American Journal of Primatology 47:15–28 (1999)

RESEARCH ARTICLE

Changes in Behavior in Free-Ranging *Lemur catta* Following Release in a Natural Habitat

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The adjustment of captive-reared and developmentally deprived ringtailed lemurs (*Lemur catta*) to supported release on St. Catherine's Island, Georgia, was studied over 7 years to examine if these animals developed behavior comparable to wild populations. Initial changes after release included decreased obesity and increased agility as well as foraging for appropriate novel plants. Ranging, daily behavior cycles, and vocalizations developed more slowly over 1–3 years, but eventually the behavior resembled that of wild groups. Group composition and social structure changed through conflict to resemble wild and captive troops in social organization, including the emergence of matrilineal dominance and male emigration. Since behavior eventually resembled that seen in the wild, some resilience of species-typical wild behavior in captivity is supported. Am. J. Primatol. 47:15–28, 1999.

Key words: release; *Lemur catta;* lemurs

INTRODUCTION

Although reintroduction is a potentially important tool for primate conservation [Griffith et al., 1989; Kleiman, 1989; Primack, 1993], few mammal reintroduction programs are successful [Beck, 1994]. The chances of success can be increased by selecting individuals for reintroduction that have necessary basic behaviors and skills, including how to navigate and utilize relevant habitat for essentials such as food and shelter while avoiding predators as well as an appropriate repertoire of social behaviors [Kleiman, 1996]. Such behaviors may be genetically hard-wired and only require circumstances for expression or may be learned so that reintroduction candidates may need to be trained [e.g., Box, 1991]. Various behaviors related to ecological and social functioning may also be highly

Contract grant sponsor: Wildlife Conservation Society; Contract grant sponsor: The St. Catherine's Island Foundation; Contract grant sponsor: Faculty Research Grants Committee of the University of the South.

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Received 27 November 1995; revision accepted 9 June 1998.

variable and reflect adaptations to local conditions, and it is important for reintroduced individuals to have the flexibility to respond to local conditions.

Captive-raised lemurs often have few of the skills needed to survive in wild when living in restricted conditions but may develop them under free-ranging conditions. Studies of semi-free-ranging *Lemur catta* released into multihectare forested enclosures at the Duke University Primate Center (DUPC) [Taylor, 1986; Pereira et al., 1990] indicate that captive-born individuals express social behavior that closely resembles that observed in the wild [Jolly, 1966; Budnitz & Dainis, 1975; Mertl-Millhollen et al., 1979; Jolly et al., 1982; Sussman, 1991]. This group also developed habitat selection typical of the species and selected novel nontoxic food items [Ganzhorn, 1985, 1986]. *L. catta* released at the DUPC, however, were an established social group that had been in an outdoor run for several years (DUPC records). It is not clear whether animals without prior opportunity to express relevant behaviors can adapt to free-ranging conditions.

It is also important to determine what aspects of a species' social and ecological repertoire remain constant across conditions and which demonstrate variability. It is known that lemur behavior and ecology varies with habitat. For example, sifakas, *Propithecus verreauxi,* defend fixed territorial boundaries in some dry southern forests but not in some moist northwest forests [Richard, 1978]. Variations in the social system with location have been reported for *L. mongoz* [Tattersall, 1978] and differences in populations of *L. fulvus rufus* in density, home range, and group size have also been found [Sussman, 1974; Overdorff, 1991]. The social organization of ruffed lemurs, *Varecia variegata,* is highly variable between populations and between the wild and captivity, ranging from long-term (at one site from 1988–1992) monogamy [Petter et al., 1977; Foerg, 1982; Tattersall, 1982; White, 1991; White et al., 1992, 1993] to multimale and multifemale [Pereira et al., 1988; Morland, 1990, 1991; White, 1991; White et al., 1992]. In wild populations of *Lemur catta,* home range size may vary according to the density of local resources. Variation in demographic parameters can have long-term consequences on group structure for this species [Sussman, 1991; O'Conner, 1987]. Although *L. catta* has been studied at multiple sites in the wild and in captivity under free-ranging conditions [Jolly, 1966; Sussman, 1972, 1974, 1991; Budnitz & Dainis, 1975; Mertl-Millhollen et al., 1979; Jolly et al., 1982, 1993; Ganzhorn, 1985, 1986; Taylor, 1986; Pereira et al., 1990; Sauther, 1991; Pereira, 1993; Sauther and Sussman, 1993], the relevance of captive studies to reintroduction to the wild has not been examined. The ability of even a deprived individual to adjust to a natural setting and show species-specific behaviors is essential to showing that these animals could be candidates for reintroduction.

We studied the supported release by the Wildlife Conservation Society (then the New York Zoological Society) of a captive-born *L. catta* group on St. Catherine's Island, Georgia, from release in 1985 until 1992 to examine whether captive, inexperienced adults could develop social and ecological behaviors appropriate to the species and to see what aspects of these behaviors were either conserved across captive and wild study populations (i.e., species-typical) or could vary with local environmental conditions.

METHODS

Subjects

The original subjects of this study were six *L. catta* (Fig. 1). The three youngest (NER, F '82; ROM, M '83; JUL, F '84) were full siblings born in successive years at the Bronx Zoo. Appearance and behavior in the absence of records suggested that the two older females (KAT, '71; POR '78) may be siblings or mother and daughter

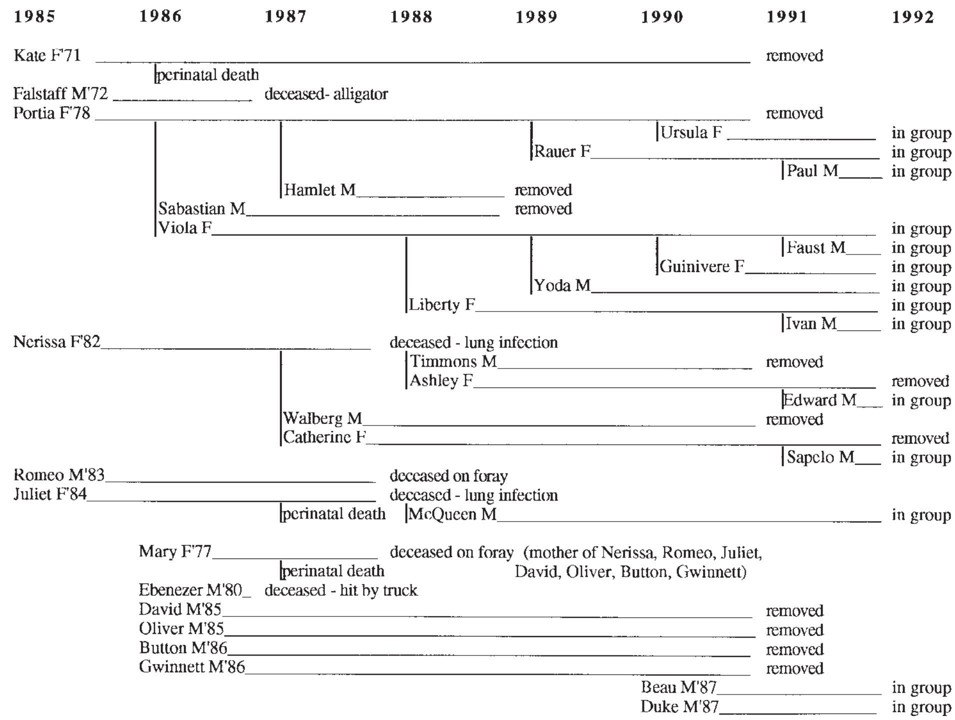

Fig. 1. Social history of *Lemur catta* released on St. Catherine's Island, including maternity, by year of release, birth in the group, or death. The date of birth of released animals is indicated following their name and sex.

and the older male (FAL '72) unrelated. The six animals had been housed in indoor walk-in cages in winter and outdoor display cages in summer at the Monkey House of the Bronx Zoo, without natural vegetation or the opportunity to disperse from each other. Three months prior to being moved to St. Catherine's Island, they were housed together indoors [Koontz, personal communication]. In April 1985, they were moved to walk-in cages on the island and then released in June 1985. All except the juvenile female (JUL) were greater than 20% above normal adult *L. catta* weight. All individuals showed limited behavioral repertoires relative to *L. catta* observed by the authors at DUPC. They were unable to climb a brick wall or large-diameter tree or to leap accurately, made no vocalizations beyond low grunts, and had no known experience with foraging. The older three animals were not observed running or leaping and typically moved at a slow walk.

An additional six subjects, including the parents (MAR, F '77; EBE, M '80) of the younger three in the first group and this pair's 1985 (DAV, OLI) and 1986 (BUT, GWI) male twins (Fig. 1), were released in December 1986 from a second site. This second group had been housed together and resembled the first group: the adult pair was obese and sedentary, and all individuals lacked agility and environmental experience and made no loud vocalizations.

Site

The study site is a largely undeveloped semitropical barrier island of 2,900 ha and approximately 16 km (N–S) by 3 km (E–W) on the Atlantic coast 22 km south of Savannah, Georgia (Fig. 2). The release site was located at 31° 38' north latitude, 81° 09' west longitude. The island is largely forested, with pine (*Pinus elliottii, P. taeda*), oak (*Quercus virginiana, Q. nigra*), and palmetto (*Sabal palmetto*) species predominating. A variety of habitats, varying from salt marsh to open forest, fresh water ponds, and open pastures, is available within 2 km of the release point. Mean annual rainfall is 126 cm, the highest daily mean temperature is 33°C in July, and the lowest is 4°C in January. The record lowest recorded temperature is –16°C.

A 6.3 × 18 m brick garage was converted to contain three 5 × 6 × 2.5 m walk-in cages connected to a 5 × 16 × 2.5 m outdoor wire run by small guillotine doors. Water was available at the garage from lick dispensers. Nest boxes with minimal heating were located indoors. The garage faces a lawn interspersed with pine, oak, and palmetto trees and is at the northern edge of the only developed part of the island, an area approximately 200 m (E–W) by 2,000 m (N–S) containing lawns, open forest, occasional small buildings, and pastures. Immediately adjacent to the garage is an overgrown grape (*Vitis rotundiflora*) arbor supported by red bay (*Persea borbonia*) trees. The mixed oak and pine forest adjoining the release site supplied additional forage, water, and sleeping sites. The second release site was located in this forest, 200 m northeast of the first site, and included a minimally heated shelter, outdoor walk-in cage space, and lick dispensers for water (Fig. 2). More detailed descriptions of St. Catherine's Island are available in Thomas et al. [1978] and Thomas [1988].

Procedure

Prior to the first release, the subjects were housed together in the garage for approximately 10 weeks. Each animal was equipped with a Telonics radio transmitter and a distinctively colored collar. The subjects were supplied once daily with several bowls of dry monkey chow, canned primate diet, vitamin supplement, and chopped fruit and vegetables on the ground at the release sites. Quantities were sufficient for at least some of the less-favored food items to be uneaten by the time of the next feeding throughout the study and without supplementation from foraging.

Following the first release in June 1985, the subjects were observed for 8–10 h per day for 50 days for short-term adjustment. Thereafter data were taken for 2 day periods spaced approximately 6 weeks apart for 7 years (1985–1992), with longer periods of observation in July 1986 and spring 1987. Data were taken in two forms, the first being scan samples at half-hour intervals which recorded for each animal behavior, location, and height above ground. Animals were considered active if the class of behavior recorded involved locomotion (e.g., walk, climb) or foraging but not sedentary activities such as mutual grooming. Temperature, weather, and light conditions were also recorded. Social contacts and plants foraged were recorded through focal animal observations lasting usually 2 h each. Over 2,000 scan samples (times the number of animals present) and 600 h of focal animal data were collected over 7 years, with even distribution of scan samples from dawn to dark and of focal animal observations from 0800–1800 h throughout the year.

Interobserver reliability was maintained by the senior observer (T.K.-L.) making 33% or more of each day's observations, reviewing all other data collected each day, and making parallel observations with each new observer. Data were analyzed using G tests of independence (with Williams correction) to examine the relative frequency of classes of behavior and Student's t-test for comparisons of weights [Sokal & Rohlf, 1981].

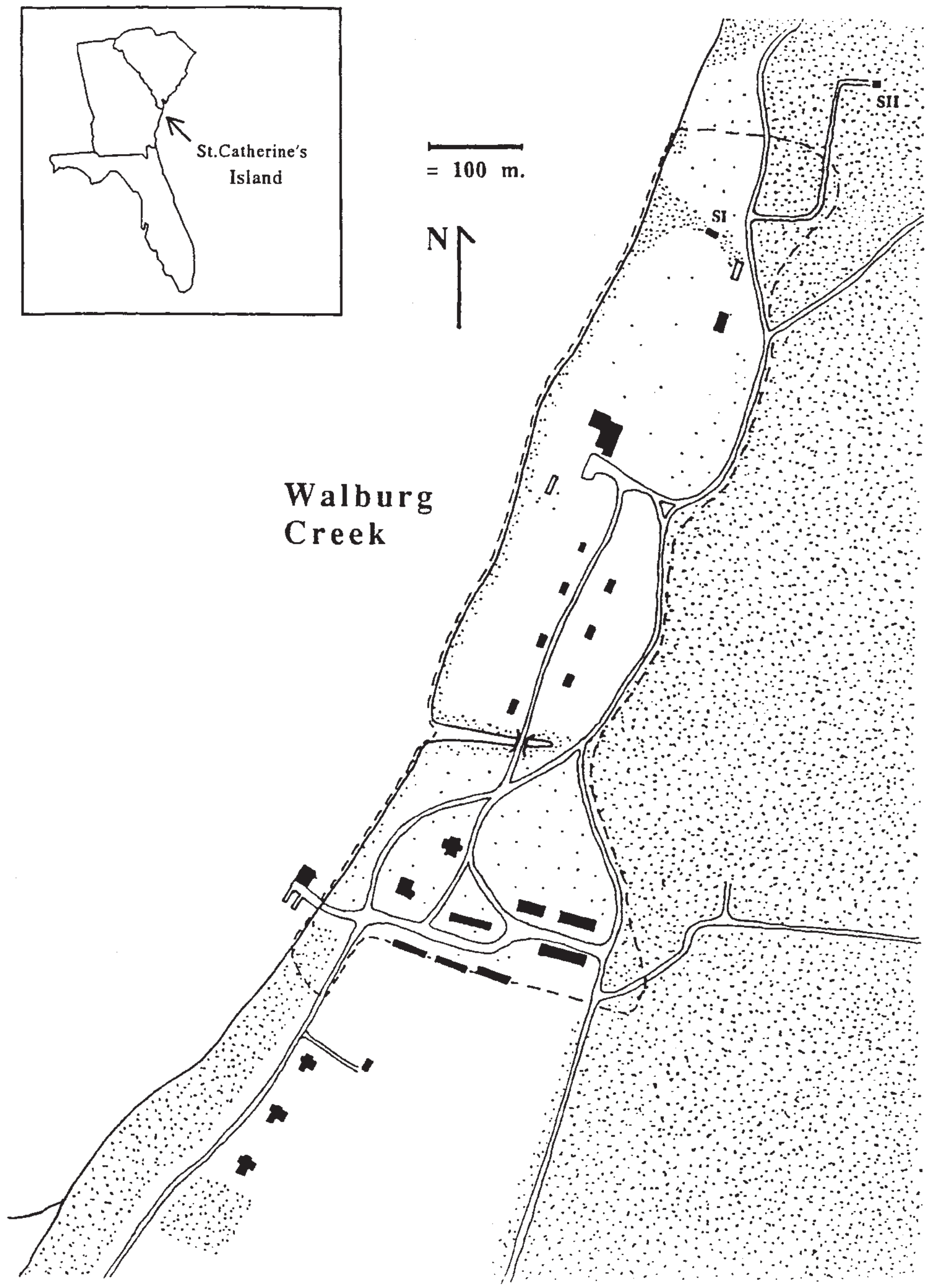

Fig. 2. Map of the release site and daily range. Relative density of forest is indicated with shading. The first and second release sites are labelled SI and SII. Daily range 1987–1992 is indicated with a dashed line.

RESULTS

Physical Condition and Activity

The physical condition and level of activity of the first group began to change within the first week following release. At the time of release, the mean weight of the five adult subjects was 3.3 kg, with a range of 2.9–3.7 kg. A comparison group of seven adult *L. catta* at DUPC had a mean weight of 2.5 kg with a range of 2.0–2.8 kg. Within 120 days, all five adult weights were between 2.95 and 2.65 kg. For the four most obese animals, this decrease was significant (t = 4.09, P < .025). The youngest female (JUL), 15 months of age and 1.8 kg at release, had increased to 2.2 kg in the same period.

Overall activity, as measured by the percent of scan samples recording leap, walk, climb, run, hang, and forage, was consistent for daytime dry weather observations at 22% for the first 60 (summer) days. Activity decreased to 16% (September–November), 13% (December–February), and 19% (March–May) of observations that followed. Overall activity increased to 55% of observations by fall 1986 and did not fall below 40% for any 3 month period through 1992 (overall activity, first 60 days vs. 1986–1991: G = 482.57, n = 19,810, P < .001). The three older animals were initially less active than the rest of the group. Their activity, however, doubled from 1.6% to 3.2% of daytime dry weather observations in the first 60 days (G = 5.23, n = 1,800, P < .05). By spring 1986, the activity of these animals had increased to 10% of observations and thereafter remained indistinguishable from the group as a whole.

Incidents of climb (requiring vertical locomotion) increased from 2% of observations to 5% over the first 50 days following release (G = 22.87, n = 1,560, P < .001) and then decreased to 2% during the winter of 1985–1986. By summer 1986, 1 year after release, climb increased again to 5% of observations. Since that time, the percent of climb has fluctuated with the season, with lows of 3% during winter and peaks of 11–18% during warmer weather (summers, late 1985 + 1986 vs. 1987–1991; G = 246.63, n = 8,100, P < .001).

Two anecdotes recorded during observation illustrate the apparent disorientation of these animals to their environment. During the first 10 days, two incidents of animals clinging to rotten branches as they fell to the ground were recorded, and members of the group were observed sunning (sitting with torso vertical, exposed ventrum, forelegs extended) while in the shade and facing away from the sun. The first incident of a horizontal leap of more than 2 m was observed after 13 days, the first climbing of a brick wall after 40 days, and the first multiple leap, in which the subject rebounded from one landing into another leap, after 54 days. The two oldest females were not recorded running or leaping during the first 60 days. From the beginning, all of the released animals sought shelter from rain and cold weather, such that only three instances of frostbite, as indicated by loss of tissue, have been recorded in 7 years.

Ranging

During the first 40 days following release, only one animal (FAL) was recorded more than 25 m from the release site, when he sat in a tree 50 m east of the release site for 48 h before being retrieved by an observer. Mean daily range, computed as a polygon covering recorded locations over each period of 3 months and excluding wet weather, did not exceed 0.04 ha during the first year. Only 4% of scan samples (N = 2,000 × 6 subjects) in the first 3 months included animals more than 18 m from the release site. Ranging behavior was observed only in the late afternoon, and lasted at most 2 h, and usually involved the entire group moving less than 200 m from the release site.

Ranging behavior increased radically with the aggressive targeting [Vick & Pereira, 1989], defined here as the subject >50 m from the nearest neighbor in 90% of scan samples, plus pursuit of a senior female (KAT) 10 months after the release. For the next 2 months, the group chased KAT occasionally as far as 800 m from the garage, but these forays were infrequent, so mean daily range not including KAT increased only to 0.6 ha. When KAT was confined to the first release site, daily range decreased to 0.02 ha but increased to 2.0 ha following the release of the second group 200 m from the first site in December 1986.

In the spring of 1987, KAT was moved to a feeding site 900 m south of the first release site. Mean daily range of the group increased to 22.5 ha and has remained stable since that time (Fig. 2). Typically, this group makes a daily circuit over an area 1,000 m × 250 m, sleeping in trees at the south end, moving to the north end while sunning and foraging en route, feeding and resting until midafternoon at the north end, and then moving back to the south in the late afternoon. Most time is spent near one end or the other. Temporary peripheral subgroups have been recorded on progressions 6 km from the home area.

Vocalization

Vocalizations audible to observers or responded to by animals at more than 20 m were not recorded before 22 days following release. Only the "purr" and "click" vocalizations described by Jolly [1996], called "contact purrs" by Budnitz and Dainis [1975] and the "contact grunts" also described by Budnitz and Dainis were noted and then at a frequency of 0.16 vocalizations per animal per hour of focal observation. The first loud (clearly audible at 250 m) vocalization was a shriek chorus at night 22 days following release when a barred owl (*Strix varia*) landed in a tree occupied by the majority of the group. The first spat calls were recorded during conflicts between males in the mating season of December 1986, when one male was seriously injured. Spat calls were notably absent in the extensive conflict between the two older and the two younger females in April and May 1986. This conflict included the aggressive targeting of one older female (KAT) and an observed kidnapping for 1 hour of one of the twin infants of the other older female (POR). Moans or mews, louder contact vocalizations, were first recorded during group pursuits of the aggressively targeted female (KAT) 14 months after release. Long range "wails" and "howls" [Jolly, 1966] did not occur with the addition of the second group but were first heared during ranging and at sunset 22 months after release. This completed the normal *L. catta* repertoire of vocalizations, with all used appropriately for the species.

Activity Patterns

Mean percent animals active (see Methods) as a function of time of day during the first 60 days varied greatly, with the only consistency being inactivity (mean below 30% animals active at any one scan) during the period 1300–1400 and greater activity (mean 50–95% active) from 1700–2000, with sunset at approximately 2000. From fall 1985 through summer 1986, the pattern included one peak of activity between sunrise and 1000 (mean 22% active), inactivity from 1200–1600 (mean 9% active), and increased activity between 1600 and sunset (mean 26% active) (1200–1600 vs. all others: G = 384.96, n = 10,860, $P < .001$). Since the summer of 1986, this approximate daily pattern has been maintained, with mean percent animals active being 45% (sunrise–1100), 20% (1200–1500), and 63% (1600–sunset) (1200–1500 vs. all others: G = 328.52, n = 12,096, $P < .001$).

Foraging

Foraging, defined here as ingesting material from the natural habitat as opposed to supplied diet, began before release, when individuals were observed eating red bay leaves (*Persea borboria*) pulled through the cage wire. During the first 6 weeks following release, forage was almost exclusively red bay leaves (37% of forage by mass) and grape leaves (*Vitis rotundipholia*) (60% by mass), with for both species at least 80% of the leaves consumed being new growth. Bay berries (2% by mass) and hackberry leaves (*Celtis occidentalis*) (1% by mass) also were eaten. Forage comprised 17% by mass of the animals' diet during this period, with 83% being the monkey chow, fruit, and vegetables supplied each day. Fourteen new plant species were added to the diet after the first 6 weeks (Table I). During the first 6 weeks, the subjects were observed to test, by licking or piercing with a canine tooth, six plants. The animals have not been observed to test or eat seven other readily available plants, including grasses (Table I).

Forage was obtained only near the release site during the first 10 months,

TABLE I. Plant Species Foraged, Tested by Licking or Piercing With a Canine Tooth and Rejected, or Plentiful But Not Observed Being Foraged or Tested

Species	Common name	Part
Foraged		
Persea borbonia	Red bay	Leaves, fruit
Vitis rotundiflora	Muscadine grape	Fruit, leaves
Celtis occidentalis	hackberry	Leaves, fruit
Pinus elliottii, taeda	Pine	Fruit, needles
Vaccinium arboreum	Sparkleberry	Fruit
Quercus virginiana	Live oak	Acorns
Magnolia grandiflora	Southern magnolia	Petals
Melia azedurach	China berry	Fruit
Morus alba, rubra	Mulberry	Fruit
Myrica ceriferawax	Myrtle	Leaves
Ficus spp.	Fig	Fruit
Carya glabra	Hickory	Bud scales
Sabel palmetto	Cabbage palm	Fruit
Prunus caroliniana	Caroina laurel cherry	Fruit
Cornus florida	Dogwood	Fruit
Chaenomeles sp.	Quince, Japanese plum	Fruit, buds, sap
Quercus virginiana	Live oak	Acorns
Tested and rejected		
Tillandsia usneoides	Spanish moss	All
Smilax laurifolia	Greenbrier	All
Ilex vomitoria	Yaupon	All
Eupatorium capillifolium	Dog fennel	All
Quercus virginiana	Live oak	Leaves
Melia azedurach	China berry	Leaves
Plentiful, not foraged		
Juniperus virginiana	Red cedar	
Yucca aloifolia	Spanish bayonet	
Serenoa repens	Saw palmetto	
Toxicodendron radicans	Poison ivy	

and foraging behavior decreased from 5% of scan samples during the summer to 2% of scan samples during the first winter, after grape leaves were no longer available. Foraging increased to 8% of scan samples in the spring, simultaneously with the increase in ranging with the aggressive targeting of KAT by the group, and remained stable with fluctuations by season thereafter. Corrected for season, the incidence of foraging has not increased since release, but the variety of plants foraged has increased with increased ranging (Table I).

Social Organization

The original group contained two subgroups, the first including two older females (KAT, POR) possibly closely related, and one older male (FAL). The second subgroup included two females and a male, all young and full siblings (Fig. 1). Mean dispersal of the original group, defined as the distance between the two most distant animals in a scan sample, was 9 m during the first 10 months. However, the animals reliably slept in two subgroups, one of the three older animals (KAT, POR, FAL) and the other of the young sibs (JUL, NER, ROM). In the first birth season, the older female (KAT) had a stillborn infant and was aggressively targeted by the young females in the group. The other older female (POR) had twins, who were the object of a kidnapping lasting 2 h. The second group released, originally intended to be socially separate, included the parents (MAR, EBE) of the young females and young male in the first group. MAR was lost on a long (6 km) foray, and EBE was killed by a truck. The four young male survivors of this group joined the first group and later were removed when they were judged to be socially peripheral by zoo personnel. This ended the second group.

Although one of the young females in the first group (NER) eventually bore two daughters, these offspring also were aggressively targeted after NER's death. This ended the competing matriline, so today the five females in the group are all direct descendants of the old female (POR) of the first group.

Removal of individuals from the group has in every case been determined by socially peripheral or aggressively targeted status. Eight males have been removed, usually following retrieval from long forays or following serious injuries in breeding season aggression. Four females have been removed, all in 1991 and 1992. KAT was aggressively targeted in 1986 and remained in varying degrees peripheral until the death of MAR and her daughters, NER and JUL, in 1988. KAT and POR became peripheral again in 1990 and were removed following conflict with VIO, POR's daughter. The advanced age of POR and KAT may have contributed to the need for removal. ASH and CAT, daughters of NER in the MAR matriline, were aggressively targeted in early 1992 following conflict with VIO and LIB of the POR matriline (see Fig. 1).

Natality and Mortality

Births began 10 months after the 1985 release with twins born to one (POR) and a stillbirth to the other (KAT) of the oldest females in the first group. Births per year have varied from five (1987, 1991) to two (1989) since release. Of 21 births surviving more than a week, all remained alive in summer 1992. Of the six animals released in 1985 and six released in 1986, two and four, respectively, were still alive in summer 1992 but had been removed from the group (Fig. 1). Of the released animals that have died, one was struck by a truck (EBE), and one was predated by an alligator while peripheral (confirmed by tracking FAL's radio collar to the alligator). Two disappeared while on a long (6 km) foray as part of a peripheral social subgroup and may have been predated or may have not found water. Two died suddenly; necropsy suggested lung infections.

Natality has exceeded mortality by 350% in this group. However, 12 animals (eight male, four female) have been removed. The group had 12 members in 1992, the same number as released in 1985 and 1986.

DISCUSSION

It is clear from the results that *L. catta* is capable of short- and long-term adjustment to a novel habitat even in the case of captive-reared adults lacking prior experience with any natural habitat. This adjustment varied for different behaviors, with some deficits in ranging and vocalizations apparent up to 22 months following release. These animals ultimately exhibited a full repertoire of both species-typical and opportunistic behavior.

The animals successfully utilized a novel habitat. The animals' behavior remained flexible, in that they were opportunistic in their foraging of new foods and overcame a lack of developmental opportunities prior to release. The study group resembled wild and semi-free-ranging conspecifics in aspects of their social organization, ranging, daily activity pattern (Table II), and vocalizations even when some of these behaviors developed long after release. Eventually, even the older animals were indistinguishable in their activity and agility from animals of similar age in a semi-free-ranging environment at DUPC all of their lives [personal observation; Taylor, 1986].

The percent time spent feeding and traveling during this study is similar to values for wild populations (Table II). It is difficult, however, to compare the amount of time spent resting due to methodological differences. Sussman [1974] reports resting and grooming separately (summed in Table II) and includes a fourth category (other) which includes sunning, playing, and fighting, whereas during this study grooming and sunning were considered as resting and playing and fighting were recorded as activity. If we assume that the majority of time in Sussman's fourth category was sunning, then the activity to rest ratios (where grooming is included as resting) becomes 0.82 for this study compared with 0.82

TABLE II. Comparison of Demographic Data From This Study and Wild Population Studies of *Lemur catta**

	This study	Berenty[a]	Beza Mahafaly[b]	Antserananomby[c]
Percent time				
Foraging	26	31		25
Resting[d]	55	50		46
Travelling	19	13		19
Other		6		10
Activity/rest ratio	0.82	0.82		0.79
Home range (ha)	22.5	10.3	25	8.8
Day range (m)	1,800	965		920
Sex ratio (M/F)	1.4	0.87	1.0	
Group size	12	13.4	13.7	19
Number of species foraged	17	24		24

*See text for calculation of activity to rest ratios.
[a]Studies by Jolly [1966], Budnita and Dainis [1972, 1974].
[b]Study by Sussman [1901].
[c]Study by Sussman [1972,1974].
[d]Resting includes grooming.

for Berenty and 0.79 for Anaseranànomby, so that the activity to rest ratios are almost identical for a wild population and this one. However, the ratios calculated here must be considered as estimates.

Ranging developed very slowly and in apparent response to social needs, the chasing of an aggressively targeted animal and contact with another group, rather than being controlled by the availability of resources as suggested by Jolly [1966], Sussman [1991], and Sauther [1991]. Ranging during social interactions appears to have resulted in the discovery of forage and sleeping sites, and these resources may help maintain this behavior. Once established, ranging has remained stable and species-typical independent of season, available forage, and contact with other groups. Very little forage is available anywhere in the range for at least two winter months of each year. In addition, there have been long periods since the original release during which there have not been other groups or even aggressively targeted individuals nearby to sustain ranging on social grounds.

The ranging behavior in this study resembles that described by Jolly [1966], Budnitz and Dainis [1975], and Sussman [1991] in both daily pattern and area. Budnitz and Dainis report 6–8 ha with a maximum of 23 ha, while Jolly reports 3–6 ha in the richer (and more crowded) habitat of Berenty. Sussman reports 32 ha in a less densely populated area. The 25 ha reported here includes substantial space that is used primarily to travel from one end of the range to the other, and these animals are not restricted by other social groups or resources.

Animals housed in small cages without neighboring groups have little use for loud vocalizations. However, the 2 year delay in adopting the full repertoire of *L. catta* vocalizations cannot be explained as due to a lack of utility. Separation of individuals from the group, intense social conflict, ranging and progressions, and contact with other social groups occurred before this time. When new vocalizations did occur, they were species-specific and used appropriately.

The daily cycle of morning and evening activity interspersed with progressions, foraging, and midday inactivity found here is identical to that reported by Jolly [1966] and Taylor [1986] at Berenty and DUPC, respectively. While the pattern was evident in terms of level of activity even before release, more than a year was needed to add the elements of progressions and foraging in a stable daily cycle.

Foraging behavior followed the opportunistic, flexible pattern described by Ganzhorn [1986] at DUPC. The plant population, both in terms of digestible and toxic species, is different, but in both cases animals tested plants, successfully rejected toxic species, and then proceeded to forage actively among a wide variety of digestible species.

The social behavior reported here, including contested dominance among females in two matrilines and peripheral status and emigration by young males, are consistent with other studies. Both this group and that studied by Taylor [1986] at DUPC have been taken over by one of the two competing matrilines. In both cases, one matriline continued high natality and social status, while the other experienced reduced natality and eventual aggressive targeting of all females from the group.

Natality has exceeded mortality in this group. Mortality among socially peripheral animals might have been higher but was minimized by the prompt removal of socially peripheral animals and particularly animals that had been retrieved from long forays that might be interpreted as attempts to emigrate to other nonexistent groups. In fact, if removed animals are considered as deceased or at least lost from the population, the stability found here would duplicate that found by Jolly et al. [1982] and Sussman [1991] in the wild.

Mortality was highest for adult released animals, while their offspring that survived neonatally are all alive in 1992. Three adult animals died while socially peripheral, and all three recorded neonatal deaths occurred accidentally (dropping, etc.) during social conflict. Emigration, when attempted, has closely emulated the pattern suggested by Jolly [1966; Jolly et al., 1982] and detailed by Sussman [1991]. Young males become peripheral and leave the group, while females remain in their natal troop. The only other emigration has followed active aggressive targeting of females, as has been observed in other both captive and wild groups [Taylor, 1986; Vick & Pereira, 1989; Koyama, 1991; Pereira, 1993]. In this case, either failure to give birth, as in the older female (KAT) in this group in 1986, or being part of a gradually losing matriline, as happened to two females (ASH, CAT) in this group in 1992, appeared to trigger aggressive targeting by other females. These social behaviors and their demographic consequence of producing a group based on closely related females appear to be conservative features of the social organization of *L. catta*.

The ability of even these inexperienced adults to develop over 22 months an appropriate behavioral repertoire supports the usefulness of studies of captive-born animals to our understanding of the species' naturally occurring behavior. This study shows that while these study animals successfully utilized a novel environment, the major characteristics of their social behavior and many features of ranging and habitat use were very similar to that observed in the wild. This consistency in pattern of species-typical behaviors is in marked contrast to reports of differences in wild and captive groups or between different wild populations of other lemur species. *L. catta,* therefore, may be less flexible in its social organization than other species studied while quite flexible in its adjustment to new habitats.

CONCLUSIONS

1. Adult, captive, inexperienced *L. catta* released into a natural habitat developed species-typical patterns in social organization, behavior, ranging, and vocalizations.
2. Different aspects of behavior developed at different times following release, with some not appearing until 22 months after release.
3. Ranging, once established, was equivalent to wild populations and remained stable even when not reinforced by foraging or social needs.
4. Although *L. catta* was flexible in its ability to utilize new forage and habitat, it may be less flexible in aspects of its social behavior than other lemurs studied.
5. The results support the use of captive animals in a large natural habitat in understanding the species-typical behavior of this species.
6. The results support the suitability of this species for reintroduction in novel habitats.

ACKNOWLEDGMENTS

We thank undergraduate observers from the University of the South too numerous to name. Three groups of individuals, without whom this project could not have been completed, have our thanks for support in many forms. We thank William Conway, director, James Doherty, general curator, and the Wildlife Survival Center staff of the Wildlife Conservation Society. We thank Frank Larkin, president, Royce Hayes, superintendent, and the staff of the St. Catherine's Island

Foundation. We thank Elwyn Simons, science director, Kenneth Glander, director, Barbara Coffman, former colony manager, and the staff of the Duke University Primate Center. This is Duke University Primate Center publication 549.

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