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INTRODUCTION

New Developments in the Behavioral Ecology and Conservation of Ruffed Lemurs (*Varecia*)

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The papers in this issue were presented at a symposium during the 25th Annual Meeting of the American Society of Primatologists held in Oklahoma City, Oklahoma, in June 2002. This symposium brought together many of the scientists who have contributed to our knowledge of ruffed lemur ecology, behavior, and conservation in the past decade. One objective was to share and compare key findings about ruffed lemurs (*Varecia*) resulting from long-term field studies at various sites in Madagascar. A second objective was to cross-fertilize work being done in the wild with that being done in captivity, with the aim of advancing a common conservation mission for this critically endangered genus. *Varecia* is a prime candidate for synthetic assessments such as these because it has now been studied in both the northern and southern reaches of its geographic range, and has also been the focus of a captive-to-wild reinforcement project. The papers in this issue contribute to 1) the establishment of reference ranges for a suite of physiological parameters in healthy wild *Varecia* populations; 2) environmental enrichment aimed at preserving species-typical behaviors in captivity; 3) an understanding of how forest structure, floristic composition, and fruiting phenology in areas with differing disturbance histories correlate with the natural occurrence and abundance of *Varecia*; 4) primary knowledge concerning dominance relations between the sexes and group leadership in wild *Varecia*; and 5) primary knowledge concerning how wild *Varecia*, with their unusual reproductive pattern and heavy reliance on fruit, modulate their activity budgets seasonally and in tandem with reproductive stages. *Am. J. Primatol.* 66:1–6, 2005. © 2005 Wiley-Liss, Inc.

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EARLY FINDINGS AND RECENT REVISIONS

Modern behavioral and ecological studies of wild lemurs began in earnest in the late 1950s and 1960s, resulting in the early publications of Jean-Jacques Petter [1962a, b] and Alison Jolly [1966]. On the basis of broad surveys and short-term observations at a variety of sites, early field reports suggested that *Varecia* was primarily crepuscular; consumed a varied diet of leaves, fruits, and flowers; and lived in cohesive, territorial family groups of two to four individuals (males, females, and their young) [Petter, 1962a, b; Petter et al., 1977; Pollock, 1979]. The dental anatomy of *Varecia* was considered well-suited for cracking and mashing hard fruits, seed pods, nuts, and stems [Seligsohn & Szalay, 1974]. Some of the unusual reproductive traits of wild *Varecia* were also noted early on (e.g., females bear litters, use nests, and orally transport their young) [Petter, 1962a, b; Petter et al., 1977]. These early characterizations of *Varecia* have been revised (in some respects quite substantially) in light of more-recently completed long-term field studies. *Varecia* is now considered the most frugivorous extant lemur (it spends 74–90% of feeding time on fruit annually) [Balko, 1998; Morland, 1991a; Ratsimbazafy, 2002; Vasey, 2002], and characterizations of its social structure and social organization have been vastly broadened. A relative consensus has emerged that *Varecia* exhibits extraordinary behavioral variation in the wild [Balko, 1998; Vasey, 1997a, 2003], and should no longer be viewed as living *en suite* in small, cohesive, territorial family groups [Morland, 1991a, b]. Group size and composition, intra- and intergroup spacing patterns, and home range size all differ considerably between localities in which long-term studies have been carried out [Balko, 1998; Britt, 1997; Morland, 1991a, b; Ratsimbazafy, 2002; Rigamonti, 1993; Vasey, 1997a] (reviewed in Vasey [2003]). This remains the case whether black-and-white ruffed lemurs and red ruffed lemurs are considered subspecies or separate species (the latter taxonomy is adopted here, following Groves [2001] and Vasey and Tattersall [2002]). For several populations in which a dispersed fission-fusion type of social organization has been observed, the term “group” has largely been dropped and the term “community” adopted in descriptions of social structure and social organization [Morland, 1991a, b; Vasey, 1997a].

NEW CONTRIBUTIONS

With the advent of long-term field studies on *Varecia* and other lemur species in the eastern rainforests of Madagascar, beginning in the mid-1980s, came the perception that this highly frugivorous genus is particularly susceptible to local extinction due to human-induced habitat loss and hunting [Rigamonti, 1996; Simons & Lindsay, 1987; Vasey, 1996]. A thorough understanding of *Varecia*’s ecological requirements and adaptations, and its responses to both natural and anthropogenic disturbances have subsequently become the focus of recent field studies [Balko, 1998; Morland, 1991a; Ratsimbazafy, 2002; Rigamonti, 1993; Vasey, 1997a]. In contrast to the marked behavioral variation evident at different sites, *Varecia* populations have been shown to share many ecological characteristics across sites. *Varecia* is highly frugivorous, uses the highest forest strata and the largest feeding trees, is active primarily by day, and is limited to rainforests. An exception to this ecological profile is found at the Réserve Spéciale (RS) de Manombo and an adjacent classified forest, where the combined effects of anthropogenic activity (e.g., subsistence agriculture and logging) and natural disasters (e.g., cyclones and windstorms) have resulted in the loss of large trees and much of the upper forest strata. At the height of forest disturbance (after

cyclone Gretelle hit in 1997), *V. variegata* at Manombo ranged primarily in the herbaceous understory and lower canopy, feeding extensively on the fruits of a non-native shrub (*Clidemia hirta*) and other low-growing, relatively small trees [Ratsimbazafy, 2002]. Given the otherwise consistent ecological profile of *Varecia*, it has been suggested that flexible social behavior may provide a means of maintaining ecological similarity across a wide variety of sites [Balko, 1998; Vasey, 1997a, 2000].

Varecia's reproductive traits (see above) were long considered enigmatic, and additional information on gestation length, growth rates, maternal investment, and other life history variables only furthered the puzzlement [e.g., Pereira et al., 1987; Rasmussen, 1985; Young et al., 1990]. Field studies have begun to unravel some of this mystery at the organismal level. In this regard, great insight has come from recognizing the common occurrence of intra-annual variation in *Varecia*. A wide array of behavioral and ecological variables (e.g., intragroup/community spacing, frequency of social interactions, diet, ranging, and micro-habitat use) shift seasonally [Britt, 2002; Morland 1991a, b; Rigamonti, 1993; Vasey, 1997a, 2000, 2002, 2004] and/or in tandem with reproductive stage [Vasey, 1997a, 2000, 2002, 2004]. Intra-annual variation in the behavioral ecology of this litter-bearing primate appears to be highly integrated with seasonal oscillations in climate and food distribution, as well as with the energy demands of different reproductive stages (gestation and lactation) [Morland, 1991a, b; Vasey, 2000, 2002, 2004]. In this issue, contributions by Overdorff et al. and Vasey advance our understanding of how *Varecia*'s reproductive adaptations are mediated ecologically and socially in relatively intact natural forests. Overdorff et al. examine dominance relations between the sexes, and group leadership in both feeding and nonfeeding contexts at the Parc Nationale (PN) de Ranomafana, while Vasey demonstrates how male and female activity budgets shift throughout the year both seasonally and in tandem with reproductive stages at the PN de Masoala.

Varecia's reproductive traits are beginning to be understood from a demographic perspective as well, although long-term demographic monitoring will require many years to yield definitive results. Given its high population growth potential relative to other lemurs, *Varecia* seems well adapted to rebound after natural demographic declines caused, for example, by natural habitat disturbance. On Madagascar, natural habitat disturbances are caused not only by relatively predictable seasonal oscillations in climate, but also by unpredictable annual variations in climate (typified by the catastrophic cyclones that frequently strike the island) [Donque, 1975; Ganzhorn, 1995]. Adaptation to episodic climatic fluctuations, in particular, may partly explain the patchy geographic distribution [Balko, 1998; Vasey, 1996, 1997b], widely fluctuating birth rates and infant mortality rates [Morland, 1990; Ratsimbazafy, 2002] (Vasey, unpublished results), and highly disparate population densities (reviewed in Vasey [1997b, 2003]) documented in wild *Varecia*. In other words, longitudinal shifts of large amplitude in *Varecia*'s demographic profile may be an intrinsic aspect of its biology. However, anthropogenic activity complicates this scenario. Anthropogenic disturbances (e.g., from agriculture and logging) have had particularly devastating effects on the distribution and abundance of *Varecia*. Quite likely, such disturbances have increased *Varecia*'s naturally patchy distribution and made demographic declines permanent. Many of the remaining populations are reduced to living in isolated forest fragments surrounded by periodically burned agricultural land [e.g., Balko, 1992; Britt, 1997; Britt et al., 1999a; Ratsimbazafy, 2002; Welch & Katz, 1992]. Not surprisingly, given its high population growth potential, *Varecia* populations show signs of staging comebacks in several

disturbed areas that have recently come under protection. Balko's article in this issue directly addresses how such a process might come about by examining how forest structure, floristic composition, and fruiting phenology in areas with differing anthropogenic disturbance histories within the PN de Ranomafana correlate with the natural occurrence and abundance of *Varecia*. Over a 5-year period, the abundance of *Varecia* increased even in the severely disturbed RS de Manombo [Ratsimbazafy, 2002]! What the PN de Ranomafana and the RS de Manombo have in common is that they are both part of the protected area network in Madagascar. With cautious hope, I advance the view that protected areas have begun to play a key role in reversing negative demographic trends in the genus *Varecia*.

In Madagascar, *V. variegata* and *V. rubra* are indicator, umbrella, and flagship species [Vasey, 2003]. In U.S. and European zoos, both species breed well and are relatively abundant and healthy [Porton, 1992]. While genetic diversity is relatively high in the captive *V. variegata* population, more founders are needed to increase genetic diversity in the captive *V. rubra* population [Porton, 2002]. These factors made *V. variegata* a promising candidate for a captive-to-wild reinforcement project that is now taking place at the Réserve Naturelle Intégrale (RNI) de Betampona. The depleted, isolated population of wild *V. variegata* (~35 individuals) that persisted at Betampona until the early 1990s likely lacked genetic diversity and long-term viability [Welch and Katz, 1992]. While many of the captive-born animals that were translocated to the RNI de Betampona during the past 7 years have not survived (mainly because of predation by *Cryptoprocta ferox*), others have successfully begun to reproduce and integrate with their wild counterparts [Britt et al., 1999b, 2003; Welch & Iambiana, 2001–2003]. Given the cautious hope expressed in the previous paragraph with respect to the key role protected areas are playing in harboring endangered populations, *Varecia*, as a taxon, and the RNI de Betampona, as a protected area, may ultimately prove to be good choices for a captive-to-wild reinforcement program. To date, *Varecia* is the only lemur taxon that has been the focus of such efforts.

Highly varied information must be gathered prior to, during, and after wildlife translocations, both to improve the immediate chances of survival for translocated animals and to optimize wildlife management in the long term. The contributions in this issue are representative of such varied efforts. Operating on the principal that captive conservation breeding programs should be concerned with the conservation of species-typical behaviors as well as genetic diversity, Kerridge compares the activity budgets and social and solitary behaviors of captive and wild *V. variegata*, articulates key ways in which they differ, and then devises an experimental study aimed at promoting species-typical feeding behaviors in captivity via environmental enrichment. Operating on the principal that baseline information on healthy wild animals is needed to optimize the care of both wild and captive *Varecia*, Junge and Louis establish reference ranges for a suite of physiological parameters in healthy wild *Varecia* populations. Such baseline information is critical on a wide variety of fronts, from determining which captive *Varecia* are the best candidates for translocation (e.g., those that pose no disease risk), to being better prepared to treat disease in both wild and captive populations, to improving the diet and general health of captive *Varecia*.

THE FUTURE

The future is uncertain for *Varecia* and other lemurs. Some populations have fared relatively well, others will get by with a lot of help from their friends, and

still others are gone but not forgotten. There is so much yet to learn. Coordinated efforts between researchers who have experience with captive populations and those who work in the wild have been enlightening and have prompted us to address critical questions that we might not have otherwise considered, and that have enabled us to integrate our conservation mission. Whether inquiries focus on ground-truthing, ecology, behavior, reproduction, demography, *in situ* management, or *ex situ* management, our common goal is to ensure that our distant relatives will be secure in the lifestyles they evolved in nature.

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