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Original Article

Strontium Isotopes are Consistent With Low-Elevation Foraging Limits for Henst's Goshawk

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ABSTRACT Apex predators play critical roles in the ecosystems they inhabit. Unfortunately, little is known about movement patterns for many species. This information is critical for evaluating vulnerability to habitat loss and the adequacy of existing or proposed protected areas. Strontium isotope ratios ($^{87}Sr/^{86}Sr$) in prey remains reflect the geology where individuals lived and were killed, and can be used to identify foraging ranges for predators. We tested the degree to which $^{87}Sr/^{86}Sr$ in consumed lemurs (Lemuroidea) can be used to track foraging ranges for Henst's goshawk (*Accipiter henstii*) at Ranomafana National Park (RNP), eastern Madagascar, Africa. This large-bodied endemic accipiter is sparsely distributed and rarely observed outside of forest or at elevations >1,200 m. A geologic boundary divides lower and higher elevations at RNP: Precambrian migmatite is at lower elevations within and to the east of RNP and Precambrian metasediments are limited to higher elevations in southwestern RNP. We collected foliage from trees and understory plants to establish $^{87}Sr/^{86}Sr$ for both geologies, and remains from 19 depredated lemurs from 4 hawk nests located along the eastern edge of RNP. Leaves from metasediments have greater $^{87}Sr/^{86}Sr$ than leaves from migmatite. $^{87}Sr/^{86}Sr$ for lemur bones suggests that 18 of the 19 predated individuals came from forests underlain by migmatite. Thus, strontium isotope data suggest that Henst's goshawk primarily hunted on migmatite at RNP, which supports a growing body of evidence that this species forages at elevations below approximately 1,200 m. Most reserves in eastern Madagascar protect forest at higher elevations. Conserving remaining forest and revegetating denuded land at lower elevations will likely be critical for survival of this species. Understanding mobility patterns is crucial for managing predator populations. Isotopic analysis of prey is a noninvasive method for monitoring foraging ranges that complements existing approaches. This geochemical tool is readily adaptable to other systems and species.

KEY WORDS *Accipiter henstii*, bone, deforestation, foraging range, lemur, Madagascar, predation, Ranomafana National Park, raptor.

Raptors play critical ecological roles in the ecosystems they inhabit, yet little more than occurrence data exist for most species (Thiollay 1985). This is especially true for the tropics, which house approximately 90% of the world's raptor species (Bildstein et al. 1998). Although the primary threat to most of these species appears to be anthropogenic habitat loss, little is known about raptor abundance, diets, or movement patterns, or the interplay between these factors and habitat modification (Thiollay 1985, Bildstein et al. 1998, Virani and Watson 1998). With increasing deforestation and fragmentation occurring worldwide, there is an urgent need to learn more about the ecology of raptors if we are to conserve their wild populations. Beyond assessing diet and abundance, it will be crucial to evaluate movement patterns, including the ability for individuals to nest and forage outside of protected areas. Without this knowledge, we cannot properly gauge their vulnerability or resilience to continued forest loss or the adequacy of existing or proposed protected areas.

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Typical methods for assessing home range distance and foraging patterns in raptors include banding and telemetry (Webster et al. 2002). However, these methods can be expensive, require direct handling that can be stressful for birds, and provide limited temporal information for only a few individuals. Tracing the provenance of prey brought back to nests may offer a novel complementary and noninvasive method for assessing mobility. Bones from consumed prey can be regularly collected from within or below nests, potentially providing information about daily, seasonal, or inter-annual mobility patterns for multiple individuals.

Faunal analysis of prey offers a first-order assessment of predator foraging strategies (Lewis et al. 2004). For example, consumption of prey with patchy distributions or distinct habitat requirements (e.g., arboreal or aquatic organisms) can indicate selected foraging locations. Although valuable, this information may not provide a good indication of the area over which prey items are acquired. Analyses of the isotopic composition of prey can help close this knowledge gap. For example, carbon, nitrogen, hydrogen and oxygen isotope values can distinguish prey that inhabited dry, hot localities from cool, moist ones (Cormie et al. 1994; Sellick et al. 2009; Crowley et al. 2011, 2015). Although these data can be used to identify home ranges for animals that forage in distinct habitats (Chamberlain et al. 1997, Bearhop et al. 2003, Cerling et al. 2005), they are less useful for distinguishing regions with relatively invariant vegetation or climate (Koch et al. 1995, Bowen et al. 2005, Crowley et al. 2011). In these contexts, $^{87}Sr/^{86}Sr$, which primarily reflects geology, may be advantageous.

Strontium is released from weathering rock into soils and surface water. It is then incorporated into plants (it readily substitutes for calcium ions), and subsequently into the tissues of consumers with negligible fractionation (Rosenthal et al. 1972, Åberg 1995, Capo et al. 1998, Flockhart et al. 2015). Consequently, $^{87}Sr/^{86}Sr$ in prey remains should reflect the surface geology of the locality where an individual lived and was killed (Beard and Johnson 2000, Price et al. 2002, Porder et al. 2003, Copeland et al. 2010). The isotopic composition of rocks varies with age and chemical composition. ^{87}Sr is produced by the radiogenic decay of ^{87}Rb (half-life $= 48.8 \times 10^9$ yr) while the ^{86}Sr isotope remains constant. Consequently, as a rock ages its $^{87}Sr/^{86}Sr$ ratio will slowly increase due to the continued decay of ^{87}Rb into ^{87}Sr. Granites and other felsic crustal rocks typically exhibit $^{87}Sr/^{86}Sr > 0.710$ (Capo et al. 1998). Basalts and other mafic rocks, including those on Madagascar, have lower $^{87}Sr/^{86}Sr$ between 0.702 and 0.707 (Storey et al. 1997, Capo et al. 1998). Carbonates have Sr isotope ratios similar to those of seawater (~0.707–0.709; McArthur et al. 2001). Clastic sediments typically have slightly greater and more variable ratios than carbonates because they contain older detrital material.

We tested the degree to which $^{87}Sr/^{86}Sr$ in consumed lemurs (Lemuroidea) can identify foraging patterns for Henst's goshawk (*Accipiter henstii*) in and around Ranomafana National Park, Madagascar, Africa. Like many tropical raptors, very little is known about this large-bodied accipiter, which is endemic to the island (reviewed in Virani and Watson 1998). Henst's goshawk is generally considered to be an obligate forest species that inhabits primary or secondary evergreen humid forest and dry deciduous forest across the island (Thiollay 1985, René de Roland et al. 1996, Karpanty 2003, Watson 2007, Gardner and Jasper 2014). Forest patch size and elevation appear to play a major role in its presence and abundance (Hawkins 1999, Goodman and Rasolonandrasana 2001, Raherilalao 2001, Watson et al. 2004). Although individuals have been observed in agroecosystems, these sightings are infrequent (Raherilalao 2001, Watson 2007, Martin et al. 2009). Hawkins (1999) classifies Henst's goshawk as a low–midaltitude specialist, but elevation limits for this species are poorly constrained. For example, Langrand (1990) stated that Henst's goshawks are found up to 1,800 m above sea level, while Kemp et al. (2014) reported that they live below 1,000 m and only exceptionally to 1,980 m. To the best of our knowledge, with the exception of a single sighting at 2,000 m in northern Madagascar, Henst's goshawk have not been observed above approximately 1,200 m (Hawkins 1999, Goodman and Rasolonandrasana 2001, Karpanty 2003).

Henst's goshawk is rare and sparsely distributed. Its population is estimated at <2,000 mature individuals (del Hoyo et al. 1994, Kemp et al. 2014). The species is listed as Near Threatened by the International Union for Conservation of Nature on the basis of its small population (BirdLife International 2012). However, current trends of increasing forest fragmentation and loss in Madagascar, coupled with our limited knowledge about this accipiter's biology, suggest that its status may warrant re-evaluation (Du Puy and Moat 1998, Harper et al. 2007). In the Ranomafana region, forest loss is prevalent and nearly all land outside of the formal park boundaries has been denuded at lower elevations (Fig. 1c). It is highly unlikely that any individuals are breeding outside of the park (Raherilalao 2001, Karpanty 2003). With these geographical limitations in mind, it is critical to determine whether goshawks are able to freely forage throughout the park's protected boundaries or whether they are limited to lower elevations, which would restrict their available foraging area to only the eastern edge of the park (Fig. 1b).

STUDY AREA

Ranomafana National Park (RNP), is at the eastern edge of Madagascar's high central plateau (21.27°S, 47.33°E; Fig. 1). It encompasses 43,500 ha of mountainous terrain, including a core protected area (41,500 ha) surrounded by a peripheral zone that includes >100 villages (Centre ValBio Research Station, RNP, unpublished data). Elevation within the park ranges from 600 to 1,513 m above sea-level and average daily temperatures ranged from 15.7° to 21.9° C (reviewed in Crowley et al. 2011). The forest was perennially moist and received on average 3,600 mm of annual rainfall (Centre ValBio, unpublished data: 2004–2009). Vegetation varied by elevation and included lowland and midaltitude evergreen forest, and high-plateau montane forest (Koechlin 1972). The region was ideally suited for strontium provenance research. A digitized and georeferenced geology map

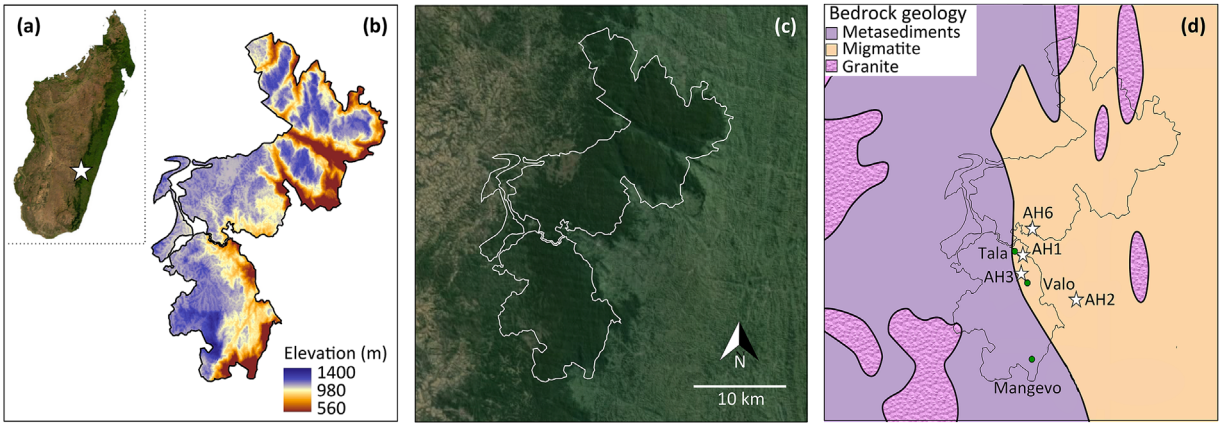

Figure 1. Maps of (a) Madagascar (star designates Ranomafana National Park; RNP), with (b) modelled elevation, (c) forest cover, and (d) geology at RNP. The scale is the same for panels b through d. Plant locality abbreviations: Tala = Talatakely and Valo = Valohoaka. AH1, 2, 3, and 6 are Henst's goshawk nests. Elevation map and park boundary by Brian Gerber used with permission from http://warnercnr.colostate.edu/~bgerber/maps.htm. Google Earth Image taken 10 April 2013. Geologic map modified from Besairie (1964).

(Besairie 1964) indicated that a contact between 2 Precambrian metamorphic bedrock geologies roughly divides the lower elevation forests in the east from higher plateau montane forest in the southwestern portion of RNP (Fig. 1d; Besairie 1964). Eastern RNP is underlain by migmatite. Southwestern RNP is underlain by metasediments (preserved as schists and gneisses). These rocks, which were likely deposited in the NeoArchaean or Late Palaeoproterozoic (prior to 2,500 million yr ago), are part of the Antananarivo Block, which covers much of central and eastern Madagascar and forms the largest Precambrian tectonic unit on the island (Collins 2006). Rocks in the Antananarivo Block were structurally and thermally altered in the Late Precambrian 700–532 million years ago when the region experienced extension, shearing, and intrusion of granitic magmas associated with the collapse of the East African Orogeny (Nédélec et al. 1995, Collins et al. 2000, Collins 2006). Outcrops of these granites are present in and around the park (Fig. 1d).

METHODS

Species Description

Henst's goshawk is highly sexually dimorphic (males ~600 g, females 960–1,140 g); body length and wingspan range from 52 to 62 cm and 86 to 100 cm, for males and females, respectively (Kemp et al. 2014). Similar to northern goshawks (*A. gentilis;* Greenwald et al. 2005), Henst's goshawks build their nests in mature trees in primary or secondary forest stands with tall canopies (Karpanty 2003). The geographic distribution for Henst's goshawk is poorly documented. It is sparsely distributed in the moist forests of eastern Madagascar, as well as in dry forests in the northwest (Langrand 1990, del Hoyo et al. 1994, Kemp et al. 2014). Gardner and Jasper (2014) documented a single breeding pair at Ranofoty in southwestern Madagascar. There are no documented occurrences in the central highlands (BirdLife International 2012), which may be attributed to the lack of forest and relatively high elevations in this region.

Male goshawks primarily hunt birds, including domestic chickens, and small-bodied lemurs <1 kg (Goodman et al. 1998, Karpanty 2003). They provide all of the food to the nest during the incubation period and into the first few weeks of the nestling period (Goodman et al. 1998). Larger bodied females can secure prey weighing up to 3.7 kg (Johnson et al. 2005, Baden et al. 2008). In the Ranomafana region, domesticated chickens were the most commonly observed individual prey species to be delivered to goshawk nests (21.8% of total individual prey deliveries), but 7 species of small-bodied lemurs accounted for the 23.2% of individual prey deliveries (Karpanty 2003). Forest-dwelling native birds, and unknown avian species comprised another 37.3% of total prey deliveries; the remaining 17.7% of individual prey delivered consisted of amphibians and reptiles (Karpanty 2003). We focused on lemur prey because they 1) comprise nearly 25% of the goshawk's diet, 2) have small home ranges and are relatively immobile (compared with birds), and 3) are limited to forested habitat (Garbutt 2007, Mittermeier et al. 2010).

Little is known about the typical foraging range for Henst's goshawks. Kemp et al. (2014) stated that it is likely <20 km on the basis of estimated nest density (1 breeding pair/24–28 km^2 in the Ranomafana region; Karpanty 2003), which is on par with home ranges reported for northern goshawks in North America (Roberson et al. 2003). However, radiotracking of individual birds indicates foraging ranges may actually be much smaller. Four radiotracked birds were repeatedly found within 800 m of their nesting sites even outside of the nesting season at Ranomafana (Karpanty 2003).

Sample Collection, Preparation, and Analysis

We (S.M.K.) opportunistically collected skeletal material from 19 depredated small-bodied lemurs from 4 Henst's goshawk nests during the incubation and nestling periods (Aug–Jan) from 1999 to 2002 (Table 1; Fig. 1). These nests —labeled AH1, 2, 3, and 6—were located below, or close to, 1,200 m in elevation along the eastern edge of RNP and represented the largest prey assemblage ever collected from

Table 1. Locality information for individual Henst's goshawk nests (1999–2002) and plant collection localities (2002–2003 for Talatakely and Valohoaka; 2008 for Mangevo) at Ranomafana National Park, Madagascar.

Material	Site name	Nest	Latitude (°S)	Longitude (°E)	Elevation (m above sea-level)	No. samples
Nests						
	Talatakely	AH1	−21.266	47.428	1,023	7
	Iambafo	AH2	−21.312	47.493	724	5
	Vatoharanana	AH3	−21.294	47.428	1,183	6
	Ambatolahy	AH6	−21.237	47.439	1,233	1
Plant localities						
	Talatakely		−21.263	47.421	900–1,100	11
	Valohoaka		−21.296	47.439	827–1,215	7
	Mangevo		−21.373	47.450	690–1,178	12

Ranomafana (Table 1; Karpanty 2003). We limited our analyses to lemurs (available from 4 of the 7 monitored nests) because these forest-dwelling primates have relatively small home ranges (Garbutt 2007, Mittermeier et al. 2010), and were most likely captured inside the park boundaries. For each individual, we powdered 20 mg of bone using a rotary tool equipped with a dental drill bit. We reacted samples with 30% H_2O_2 for 72 hours at room temperature to remove organics and rinsed 5× with ultrapure water. We soaked samples in 1 M acetic acid buffered with Ca-acetate for 24 hours at 4°C to remove non-lattice bound carbonates. We again rinsed samples 5× with ultrapure water and lyophilized them.

We (A.L.B. and S.A.N.) systematically collected foliage samples from 30 trees and understory vegetation at 3 RNP localities for nutritional research (Arrigo-Nelson 2006, Baden and Crowley 2009); we used these samples to establish bioavailable $^{87}Sr/^{86}Sr$ for Precambrian migmatite and metasediments (Table 1; Fig. 1). These sites included Talatakely, which was selectively logged between 1986 and 1989, and undisturbed primary forest at Valohoaka and Mangevo. We collected foliage between August 2002 and December 2003 at Talatakely and Valohoaka, and in February 2008 at Mangevo. Foliage samples were not available from localities underlain by granite. We homogenized dried leaves using an agate mortar and pestle. We then weighed approximately 150 mg of each sample into a ceramic crucible and ashed it at 400°C for 8 hr. We collected and exported all samples with permission from the Madagascar government (collection permit Nos. 156-MEF/SG/DGEF/DADF/SCBF 2000, 151-MEF/SG/DGEF/DADF/SCBF 2001, 153-MEF/SG/DGEF/DADF/SCBF 2003, 045-MEF/SG/DGEF/DADF/SCBF 2003, 139-MEF/SG/DGEF/DADF/SCBF and 041/08 & 223/08-MET/SG/DGEF/DSAP/SSE; export permit Nos. 0023N-EV01/MG02, 0475N-EA12/MG02, 0010-EAL/MG00/CWN, 0407N-EV11/MG02 and 250N-EA12/MG08).

We analyzed all samples at the Multicollector Inductively Coupled Plasma Mass Spectrometry (MC-ICPMS) Laboratory in the Geology Department at the University of Illinois Urbana-Champaign, USA. To isolate strontium, we dissolved 3–5 mg of bone and 5–7 mg of ashed leaves in 0.5 mL of 3N HNO_3 and loaded samples into teflon cation-exchange columns. We filtered dissolved samples through 0.2 mL of Eichrom Sr spec resin (100–150 μm) and eluted them with a combination of ultrapure water and 0.05 N HNO_3 into 4-mL autosampler vials. We measured $^{87}Sr/^{86}Sr$ on a Nu plasma High Resolution MC-ICPMS (Nu Instruments Ltd, Wrexham, Wales, UK). Analytical precision was ±0.00005 to ±0.00007. We corrected data for mass bias fractionation using an internal normalization to $^{86}Sr/^{88}Sr = 0.1194$. We further normalized data using NBS 987 (accepted $^{87}Sr/^{86}Sr = 0.710255$), which we ran every fifth sample, and 2 internal standards—"Coral" ($^{87}Sr/^{86}Sr = 0.70918$) and "E&A" ($^{87}Sr/^{86}Sr = 0.70804$). The average difference in $^{87}Sr/^{86}Sr$ between duplicate analyses for 5 samples was 0.00015.

After confirming homoscedasticity among localities using Levene's test, we used nonparametric Kruskal–Wallis tests coupled with Steel–Dwass *post hoc* Honestly Significant Difference tests to assess differences in average $^{87}Sr/^{86}Sr$ among plant localities as well as nests. We performed all statistical tests using JMP Pro version 12.0 (SAS Institute Inc., Cary, NC, USA), with significance set at $\alpha = 0.05$. Lastly, we used IsoError version 1.04 (www.epa.gov; Phillips and Gregg 2001) to estimate the proportion of prey that came from metasediments versus migmatite for each hawk nest.

RESULTS

Plants at each locality exhibited a considerable range in $^{87}Sr/^{86}Sr$ (Fig. 2), but these values were within the ranges observed in other studies (Porder et al. 2003). We suspect that this isotopic variability reflects variable mineralogy, terrain, soil cover, and rooting depth among plants (Jobbágy and Jackson 2001, Poszwa et al. 2004, Porder and Chadwick 2009), but were unable to tease apart these factors. Talatakely and Valohoaka, which sit on Precambrian migmatite (Besairie 1964), had similar $^{87}Sr/^{86}Sr$ ranges (0.71658–0.72684 and 0.71695–0.72290, respectively; Table 2). Strontium isotope ratios $^{87}Sr/^{86}Sr$ for plants from Mangevo, which sits on Precambrian metasediments, were considerably greater (0.72145–0.73643). Significant differences in median $^{87}Sr/^{86}Sr$ among plant localities were found ($\chi^2_2 = 14.54$, $P = 0.007$; Table 2). Leaves from Talatakely and Valohoaka had lower average $^{87}Sr/^{86}Sr$ than those from Mangevo (Table 2; Fig. 2).

We assume that $^{87}Sr/^{86}Sr$ data for plants from these 3 sites were representative of the 2 geologies at RNP because other studies have found little evidence to suggest substantial

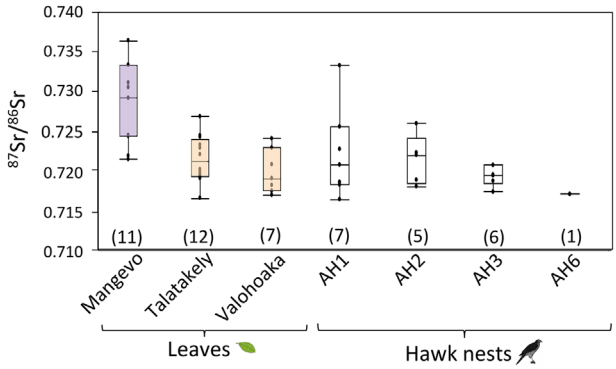

Figure 2. Comparisons of $^{87}Sr/^{86}Sr$ for plant localities and Henst's goshawk nests (AH) at Ranomafana National Park, Madagascar. Boxes include medians, first and third quartiles; whiskers extend 1.5× the interquartile range from boxes. Colors for plant localities correspond with geologies in Figure 1.

geographic variability in bioavailable $^{87}Sr/^{86}Sr$ within the same lithology (Hoppe et al. 1999, Radloff et al. 2010, Widga et al. 2010, Copeland et al. 2011). Further, it is not uncommon to use data from 1 or 2 localities to establish expected $^{87}Sr/^{86}Sr$ for a given lithology (Hoppe et al. 1999, Copeland et al. 2011). No comparative data were available for Cambrian granites from Madagascar. On the basis of their age difference, we would expect Cambrian granites to have lower $^{87}Sr/^{86}Sr$ than either Precambrian geology; published $^{87}Sr/^{86}Sr$ for plants and water on granites elsewhere typically range between 0.710 and 0.715 (Blum et al. 1993, English et al. 2001, Porder et al. 2003).

There were no differences in $^{87}Sr/^{86}Sr$ among Henst's goshawk nests ($\chi^2_3 = 3.48$, $P = 0.32$). Comparing plant and lemur data, all but one of the depredated lemurs retrieved from nests had $^{87}Sr/^{86}Sr$ that were most consistent with Talatakely and Valohoaka (Table 3; Fig. 2). The exception was a single *Cheirogaleus* from AH1, whose $^{87}Sr/^{86}Sr$ was comparable to those obtained for plants from Mangevo (Fig. 2). The Sr isotope ratio for the single *Avahi peyrierasi* retrieved from AH6 (0.71737) was low but within the range of $^{87}Sr/^{86}Sr$ for plants collected at Valohoaka and Talatakely. It is also possible that this individual came from a locality on Cambrian granite in the northeastern portion of RNP (Table 3; Fig. 2). Estimated proportions of lemur remains from each nest corroborate that the majority of lemurs came from localities underlain by migmatite (Table 4). We concede that the error around these modelled proportions is

Table 2. Strontium isotope data for individual plant samples collected at Ranomafana National Park, Madagascar. Foliage was collected between August 2002 and December 2003 at Talatakely and Valohoaka, and in February 2008 at Mangevo. For species authorities, see the Missouri Botanical Garden online database (www.tropicos.org).

Locality	Family	Genus and species	Common name	$^{87}Sr/^{86}Sr$
Mangevo	Burseraceae	*Canarium madagascariense*	Ramy	0.72919
	Burseraceae	*Canarium madagascariense*	Ramy	0.73643
	Euphorbiaceae	*Psychotria* sp.	Fanorafa	0.73336
	Lauraceae	*Cryptocarya* sp.	Tavolo malady	0.72189
	Lauraceae	*Cryptocarya* sp.	Tavolo malady	0.72436
	Moraceae	*Ficus* sp.	Nonoka	0.73051
	Moraceae	*Ficus* sp.	Nonoka	0.73111
	Rubiaceae	*Breonia* sp.	Valotra	0.72919
	Rubiaceae	*Psychotria* sp.	Fanorafa	0.72145
	Rubiaceae	*Psychotria* sp.	Fanorafa	0.73636
	Sapotaceae	*Chrysophyllum biovinianum*	Rehakaka	0.72448
			Range	0.72145–0.73643
			Average ± 1σ	0.72894 ± 0.0053
Talatakely	Apocynaceae	*Mascarhenasia* sp.	Herodrano	0.72444
	Asclepiadaceae	*Secamone* sp.	Vakikondro	0.71906
	Asclepiadaceae	*Secamone* sp.	Vakikondro	0.72207
	Asclepiadaceae	*Secamone* sp.	Vakikondro	0.72684
	Fabaceae	*Albizia* sp.	Albizia	0.71658
	Fabaceae	*Viguieranthus* sp.	Ambilazona	0.71955
	Fabaceae	*Viguieranthus* sp.	Ambilazona	0.71928
	Loranthaceae	*Bakerella* sp.	Tongoalahy	0.71984
	Loranthaceae	*Bakerella* sp.	Tongoalahy	0.72428
	Loranthaceae	*Bakerella* sp.	Tongoalahy	0.72018
	Myrsinaceae	*Maesa* sp.	Voarafy	0.72327
	Pittosporaceae	*Pittosporum verticillatum*	Ambouitsika	0.72290
			Range	0.71658–0.72684
			Average ± 1σ	0.72152 ± 0.0029
Valohoaka	Apocynaceae	*Mascarhenasia* sp.	Herodrano	0.71904
	Apocynaceae	*Mascarhenasia* sp.	Herodrano	0.71695
	Fabaceae	*Albizia* sp.	Albizia	0.72407
	Fabaceae	*Albizia* sp.	Albizia	0.72079
	Fabaceae	*Viguieranthus* sp.	Ambilazona	0.71746
	Fabaceae	*Viguieranthus* sp.	Ambilazona	0.71818
	Fabaceae	*Viguieranthus* sp.	Vahihenotra	0.72290
			Range	0.71695–0.72290
			Average ± 1σ	0.71991 ± 0.0028

Table 3. Strontium isotope data for individual *Avahi peyrierasi, Microcebus rufus,* and *Cheirogaleus* spp. retrieved from Henst's goshawk nests along the eastern edge of Ranomafana National Park, Madagascar, during the incubation and nestling periods (Aug–Jan) from 1999 to 2002. The *Cheirogaleus* individuals could be *C. major* or *C. crossleyi;* both are found at Ranomafana (Mittermeier et al. 2010), and are difficult to distinguish on the basis of fragmentary skeletal material. Dates are presented as day month year.

Nest	Species	ID	Collection date	$^{87}Sr/^{86}Sr$
AH1	*Avahi peyrierasi*	17	14 Dec 1999	0.71888
	Cheirogaleus sp.	18	14 Dec 1999	0.72305
	Cheirogaleus sp.	30	5 Jan 2000	0.73360
	Cheirogaleus sp.	34a	7 Dec 1999	0.71855
	Cheirogaleus sp.	37	31 Dec 1999	0.72107
	Cheirogaleus sp.	38a	5 Jan 2000	0.71673
	Avahi peyrierasi	38b	5 Jan2000	0.72589
AH2	*Avahi peyrierasi*	No number	12 Dec 2000	0.71835
	Avahi peyrierasi	02-4	4 Jan2002	0.72628
	Cheirogaleus sp.	48	27 Dec 2001	0.72230
	Cheirogaleus sp.	57	26 Dec 2001	0.71916
	Avahi peyrierasi	58	30 Dec2001	0.72260
AH3	*Avahi peyrierasi*	02-2	28 Oct 2002	0.71982
	Avahi peyrierasi	02-5	23 Sep 2002	0.71765
	Avahi peyrierasi	02-7 #1	18 Oct 2002	0.72101
	Avahi peyrierasi	02-7 #2	18 Oct 2002	0.72103
	Avahi peyrierasi	67	14 Dec 2001	0.71904
	Cheirogaleus sp.	72.2	20 Dec 2001	0.71970
AH6	*Avahi peyrierasi*	02-3	6 Sep 2002	0.71737

quite large, which likely reflects variability in plant data at each site, as well as relatively small sample sizes. Although modelled proportions are by no means definitive, these estimates do serve the purpose of demonstrating that there is a much greater likelihood that Henst's goshawks captured lemurs on migmatite than metasediments.

DISCUSSION

Strontium isotope data suggest that Henst's goshawks primarily hunted lemurs on migmatite. Migmatite outcrops are found only at lower elevations at RNP; therefore, it would appear that goshawks do not frequently hunt at higher elevations in the park, at least not during the nesting and breeding seasons. These results are somewhat surprising considering the presumed proximity of AH2 and AH3 nests to metasediments. It is possible that the actual contact between these 2 lithologies is not identical to that mapped by Besairie (1964); vegetation and topography in the region make bedrock mapping challenging. Nevertheless, $^{87}Sr/^{86}Sr$ data for plants were consistent with the geologic contact lying somewhere between Talatakely, Valohoaka, and Mangevo. We recognize that our spatial sampling of plants from different localities at Ranomafana is quite limited. However, we feel secure that observed differences in $^{87}Sr/^{86}Sr$ among sites are due to differences in geology. Variability in rooting depth could lead to isotopic differences among plants (Poszwa et al. 2004, Reynolds et al. 2012), but this should not significantly affect our results because we included data for deep-rooted canopy trees at all 3 sites. Additionally, variable weathering rates related to topography or vegetation cover could influence bioavailable strontium (Porder et al. 2006, Bern et al. 2007); however, because all 3 of the sites were characterized by steep slopes and vegetation samples were collected in primary forest, this should also be of negligible concern in the present study. Thus, although our results must be viewed as somewhat preliminary, they substantiate previous observations that Henst's goshawks select elevations below approximately 1,200 m (Hawkins 1999, Goodman and Rasolonandrasana 2001), and point to the need for additional research. A more thorough analysis of spatial isotopic variability in the region is warranted, but beyond the scope of the present study.

Why do Henst's goshawks select elevations below 1,200 m? We suspect this is directly related to forest structure. Northern goshawks nest in dense stands of mature or secondary forests with large trees and high, relatively closed canopies (Greenwald et al. 2005). They are "sit and wait" ambush predators that rely on canopy trees to search for prey and use understory vegetation to hide (Roberson et al. 2003). Henst's goshawks also nest in mature trees with tall, closed canopies (Karpanty 2003). Nothing is known about their foraging strategies. However, it is reasonable to assume that, like northern goshawks, they are ambush predators that perch in forest canopies and utilize understory vegetation for cover.

Canopy height and understory vegetation above 1,200–1,300 m may not be particularly suitable for goshawk foraging at RNP. Midaltitude evergreen forest, which extends from 700 to 1,500 m in eastern Madagascar, is characterized by a 15–30 m canopy, abundant vines and epiphytes, and a dense shrub layer (Hawkins 1999). However, lower montane forest, which is characterized by a lower canopy (5–20 m) and a reduced shrub layer, overlaps with the upper portion of this range (extends from 1,000 to 1,800 m); and sclerophyll forest, which is defined by very dense vegetation and an even shorter canopy (1–5 m), is present between 1,400 and 2,200 m (Hawkins 1999). Forest structure in western RNP has not been extensively surveyed. However, preliminary studies suggest that canopy is, indeed, lower in this part of the park (S.A.N. unpublished data; S. Johnson, University of Calgary, personal communication).

Additionally, 1,200 m is a natural cutoff for many other bird and mammal species in eastern Madagascar, and species richness declines quickly at higher elevations (Hawkins 1999,

Table 4. Estimated proportion of lemur remains recovered from metasediments versus migmatite for individual Henst's goshawk nests at Ranomafana National Park, Madagascar (1999–2002). Proportions were estimated using IsoError 1.04 (Phillips and Gregg 2001).

	Estimated proportion of prey from metasediments		Estimated proportion of prey from migmatite	
Nest	$\bar{x} \pm 1\sigma$ (%)	95% CI	$\bar{x} \pm 1\sigma$ (%)	95% CI
AH1	20.1 ± 29.5	0.0–88.2	79.9 ± 29.5	11.8–1.0
AH2	10.1 ± 21.6	0.0–61.1	89.9 ± 21.6	38.9–1.0
AH3	-15.3 ± 17.3*	0.0–24.6	115.3 ± 17.3*	75.4–1.0
AH6	-44.4 ± 21.6*		144.4 ± 21.6*	

*These models estimated that <0 and >100‰ of predated lemurs came from metasediments and migmatite, respectively. Although such proportions are not physically possible, we have chosen to include them as they illustrate the degree of likelihood that prey were hunted on each type of geology.

Irwin et al. 2005). Lemurs are present at higher elevations in RNP, but they are less abundant than at lower elevations, most likely because of a decline in their preferred food trees (Herrera 2016). Hunting for patchily and sparsely distributed prey in sub-ideal habitat at higher elevations may be less effective than foraging at lower elevations at RNP.

If Henst's goshawks geographically limit their foraging efforts, this has important implications for their conservation and management, as well as the conservation and management of the species they consume. On the basis of estimated population size (670–2,000 mature individuals), this accipiter is rare. Using forest cover and nest density at Ranomafana, Karpanty (2003) estimated that there are 15–18 breeding pairs of hawks in the park. However, no nests have been observed in western RNP, and $^{87}Sr/^{86}Sr$ data further suggest that individuals may not even forage within much of the park's protected boundaries. Very little of Madagascar's forests remain intact and only a portion of them are protected (Du Puy and Moat 1996, Harper et al. 2007). Protecting remaining forest and revegetating denuded land, particularly at lower elevations, will likely be critical for persistence of Henst's goshawks.

It has been previously noted that Henst's goshawks depredate populations of critically endangered lemurs (Wright 1998, Karpanty 2006, Goodman et al. 2014). Goshawks may disproportionately affect lemurs living at lower elevations in protected areas or unprotected fragments. Additionally, although goshawks consume forest-dwelling species, they also rely heavily on domesticated chickens in the Ranomafana region (Karpanty 2003). Chickens likely provide an easy target for goshawks along the eastern boundary of RNP (Valeix et al. 2012), which may further limit the need for individuals to seek out less productive, high-altitude hunting ranges. Revegetating denuded land and increasing forest protection along the eastern margin of the park may help decrease hunting of chickens and reduce conflict between Henst's goshawks and people.

Here we have demonstrated the utility of a noninvasive geochemical tool for determining origin of prey and tracking predator foraging ranges. To the best of our knowledge, just 2 other studies have used a similar approach (Porder et al. 2003, Copeland et al. 2010). Copeland et al. (2010) used $^{87}Sr/^{86}Sr$ in tooth enamel from rodents collected from a barn owl (*Tyto alba*) roost at Gladysvale Cave in South Africa to determine the relative proportion of local versus distantly derived prey. They then examined $^{87}Sr/^{86}Sr$ for fossil rodent assemblages at the cave to confirm that proportions of local and distantly derived prey were similar in the past. Porder et al. (2003) used $^{87}Sr/^{86}Sr$ in herbivore bone assemblages at 2 caves in Yellowstone National Park, USA, to determine that foraging ranges for predators have been relatively consistent over the past 3,000 years. This geochemical tool could easily be applied to other species and systems. The geologic heterogeneity at Ranomafana is not unusual. Any area that has variable bedrock geology, or variable overburden (e.g., alluvium, glacial till), will likely be suitable for strontium isotope analysis. Because vegetation structure and composition is frequently linked to underlying geology (Du Puy and Moat 1996), strontium isotopes may be useful for tracking predator use of different habitats. We anticipate that this method would be fruitful for assessing mobility of individuals, validating proposed protected areas, identifying important unprotected regions, and monitoring use of agricultural land or revegetated corridors.

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