LEMURIDAE: *VARECIA*, RUFFED LEMURS, *VARIKANDANA*, *VARIJATSY*

N. Vasey, A. L. Baden, and J. H. Ratsimbazafy

Varecia (family Lemuridae) occurs at low to medium elevations, under 1350 m, throughout most of Madagascar's eastern moist evergreen forest corridor and on the Masoala Peninsula. Despite having an extensive latitudinal range, populations are patchily distributed (Vasey 1997a; Irwin et al. 2005; Lehman et al. 2006c) and vary in density (Table 14.29). Two species are currently recognized, *V. variegata* (Black and White Ruffed Lemur) and *V. rubra* (Red Ruffed Lemur) (Figure 14.51). Gray (1863) proposed this taxonomy when he first introduced the genus *Varecia*, but the genus name was not immediately accepted, and nearly 100 years elapsed before the generic distinction between *Lemur* and *Varecia* was reintroduced (J.-J. Petter 1962; Tattersall 1982). For much of the 19th and 20th centuries, *V. rubra* was considered a variant or subspecies of *V. variegata* (known during that time as *Lemur varius*). Subsequently, a geographic divide between the two forms was identified, the Antainambalana River in northeastern Madagascar (J.-J. Petter et al. 1977). *Varecia rubra* occurs east of the Antainambalana River and on the Masoala Peninsula, with the northernmost records ~30 km south of Andapa in the Besariaka forest corridor (Ranorovelohanta 1996) and at the Antohakalava private reserve (E. Patel, unpublished data). *Varecia variegata* has a much larger latitudinal range, extending from west of the Antainambalana River (J.-J. Petter et al. 1977; Lindsay and Simons 1986; H. J. Simons and Lindsay 1987) to south of the Mananara River, with the southernmost records at Ambalavero in the Vondrozo–Midongy du Sud forest corridor and in the Vohitrambo and Marakopila Forests in the commune of Bevata (Vasey and Tattersall 2002; Rakotonirina et al. 2013; I. Tattersall, unpublished data).

TABLE 14.29. **Population densities of *Varecia variegata* and *V. rubra* in continuous versus isolated forests (i.e., surrounded by nonforest matrix) by elevation**

SITE	SPECIES/VARIANT	ELEVATION (m)	DENSITY (ind/km)[1]	REFERENCE
CONTINUOUS FORESTS				
Nosy Mangabe	*V. v. subcincta*[2]	0–331	29–43	Morland (1991a)
Andranobe (Masoala)	*V. rubra*	110–260	31.2–53.4	Vasey (1997a)
Ambatonakolahy Forest	*V. rubra*	450–650	21.5–23.2	Rigamonti (1993)
Mangevo (Ranomafana)	*V. v. editorum*	800–1200	24.3	Baden (2011)
Analamazaotra	*V. v. variegata*	800–1300	<4	Pollock (1975a)
Valohoaka (Ranomafana)	*V. v. editorum*	1200–1300	6	Balko (1998)
Vatoharanana (Ranomafana)	*V. v. editorum*	1200–1300	3	Balko (1998)
ISOLATED FOREST FRAGMENTS				
Manombo	*V. v. editorum*	0–137	0.4–2.5	Ratsimbazafy (2002)
Kianjavato Forests[1]	*V. v. editorum*	70–390	0.11–0.18	Narváez-Torres (2018); P. R. Narváez-Torres et al. (unpublished data)
Vatovavy Forest	*V. v. editorum*	100–322	32	Balko (1992)
Betampona	*V. v. variegata*	275–650	1.6–2.2	Welch and Katz (1992)
Betampona	*V. v. variegata*	275–650	2.5–3.1	Britt (1997)
Antanamalaza Classified Forest	*V. v. variegata*	600–700	10–15	Britt et al. (1999)

[1] Density estimate represents the combined densities of five forest fragments in 2014, 2015, and 2016; the fragments include Vatovavy, Sangasanga (also known as Kianjavato), and Tsitola.

[2] *V. v. subcincta* was introduced to Nosy Mangabe in the 1930s (Kuhn 1972). As it is a small island (520 ha), it is not easily classified as either a continuous forest or an isolated fragment. Ecologically, the forest is relatively intact.

FIGURE 14.51 **The two species of *Varecia*. A) *Varecia variegata* in the forest canopy at Mangevo, Ranomafana National Park. This individual expresses the "editorum" coat pattern (see text). B) A mixed-age subgroup of *Varecia rubra* individuals in the forest canopy at Andranobe, Masoala National Park. The animals are actively feeding on *Lepidotrichilia* sp. (Meliaceae). Markings shown include a white ankle band (top left individual) and white patches on the dorsum (the two individuals below).** (PHOTO A by F. Bendell, and B by N. Vasey.)

Since the precursor of this book, which contained a contribution on *Varecia* (Vasey 2003), a considerable amount has been learned about this genus of lemur, summarized herein.

TAXONOMY

The variegated coat patterns of *V. variegata* and of *Varecia* hybrids (captive and wild-caught), coupled with incomplete information on the geographic distribution of pelage variants, have long prevented taxonomists from arriving at a firm consensus concerning specific and subspecific variation in the genus (Vasey and Tattersall 2002). Since at least 1868, the two *Varecia* species have hybridized in menageries and zoological gardens and were assumed to do so in the wild. Largely on this basis, by the mid- to late 19th century, the Red Ruffed Lemur was downgraded to a variant or subspecies of *Lemur varius* (Schlegel 1866; Pollen 1868; Schwarz 1931; Hill 1953). This fueled queries about the existence of a natural hybrid zone. Based on local reports of a rufous-brown form north of the Bay of Antongil (Tattersall 1977) and study of museum holdings and collection records (Tattersall 1982; Buettner-Janusch and Tattersall 1985), it was suggested that the black-and-white and red forms are in secondary contact between the confluent Vohimaro and Antainambalana Rivers. A review and synthesis of historical documents and illustrations, taxonomic literature, museum collections, and survey work indicated a more widespread hybrid zone, extending across two additional river drainages farther east (the Andranofotsy and the Mahalevona), but one in which hybridization is rare (Vasey and Tattersall 2002).

In the late 19th and early 20th centuries both Black and White and Red Ruffed Lemurs were collected near Maroantsetra, as were a handful of hybrids from two localities within the three watersheds (Bevato and Malewo). Sightings have since accumulated of *Varecia* individuals with "hybrid" coat patterns east of the Antainambalana River at Ambodivoangy in 2008 (R. Kramer, unpublished data) and farther north at Antohakalava in 2009, 2012, and 2019, and at Maherivaratra in 2018 (E. Patel, unpublished data). However, within the same time frame, long-term demographic records on the Masoala Peninsula (Andranobe Forest) document a small number of *V. rubra* individuals with similarly unusual coat patterns (N. Vasey, unpublished data). This casts open, once again, the question as to whether a hybrid zone exists; the unusual coat patterns may alternatively represent rare, previously undocumented pelage variations attributable to genetic drift and/or reduced gene flow.

Lemur trapping and extensive swidden agriculture have led to habitat fragmentation and the partial or complete isolation of *Varecia* populations north of the Bay of Antongil (Lindsay and Simons 1986; H. J. Simons and Lindsay 1987; Hekkala et al. 2007). Near the Mahalevona River in the northwestern reach of the Masoala Peninsula (in the Ambatoledama forest corridor), the *V. rubra* population has recently undergone a genetic bottleneck (Razakamaharavo et al. 2010). Population and habitat surveys are currently underway to determine the extent of the geographic range of *Varecia* in northeastern Madagascar, to document the pelage patterns therein, and importantly, to obtain tissue samples suitable for comparative genomic analysis to be paired with those from San Diego Zoo's Frozen Zoo. Such analyses using samples gathered across the entire extant range of *Varecia* should resolve the question of species delimitations and allow examination of in situ and ex situ population health. Herein we treat the two forms as distinct species and discuss the question of variants defined by pelage below.

It is important to know the number of taxonomic units we aim to protect and their geographic distribution. To determine specific and subspecific divergence, less emphasis on pelage and more reliance on craniometry (which is notably lacking) and neutral genetic variation are warranted. Sequence variation in the mtDNA control region suggests that *V. variegata* contains two geographic forms: a southern unit, based on samples from the protected areas of Manombo and Ranomafana, and a northern unit, based on samples from Betampona (Wyner et al. 1999b). Population structure inferred from microsatellites and mtDNA from samples spanning the geographic range of *V. variegata* (19 sites) similarly indicates two subspecies, separated by the largest river in eastern Madagascar, the Mangoro (Baden et al. 2014). These different data call into question the generally accepted three subspecies of *V. variegata* (as listed in Table 14.29).

PHYSICAL FEATURES

Varecia species are the largest members of the family Lemuridae (wild adult weights: *V. rubra*, 2.1–3.6 kg, n = 25, Vasey 2003, Dutton et al. 2008; *V. variegata*, 2.5–4.8 kg, n = 98, Baden et al. 2008), and the sexes show no difference in pelage coloration or size. The long, lavishly furred tail of these species slightly exceeds body length, averaging about 60 cm. The rest of its coat is also long and luxuriant. Both species have black fur on the ventrum, tail, manus, pes, crown, forehead, and face. Surrounding the face and ears is a ruff of long fur, white in *V. variegata* and red or honey blond in *V. rubra*. Consistency in coat color and pattern ends there. In *V. rubra* the dorsum is typically a single color but varies in any given individual from dark blood red to red orange to honey blond. The nape bears a large distinct patch of white fur, and white or honey-blond fur may encircle the base of the tail or appear in a patch on the dorsum. The tarsus, metatarsus, and pedal digits often have bands of white fur in these otherwise black areas. White fur may also appear on the lateral aspect of the ankle or extend up to the knee or midthigh. In comparison, individuals of *V. variegata* show highly personalized patches or bands of white or light fur on the dorsum and appendages (Figure 14.51).

Three principal variants of *V. variegata* have long been recognized (e.g., Geoffroy Saint-Hilaire 1851). While the overall amount of black in the dorsal pelage seems to be reduced in favor of white in the southern part of the species' geographic range, there is no straightforward north–south cline (J.-J. Petter et al. 1977; Tattersall 1982), and dark regions are not always pure black but may grade into or be light brown or dark brown. In the lightest form ("variegata") the dorsal fur is white, with black restricted to the shoulder, upper arm to elbow, and front of thigh; whereas in the darker form known from the north ("subcincta"), the dorsum is mainly black, with two variably thick bands of white fur—one band encircles the torso and sometimes extends longitudinally toward the nape of the neck, and the other band extends across the rump, down the posterior aspect of the thigh, and onto the lateral surface of the lower leg. In another form ("editorum") the black shoulder patches extend onto the dorsum, forming a black mantle across the back and shoulders. In addition to these three variants, others have been described. J.-J. Petter et al. (1977) described eight forms based on museum specimens and field observations. I. Tattersall (unpublished data) recognized as many as 10 repeated variants, and based on those, with associated provenance in combination with field observations, Vasey and Tattersall (2002) illustrated broad areas within which more than one pelage variant is found. In the absence of any clear geographic patterning across the latitudinal range in which the Black and White Ruffed Lemur occurs, these authors view *V. variegata* as a species embracing multiple largely discrete pelage patterns rather than one that is divisible, based upon pelage, into discrete geographic subspecies. Thus, while the IUCN currently recognizes three subspecies of *V. variegata* based on the three principal pelage variants (*V. v. variegata*, *V. v. editorum*, and *V. v. subcincta*), following Groves (2001), we do not concur. It may prove more profitable to study the pied and patterned pelage variation in *V. variegata* in terms of why it is so attractive (i.e., conspicuous), a question of adaptation as opposed to taxonomy. An adaptive role has recently been proposed, in that the pelage of the different forms of *Varecia*, as measured from museum specimens, is correlated with tree cover and precipitation, suggesting that countershading may be useful in the dense moist evergreen forest its populations inhabit (Spriggs 2017).

LIFE HISTORY AND POPULATION DYNAMICS

Varecia species have an unusual set of reproductive traits for medium-size, gregarious, day-active primates, including the bearing of litters, nesting of altricial young, and an absentee parenting system (which consists in the oral transport of nonclinging young combined with "infant stashing"; Vasey 2007). Only a handful of small-bodied, nocturnal strepsirrhines share this suite of traits. Uniquely, however, *Varecia* nests are built exclusively to care for young, whereas those of nocturnal litter-bearing strepsirrhines are also used throughout the year for sleeping (Kappeler 1998b; Bearder et al. 2003). *Varecia* reproductive traits were first documented in captivity, and study is ongoing (Dechambre 1935; Zehr et al. 2014 and references therein). Though fewer in number, long-term field studies have contextualized *Varecia* reproduction in the wild.

The mating season occurs between May and July, and infants are born from September to early November (Morland 1990; Vasey 2007; Baden et al. 2013). In captivity, gestation averages 102 days (D. T. Rasmussen 1985), interbirth interval is one year, and age at sexual maturity is 18–20 months for females and 36–48 months for males (Foerg 1982). In the wild, gestation is 102–109 days (Vasey 2007; Baden 2019), interbirth interval varies considerably (see below), and female age at sexual maturity is 32 months (Morland 1991a). *Varecia* species bear litters of two to three infants in the wild (averages are 2.1 in *V. rubra*, Vasey 2007; and 2.7 in *V. variegata*, Baden et al. 2013), and each infant at birth weighs just under 100 g (averages are 98.2 g in *V. rubra*, and 87.2 g in *V. variegata*; Brockman et al. 1987). Locomotor independence occurs at 10 weeks, intake of solid food at 5–8 weeks, and weaning at 3–4 months, though suckling may continue as late as 7–8 months (Morland 1990, 1991a; Vasey 2007). Relatively altricial young grow extremely rapidly, attaining 70% of adult weight at four months of age (Pereira et al. 1987).

Mothers nurse on schedule versus on demand, producing milk that is higher in dry matter, fat, protein, and gross energy (kcal/g) than that of other lemurids, with protein concentrations similar to those of lorisoid milks, which are more concentrated in nutrients than the milks of any other group of primates (Tilden and Oftedal 1995, 1997). Despite being the largest living lemurid, *Varecia* has shorter gestation periods, larger litters, more rapidly developing infants, and richer milk than other members of its family. Thus, its prenatal (A. L. Young et al. 1990) and perhaps also postnatal energetic investment in reproduction is greater than in any other primate.

Field observations of mating and parenting behavior, and a synthesis of data on captive animals, demonstrate that *Varecia* species mate polygamously and exhibit extensive alloparenting behavior (Morland 1990; Vasey 2007; Baden et al. 2013). In combination with absentee parenting, alloparenting mitigates the very high maternal reproductive costs in *Varecia*, allowing lactating females to range great distances from stashed young (Vasey 2006). Mothers sometimes cache their litters in a single communal nest or stash site—a crèche—or with a male affiliate (Vasey 2007; Baden et al. 2013; Baden 2019). These mothers may be kin or nonkin. Although this behavior is facultative (i.e., not all females use crèches), females that place their infants in crèches are able to spend more time away from their young feeding and foraging, and their infants experience lower mortality (Baden et al. 2013). On this basis, *Varecia* is characterized as having a cooperative, or alternatively, a communal, breeding system.

Newborns are kept in a nest made by the mother (the natal nest; Baden et al. 2013) for three to 22 days and then periodically transported orally to other arboreal sites (Vasey 2007; Baden et al. 2013; Baden 2019). At Mangevo (Ranomafana National Park), gestating females of *V. variegata* individually construct multiple nests (n = 8) in the cruxes of trees (near the trunk) by chewing off branches and carrying them orally to drop among lianas and/or previously collected nesting material (Baden 2019). At Andranobe, nest and stash sites also occur in tree crowns, where they are often concealed and sheltered by dense foliage and old-growth woody vines (Vasey et al. 2018). Nests take on the form of platforms or shallow bowls just over 1 m wide (Morland 1990; Vasey 2007; Baden 2019). At Mangevo, nest and stash trees (average ~34 per female) are spread throughout each female's home range in proximity to feeding trees that are used throughout the year (Baden 2019). For *V. rubra* at Andranobe, nest and crèche trees (average ~40 per female) are clustered in different adjacent valleys within seasonally nonoverlapping core areas, and just 12 genera (24 species) make up 73% of trees used, all of which are known food species (Vasey et al. 2018). At this site, nest and crèche trees are the largest trees in the forest, even larger than those used for feeding (mean dbh [diameter at breast height] of nest and stash trees: 75.8 cm; mean dbh of feeding trees: 55.3 cm; Vasey et al. 2018).

Birth rates and infant mortality vary widely from year to year, both within and among populations of both species. For *V. variegata* on Nosy Mangabe, birth rate varied from 0.20 to 0.86 over two annual cycles, and infant mortality rate was 0.64 in one of those years (Morland 1990). For *V. rubra* at Andranobe, birth rate was 0.86 in one year, and there was no infant mortality over two annual cycles (Vasey 2007). At the other end of the spectrum, *Varecia* populations of both species collectively abandon reproduction for years at a time in the aftermath of major cyclones that reduce plant productivity (Ratsimbazafy 2002; Vasey and Borgerson 2009; Baden et al. 2013); interbirth intervals between one and six years are documented. These demographics may in part underlie variations in density (Table 14.29) and contribute to the ruffed lemurs' patchy distribution. Dramatic population growth can occur in adequate habitat and/or in productive fruiting years, especially given the capacity of these lemurs to produce litters. Such population growth potential may buffer them from local extinction in years or sequences of years when, owing to natural reasons, birth rate is low (or nil) and infant mortality is high. However, the patchy distribution of *Varecia* today is more complex, factoring in anthropogenic impacts (see Conservation, below).

HABITAT USE AND DIET

Varecia species show a similar microhabitat profile across many intact moist evergreen forest sites, regardless of other sympatric lemur species present. Members of this genus use mainly mid- to upper forest strata and relatively large feeding trees, and are active primarily by day (Vasey 2000b and references therein). Both species spend most of their time in tree crowns (94% of time on an annual basis) but show seasonal departures and daily rhythms during the hot seasons attributable to predator-avoidance tactics, reproduction, and thermoregulation (Vasey 2000b, 2004; Vasey et al. 2018; Beeby and Baden 2021). Locomotion and posture are cost-efficient for a high-canopy dweller; quadrupedal spring leaping allows *Varecia* species to travel through the often-discontinuous upper canopy without descending to seek out continuous arboreal pathways, and suspension allows access to plant foods located in the crown periphery (Britt 1997, 2000). Given the similarity in microhabitat use across studies, *Varecia* species appear to have relatively inflexible ecological requirements (Vasey 2000b). This ecological inflexibility has undoubtedly contributed to their vulnerability when faced with habitat alteration and loss, as *Varecia* species have fewer dispersal and habitat options than other lemurs (only *Eulemur rubriventer* is similarly both highly frugivorous and limited to eastern rain forests). Both *Varecia* species rarely come to the ground (Vasey 2002; Vasey et al. 2018) and are unlikely to traverse large open areas. Thus, habitat fragmentation and fragment isolation pose some of the most significant dispersal barriers to the genus (Holmes et al. 2013; Baden et al. 2014). Indeed, anthropogenic landscape features (i.e., habitat quality and human habitation) impede *V. variegata* gene flow more than natural barriers to gene flow such as rivers (Baden et al. 2019).

Yet, in degraded habitat where both lemurs and forest have fallen under protection, *Varecia* species have proven to be somewhat resilient, at least in the short term. At Manombo, an isolated forest fragment where *V. variegata* group sizes were halved and 85% of the canopy lost due to the unbuffered effects of a large-scale cyclone, the population rallied by broadening its diet, including more leaves and the fruits of two introduced, light-loving pioneer plants (*Miconia crenata* [previously known as *Clidemia hirta*], Melastomataceae; and *Cecropia peltata*, Urticaceae), which totaled 38% of their diet. They had no option but to use lower forest strata and began to reproduce again after a hiatus of four years (Ratsimbazafy 2002, 2006). In the Ambatoledama forest corridor of Masoala, a restoration site designed to connect wildlife populations separated by agricultural land and deforestation, *V. rubra* not only foraged in the recently planted corridor, dispersing native seeds, but also came to the ground frequently to feed on the ubiquitous *Miconia crenata* (Martinez 2010; Martinez and Razafindratsima 2014). Even in intact habitat, *Varecia* species show some degree of attraction to natural disturbance in that they are more frequently observed in close proximity to canopy gap edges created by cyclone-driven tree-fall gaps. At these tree-fall gaps, vegetative regrowth increases the quantity of fruit and young leaves at the canopy level (Mogilewsky 2020). Given the regularity of cyclones making landfall on Madagascar, co-adaptation to natural disturbance makes evolutionary sense for a canopy-dwelling frugivore such as *Varecia*.

Varecia species are among the most frugivorous living lemurs, spending 61–96% of feeding time on fruit. Mature leaves (0–17%), young leaves (2–6%), flowers (0–37%), and nectar (0–21%) are consumed less often (percentages are drawn from studies that sampled across all seasons over one or more annual cycles: Morland 1991a; Balko 1998; Vasey 2000b, 2002; Ratsimbazafy 2006; Erhart et al. 2018; Beeby and Baden 2021). At the highly disturbed sites of Kianjavato and Vatovavy, *Ravenala* (Strelitziaceae) flowers and nectar compose a large portion of the diet of *V. variegata* (23–34% annually; Holmes et al. 2016). At Andranobe, *V. rubra* fruit intake does not drop below 75% in any season and reaches 100% when females are neither gestating nor lactating, during the resource-scarce cold seasons (Vasey 2000b, 2002). At Mangevo, in contrast, frugivory in *V. variegata* reaches 100% in some months during the warm, wet, resource-rich season and dips as low as 25% in the cool, lean season. Leaf consumption is equally variable across years and seasons here, reaching 56% in some lean-season months (Beeby and Baden 2021), notably higher than that at other sites. Foliage intake, even in small proportions, may confer benefits at key times. During lactation, when protein requirements are greatest, *V. rubra* females at Andranobe show a daily rhythm, feeding more often on young leaves late in the day, when soluble carbohydrates in leaves peak, and before ensuing night-time inactivity, during which the leaves' protein and other nutrients can be slowly extracted (Vasey 2004). Moreover, compared to males, pregnant and lactating females more often diversify their diets with seasonally available young leaves and flowers, presumably low-fiber protein items (Vasey 2000b, 2002). These sex differences are attributed to high reproductive costs of *Varecia* females, as are sex differences in activity budgets and distances traveled between food patches (Vasey 1997b, 2005a).

At Mangevo and Andranobe, intact moist evergreen forest sites, *V. variegata* and *V. rubra* consumed the parts of 111 and 132 different plant species from 19 and 36 plant families, respectively (Vasey 2000a; Beeby and Baden 2021). Over a three-year period, dietary diversity of *V. variegata* was lower than that of *Propithecus edwardsi* or *Eulemur albifrons* (Erhart et al. 2018), as is common for frugivorous primates. Rigamonti (1993), Balko (1998), Ratsimbazafy (2006), and P. C. Wright et al. (2011) provide lists of plant species eaten by *Varecia* species. Plant taxa frequently consumed at most sites include *Canarium* (Burseraceae), *Chrysophyllum* (Sapotaceae), *Cryptocarya*, *Ocotea*, and *Ravensara* (Lauraceae), *Eugenia* (Myrtaceae), and *Ficus* (Moraceae). Some of these taxa are viewed as fallback foods, as they are eaten over a protracted period in times of relative resource scarcity (Vasey 2000a; Balko and Underwood 2005; Beeby and Baden 2021). Balko and Underwood (2005) note that areas of Madagascar that contain high tree-species richness (e.g., Masoala and Nosy Mangabe) also support some of the highest densities of *Varecia* species (Table 14.29). They speculate that these lowland moist evergreen forests, which experience a lot of natural disturbance, can support elevated densities of *Varecia* because high tree-species richness increases the probability of year-round fruit availability, which buffers the effects of asynchrony in the fruiting phenology of Malagasy forests.

SOCIAL SYSTEM AND RANGING PATTERNS

Wild *Varecia* populations of both species exhibit considerable behavioral variation. A wide array of community (or group) sizes, social structures, social organizations, and home-range sizes, as well as differences in territorial behavior, have been documented. On the basis of surveys at Analamazaotra, Fanovana, and Ambodiriana (in July and October) and of short-term observations at several other localities, early field reports suggested that members of this genus live in cohesive, territorial family groups of two to four individuals (J.-J. Petter 1962; J.-J. Petter et al. 1977; Pollock 1979). A two-month study during the austral winter at Ranomafana reported that two *V. variegata* individuals lived as a cohesive, monogamous pair in an enormous home range of 197 ha (F. J. White 1991). A subsequent longer-term study in the same region documented cohesive, territorial, multi-female and/or multi-male groups of four to nine animals, in home ranges of 100–150 ha (Balko 1998), that grew dispersed over the course of several years (Balko and Underwood 2005). In an eight-month-long study in Betampona, *V. variegata* was found in dispersed monogamous groups of two to five individuals (an adult pair and presumed offspring) in home ranges of 28.9–43.1 ha (Britt 1997).

In all other long-term-study populations, both species of *Varecia* live in multi-female and/or multi-male communities with a fission-fusion type of social organization that has both daily and seasonal components (Nosy Mangabe, Morland 1991a, 1991b; Ambatonakolahy Forest on Masoala, Rigamonti 1993; Andranobe Forest on Masoala, Vasey 2006; Mangevo at Ranomafana, Baden et al. 2016; Kianjavato Forest, Holmes et al. 2016). Subgroup transitions (either fissions or fusions) occur on average every 90 minutes, on the same order of magnitude as in the highly dynamic fission-fusion social systems of chimpanzees, bonobos, and spider monkeys (Baden et al. 2016). Yet, compared to these haplorrhine taxa, both species of *Varecia* form smaller subgroups, have dramatically lower rates of social interaction (solitary 48% of the time), and have a female-centered social organization (Morland 1991a, 1991b; Baden et al. 2016). Interestingly, neither social associations nor social preferences in *Varecia* can be explained by kinship; rather, associations are best explained by shared range use (Baden et al. 2021). Some, though not all, of the behavioral variation found in different populations of members of this genus may be an artifact of short-term observations in early studies and a lack of sampling during the hot rainy season, when fission-fusion dynamics are elevated and it is possible to clearly discern that small aggregations (i.e., two to four individuals) are part of a larger community network (Vasey 2003, 2006). Low population density and its underlying causes (e.g., resource distribution and floristic diversity, hunting pressure, presence of other day-active frugivorous lemurs) may also contribute to the formation of stable, cohesive groups at some sites (Table 14.29; Vasey 2006; Baden et al. 2016).

The *V. variegata* population on Nosy Mangabe communally defends food resources but is not territorial (Morland 1991a, 1991b), whereas at Mangevo, Andranobe, and (possibly) Ambatonakolahy, members of this genus are territorial, communally defending exclusive home-range boundaries (Rigamonti 1993; Vasey 2006; Baden et al. 2016). Females play the most active role in defending food resources and/or home-range boundaries, and despite the variation in territorial behavior, all four populations mentioned above are similar in their seasonal ranging patterns and, concomitantly, their fission-fusion social organization. For example, in these studies *Varecia* communities are formed of core groups with discrete core areas; core groups disperse into separate core areas in the food-scarce cold season, and individuals travel shorter daily distances in cold versus hot months. Shifts in ranging correspond with seasonal food distribution and/or reproductive stages, albeit to a much larger extent in females than in males (Vasey 2006; Baden et al. 2021). Thus, the ranging pattern of both species of *Varecia* appears to be the outcome of its reproductive pattern combined with its reliance on a spatiotemporally patchy diet of ripe fruit, flowers, and young leaves (Vasey 1997a, 2006). This co-adapted interaction between reproduction and foraging ecology may necessitate flexibility in its social behavior. In turn, flexible social behavior appears to provide the means for maintaining ecological similarity across sites (see Habitat Use and Diet).

COMMUNICATION

Like other diurnal lemurs, ruffed lemurs use vocal, visual, and olfactory modes of communication. Little research on *Varecia* communication has accumulated since the precursor of this contribution, so we refer readers to that review (Vasey 2003) and limit our discussion to a few notable traits. Female greeting displays are spectacular, involving anogenital scent marking of each other's backs, jumping over one another in a leapfrog fashion, writhing together, and emitting soft squealing sounds (Morland 1991a; Vasey 2006). These displays occur during the hot season, when female ranges overlap extensively and fission-fusion dynamics are elevated (Vasey 2006). *Varecia* is further distinguished by its highly aggressive antipredator behavior that involves mobbing accompanied by loud calls that continue long after the stimulus (i.e., predator) has departed. Ground predators evoke "pulsed squawks," while aerial predators elicit the contagious "abrupt roar." These antipredator tactics are seen in part as an effect of larger body size but also as a consequence of having young bound to nest and crèche sites, which prevents adults from fleeing predators without risking reproductive loss (Macedonia 1993a). Field observations suggest that the "roar/shriek chorus" (a group-advertisement loud call) facilitates dispersed intra-community communication within large home ranges by permitting, for example, coordination of individual schedules during infant-stashing season via vigilance displays (Vasey 2007) and time-sharing of highly prized masting fruit trees by subgroups during certain times of year (Vasey 2000b). Another remarkable trait is that some *Varecia* females possess trichromatic vision—those that are heterozygous at the X-linked M/L opsin gene locus (Y. Tan and Li 1999; G. H. Jacobs and Deegan 2003). These females may have an advantage in detecting young leaves that flush red against a background of mature green foliage (Dominy and Lucas 2001; Vasey 2004). The vocal, visual, and olfactory communication systems of *Varecia* clearly warrant further research.

CONSERVATION

Both *V. rubra* and *V. variegata* are classified as Critically Endangered (IUCN 2020). Hunting and anthropogenic habitat loss (e.g., due to swidden agriculture and logging) have reduced their numbers in many areas of their range (Rigamonti 1996; Lehman et al. 2006c; Hekkala et al. 2007). These factors quite likely increase the naturally patchy distribution of *Varecia* species and make demographic declines permanent (Vasey 2005b). Many *Varecia* populations have been reduced to living in physically and genetically isolated forest fragments surrounded by periodically burned agricultural land (e.g., Manombo, Louis et al. 2005; Vatovavy Forest, Holmes et al. 2013). Isolated forest fragments have poor prospects for recovery after natural cyclone damage, as fires can rage unchecked, consuming fallen trees, and the influx of animal-dispersed seeds or pollen can be greatly reduced. Degraded forest seems unable to support top frugivores such as *Varecia* species, and these lemurs' numbers are greatly diminished or absent in such areas (Table 14.29). Habitat fragmentation has had a strongly negative effect on the occurrence of *V. variegata* in particular (Eppley et al. 2020).

Although total remaining population size is unknown, it is clear that the occurrence of *Varecia* is tied to the presence of moist evergreen forest habitat. Deforestation is projected to eliminate *Varecia* habitat before 2080 and therefore presents the most immediate threat to their survival, surpassing the projected adverse effects of climate change (Morelli et al. 2020). What makes *Varecia* species especially vulnerable is their need for numerous exceptionally large trees in which to nest and stash their litters, leading Vasey et al. (2018) to propose that logging directly precipitates local extinctions by impeding these lemurs' ability to reproduce. Indeed, *V. rubra* is negatively impacted by altered habitat even more than by hunting, as compared to the sympatric *Eulemur albifrons* (Borgerson 2015). Nonetheless, *Varecia* is intentionally trapped for food (Golden 2009; Borgerson 2016) and for the bushmeat and pet trades (Vasey 1996; Reuter et al. 2019), even in protected areas, and harvest rates are not sustainable, putting the genus at significant extinction risk (Golden 2009; Brook et al. 2018).

Varecia rubra has been afforded protection within Madagascar's two largest protected areas, Masoala and Makira, whereas *V. variegata* occurs in at least 17 protected areas throughout Madagascar's eastern moist evergreen forest corridor (Goodman et al. 2018b). Both species are the subjects of reintroduction and translocation projects: a captive-to-wild reinforcement effort for *V. variegata* at Betampona (e.g., Britt et al. 2004); a translocation of wild *V. variegata* to Analamazaotra, where the species had been locally extinct since 1976 (Day et al. 2009); and a translocation of wild *V. rubra* to Fanankaraina reserve (a private holding managed by a local NGO, Antongil Conservation; GERP 2016), where the species has been locally extinct for several decades (T. Alexis, unpublished data).

Both species of *Varecia* are flagship taxa for conservation efforts. Their habitat requirements are strict, such that they disappear early in the process of anthropogenic habitat degradation; they have large home ranges that encompass a myriad of other plant and animal taxa; and lastly, they are charismatic, beautiful animals that scientists and nonscientists alike can appreciate. Bust-boom reproduction is a defining life-history trait of *Varecia*, and the genus is thereby equipped to rebound after natural catastrophes. Moreover, in degraded habitats where both lemurs and forest have fallen under protection, *Varecia* has proven to be somewhat ecologically resilient, at least in the short term. Should we be successful in maintaining the protected area network and connecting populations of this genus throughout eastern Madagascar, it will benefit the larger mission of biodiversity conservation on Madagascar as a whole.

Subject editors: Jörg U. Ganzhorn and Steven M. Goodman

INDRIIDAE: *AVAHI*, WOOLLY LEMURS, *FOTSY-FE*, *TSARAFANGITRA*, *DADINTSIFAKY*

G. Donati, I. Norscia, M. Balestri, A. Zaramody, E. E. Louis Jr., and U. Thalmann

The woolly lemurs, *Avahi* species, are the only nocturnal members of the family Indriidae, which also includes *Propithecus* species and *Indri indri*. The English vernacular name refers to the curly, woolly appearance of the dense fur, whereas the genus name is a transcription of its typical high-pitched and rapid, loud call (*wo-he, va-hií, vou-hií*). In southeastern and eastern Madagascar, *Avahi* species are usually called *fotsy-fe* ("white thigh" in Malagasy), reflecting the white fur coloration on the inner backside of their thighs. In the west of the island, lemurs of this genus have locally varying names. For example, in the region of Mahajanga they are called *tsarafangitra*, meaning "well-dressed hair" in Malagasy, while in the central western region they are called *dadintsifaky*, which translates to "grandparent [or ancestor] of the *sifaka*" (*Propithecus*).

TAXONOMY

As has happened in other lemur groups, particularly nocturnal genera, the taxonomy of the monophyletic genus *Avahi* was significantly revised in recent years, resulting in the current identification of nine species (IUCN 2020). These species are: *A. betsileo* (Betsileo Woolly Lemur; Figure 14.52f), *A. cleesei* (Bemaraha Woolly Lemur; Figure 14.52a), *A. laniger* (Eastern Woolly Lemur; Figure 14.52e), *A. meridionalis* (Southern Woolly Lemur; Figure 14.52i), *A. mooreorum* (Masoala Woolly Lemur; Figure 14.52d), *A. occidentalis* (Western Woolly Lemur; Figure 14.52b), *A. peyrierasi* (Peyriéras' Woolly Lemur; Figure 14.52g), *A. ramanantsoavani* (Manombo Woolly Lemur; Figure 14.52h), and *A. unicolor* (Sambirano Woolly Lemur; Figure 14.52c) (Thalmann and Geissmann 2005; Zaramody et al. 2006; Andriantompohavana et al. 2007; Lei et al. 2008). For well over a century, *A. laniger* was considered to be the only species in the genus. Rumpler et al. (1990) demonstrated that western and eastern populations should be distinguished from one another based on cytogenetic characters and suggested the recognition of two different species: *A. occidentalis* and *A. laniger*. As for the western forms, *A. unicolor* and more recently *A. cleesei* were later identified as separate species from *A. occidentalis* based on morphological differences and vocalizations (Thalmann and Geissmann 2000, 2005). As for the eastern forms, on the basis of mtDNA analyses, *A. meridionalis* and *A. peyrierasi* were first identified as different species from *A. laniger* (Zaramody et al. 2006), and this was followed by a further split from *A. peyrierasi* of *A. betsileo*, *A. ramanantsoavani* (Andriantompohavana et al. 2007), and *A. mooreorum* (Lei et al. 2008).

An analysis of complete mitochondrial genome indicates that within the Indriidae, the nocturnal *Avahi* and the diurnal *Propithecus* separated about 13 Mya (Finstermeier et al. 2013). Chromosomal and molecular analyses suggest that the genus *Avahi* first diverged in an eastern group and a separate western group followed by differentiation on the mitochondrial level but without any chromosomal changes (Rumpler et al. 2011). Within the western region, the Betsiboka River seems to constitute a major geographic barrier separating northern from southern taxa. Within the eastern region, the main barrier between the northern and the southern forms appears to be the Mangoro-Onive River system (Rumpler et al. 2011). Based on an illustration from Sonnerat (1782), *A. laniger* was described by Gmelin in 1788. Sonnerat's itineraries would place the most plausible type locality of *A. laniger* in northeastern Madagascar, specifically the Maroantsetra region (Zaramody et al. 2006).

ACTIVITY

It has been hypothesized that *Avahi* is secondarily nocturnal and that its gregarious lifestyle is retained from a former diurnal activity pattern (Ganzhorn et al. 1985; A. E. Müller and Thalmann 2000). Both *A. laniger* and *A. occidentalis* have been described as mainly nocturnal, with a decrease in activity in the central hours of the night and a correlation between night length and overall amount of activity (Ganzhorn 1985; Thalmann 2006). A more recent study,