including food provisioning (Fuentes et al. 2008; Sha et al. 2009). Any shift in macaque stable carbon or nitrogen isotope ratios would reflect a change in habitat use or trophic level, respectively, documenting a perturbation affecting one of the most common primate species in the world.

Methods

I collected hair samples from eight live long-tailed macaques in Singapore and from six long-tailed macaque specimens at the Raffles Museum of Biodiversity Research that were originally collected in Singapore (Table 1). Contemporary samples were taken from live macaques that were trapped as part of a disease project by Lisa Jones-Engel from 5 to 7 July 2009. For all samples, hair was pulled from the back of the animal, directly between the shoulder blades. Hair samples were cleaned using repeat sonication with water and acetone, dried in a drying oven, and then cut and/or folded into tin capsules. Dual $\delta^{13}C$ and $\delta^{15}N$ isotope analysis was performed at the UC Davis Stable Isotope Facility. Statistical comparisons between time periods were made using the Mann–Whitney U test and tests for outliers were made using Grubb's test in the statistical program R Version 2.11.1 (R Development Core Team 2010).

Results

Stable carbon isotope values were strikingly similar between groups (Table 1, 2009: mean ± SD = −22.63 ± 1.48; 1893–1944: mean ± SD = −22.64 ± 1.65), and there was no significant difference ($U = 22$, $p = 0.85$). However, stable nitrogen isotope values varied between time periods (1893–1944: mean ± SD = 4.31 ± 3.73; 2009: mean ± SD = 3.86 ± 0.86), a significant difference ($U = 8$, $p = 0.044$). Furthermore, because of the high variance in the 1893–1944 group, I checked for outliers and found that sample 129 was an outlier ($G = 2.01$, $U = 0.034$, $p = 0.0013$). After omitting the outlier, the 1893–1944 mean increased to 5.81 ± 0.77 and the difference between groups became more significant ($U = 0$, $p = 0.0041$).

Discussion

This study demonstrates the potential utility of museum specimens for identification of shifts in diet and habitat use over time. As agricultural and urban developments continue to expand and disturb or degrade forests and other habitats, it becomes increasingly important to understand their effects on ecosystem functioning and on the behavior of individual species. To fully understand the effect of past and ongoing habitat modifications on animal communities, museum specimens provide a useful baseline point of reference (Winker 2004; Becker and Beissinger 2006; Norris et al. 2007; Farmer and Leonard 2011).

By comparing living macaques with museum specimens, I found that stable carbon isotope ratios remained unchanged over time, suggesting that macaques occupied similar forest habitat types during both time periods. Although this may be surprising, given the extensive

Table 1 Stable carbon and nitrogen isotope ratios for macaques sampled in Singapore

Time period	ID	Year	Location	Sex	Age	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
1893–1944	127	1944	Botanical Gardens	M	Adult	−22.24	6.54
	128	1912	Botanical Gardens	F	Un	−22.43	5.36
	129	1925	Botanical Gardens	F	Subadult	−25.79	−3.18
	130	1910	Punggol	F	Adult	−21.67	4.98
	133	1922	Sembawang River	F	Un	−21.04	5.46
	134	1943	Unrecorded	Un	Infant	−22.69	6.70
	Mean ± SD					−22.64 ± 1.65	4.31 ± 3.73
2009	096	2009	Sisters Island	M	Older juvenile	−21.64	4.12
	097	2009	Sisters Island	M	Older juvenile	−20.84	4.63
	098	2009	Sisters Island	M	Older juvenile	−20.27	4.41
	099	2009	Upper Seletar	M	Subadult	−23.78	3.86
	100	2009	Upper Seletar	M	Subadult	−23.81	4.41
	101	2009	Rifle Ridge Road	F	Older juvenile	−23.87	2.56
	102	2009	Rifle Ridge Road	F	Young juvenile	−23.11	4.41
	103	2009	Rifle Ridge Road	M	Older juvenile	−23.68	2.49
	Mean ± SD					−22.63 ± 1.48	3.86 ± 0.86

Unidentified sexes and ages are labeled as "Un"

deforestation and habitat alteration in Singapore in the past century, it is important to note that deforestation and extinctions were largely complete by the end of the nineteenth century and so the 1893–1944 time period may already represent a macaque population inhabiting degraded forest (Corlett 1992). Further, because of conflict with humans, macaques today are essentially confined to forests and may therefore be less representative of animals living in other, more degraded habitats in Singapore (Sha et al. 2009).

In contrast, nitrogen isotope analysis revealed a decreasing trend in $\delta^{15}N$ values over time, suggesting that macaques today probably feed at a lower trophic position than a century ago. Although my project was limited by the small sample sizes obtained from limited museum collections and live trapping efforts, results nonetheless showed a significant difference. This important finding warrants further research.

One possible explanation for the decrease in $\delta^{15}N$ values is increased availability of fruit. Macaques consume mostly leaves, seeds, and fruit supplemented with some invertebrates and vertebrates (reviewed by Stewart et al. 2008), and increased fruit abundance may cause a proportional decrease of invertebrates and small vertebrates in their diet. Lucas and Corlett (1991) found that during peak fruit production, long-tailed macaques increased their consumption of fruit and reduced their consumption of insects.

Alternatively, or in addition, the different nitrogen isotope values may reflect changes in species composition over time. A large portion (estimated to be 42–78%) of mammals are now extinct in Singapore (Brook et al. 2003), including primates and other mammals that normally compete with macaques for fruit (Lucas and Corlett 1998); the absence of these species, and several frugivorous birds, may have enabled macaques to increase their consumption of fruit. Further, the loss of some vertebrate species found in the diet of macaques elsewhere in Southeast Asia may have caused macaques to forage for other items lower on the trophic pyramid (reviewed by Stewart et al. 2008). In these ways, extinction of mammals and other vertebrates in Singapore may have contributed to the macaque's centennial decline in trophic level.

This study highlights the effect of continued habitat modification and associated biodiversity loss on animal communities. The ability of species such as the long-tailed macaque to persist despite extensive forest degradation may be possible because of their ability to alter their behavior, by foraging at a lower trophic level as described here. In Singapore, where many vertebrate seed dispersers are now absent, macaques may serve as critical dispersers that help propagate plant seeds (Corlett 1998; Lucas and Corlett 1998). Long-tailed macaques are one of the most widespread non-human primate species, and their persistence in degraded forest habitats may be critical to the preservation of key ecosystem functions such as seed dispersal, in Singapore and beyond. As human environmental pressures continue to expand throughout the tropics, particularly in Southeast Asia (Sodhi et al. 2010), our understanding of how species adapt in degraded tropical forests will help us to predict future community organization and ecosystem functioning.

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