

INTER- AND INTRASPECIFIC INTERACTION RATES OF THREE SPECIES OF LEMURS (SUBFAMILY LEMURINAE) IN AN ENCLOSURE AT THE MEMPHIS ZOO AND AQUARIUM

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ABSTRACT—The use of mixed-species exhibits in zoological parks may influence the types and rates of interactions between individuals housed in such enclosures. Inter- and intraspecific behavioral interactions were observed for three species of lemurs (ring-tailed lemur, *Lemur catta*; black lemur, *Eulemur macaco macaco*; and black-and-white ruffed lemur, *Varecia variegata variegata*) in an enclosure designed to simulate characteristics of their natural habitat. Intraspecific interactions occurred more frequently than interspecific interactions, and little aggression was observed, either between or within species. Intraspecific interactions among black lemurs increased with decreasing ambient temperature. Black lemurs performed more intraspecific mutual contacts than either agonistic behaviors or vocal communication. Sky conditions, body size, and residence time within the exhibit did not influence frequencies of inter- or intraspecific interactions. The observations indicate the feasibility of mixed-species exhibits of limited size and provide a baseline data set with which to compare behavioral changes occurring after the introduction of a fourth species into the enclosure.

Zoological parks have assumed an increasing role in maintaining genetic variability within a species through Species Survival Plans and studbook listings. Yet, spatial and financial constraints frequently force zoos to house members of two or more different species within the same exhibit, a practice that may increase levels of individual stress resulting from inter- or intraspecific interactions. The close confines also may increase the probability of interspecific hybridization, which undermines the Species Survival Plans' goal of maintaining 90% of a species' genetic diversity over a 200-year period (Primack, 1993). Descriptions of behaviors performed in enclosures housing three or more lemur species are absent from the available literature. The present study describes the types and respective rates of inter- and intraspecific interactions occurring between members of three species of lemurs maintained in a large enclosure.

The rates and types of interactions between individual lemurs may be dependent upon a variety of environmental and social factors, including resource availability, social hierarchy, temperature, and threat of predation (Jolly, 1966; Budnitz and Dainis, 1975; Goodman et al., 1993; Macedonia, 1993). Ring-tailed lemurs, *Lemur catta* L. 1758, live in matriarchal troops (Jolly et al., 1993), whereas levels of sociality in black-and-white lemurs, *Varecia variegata variegata* Kerr 1792, and black lemurs, *Eulemur macaco macaco* L. 1766, may vary seasonally (Morland, 1993; van Schaik and Kappeler, 1993). Interactions among individuals of *L. catta*, *E. m. macaco*, and *V. v. variegata* (all in Subfamily Lemurinae) were studied in a large enclosure simulating natural habitat at the Memphis Zoo and Aquarium, Memphis, Tennessee. In their native Madagascar, *L. catta* and *V. v. variegata* exhibit parapatry, while *E. m. macaco* is allopatric to the other two species (Tattersall, 1982). To test the hypotheses that the type and frequency of interaction between conspecific

individuals is different from that of heterospecifics, the following questions were addressed: what types of interactions occur between species and between individuals within species; how do the rates of inter- and intraspecific interactions differ between species; are the rates or types of interactions a function of the species' body size, residence time in the enclosure, or ambient temperature. The answers to these questions are discussed in relation to the tenability of mixed-species exhibits of primates in zoological parks.

MATERIALS AND METHODS

The Madagascar exhibit at Memphis Zoo and Aquarium encloses 371.6 m², being 30.5 m long and between 9.1 and 15.2 m wide. The enclosure is separated into two approximately equal sections by an artificial stream of treated water. Each section is planted with mixed grass species, and a variety of temperate shrubs line the margins of the exhibit. Two young yellow-poplars (*Liriodendron tulipifera*) are planted near the center of each section of the exhibit, and the enclosure is otherwise dominated by a jungle-gym of telephone poles with anchoring rope strung between them. The walls of the enclosure are indented at an average height of 1.5 m, providing a shelf on which the lemurs can rest or bask.

Morphometric characteristics, date of introduction to the exhibit, and number of individuals representing each sex for the eight lemurs housed in the enclosure are presented in Table 1. *E. m. macaco* are sexually dimorphic and only female *L. catta* were present in the enclosure. However, no attempt was made to differentiate among the sex of the individuals because individual identification of *V. v. variegata* could not be reliably assessed during repeated observations. For similar reasons, differences in

TABLE 1. Morphometric characteristics, time of residency (days), and number of individuals representing each sex (male: female) for the lemur species observed in the Madagascar exhibit of the Memphis Zoo and Aquarium, Memphis, Tennessee, between 24 September and 18 November 1995.

Species	Mean body mass (g)	Mean total length (mm)	Residence time	Number of each sex
<i>Lemur catta</i>	2,760	595	26	0:3
<i>Eulemur macaco macaco</i>	2,406	550	149	1:1
<i>Varecia variegata variegata</i>	3,785	602	149	2:1 ¹

¹ Zoo staff implanted female *V. v. variegata* with a contraceptive to prevent her from going into estrous.

the types or rates of interactions for each individual in the enclosure were not recorded. To reduce the possibility of presumed, increased agonistic territoriality between male *V. v. variegata* in the enclosure during periods of female estrous, staff veterinarians had implanted the female with a time-lapse contraceptive before placing her in the exhibit.

Interactions between lemurs were observed, usually twice weekly, between 24 September and 18 November 1995. Interactions were scored for a period of 1 h, preceded by a minimum of 20 min of acclimation period while a single observer was present in the exhibit. At the conclusion of the acclimation period, the temperature (°C) and the degree of cloud cover were recorded. Cloud cover was described using a discrete scale: 0 = overcast/raining; 1 = mostly cloudy; 2 = partly cloudy; 3 = mostly sunny; 4 = clear. Observations were conducted only at times when all individuals were locked out on exhibit (i.e., access to an off-exhibit home cage was denied); however, to avoid any conditioning bias associated with their keepers' schedule (i.e., feeding times; Grant and Evans, 1994), lemurs were not observed within 1 h of the time when they were removed from the exhibit for the day. Observations were made between 1130 and 1430 h; interactions occurring at the moment the 1-h period began were not recorded.

During each observation period, the observer was seated in the same spot within the enclosure and remained as motionless as possible while recording all interactions. While small portions of the exhibit were obscured from view, the position in the enclosure allowed observation of >80% of the area encompassed by the exhibit (equal to ca. 300 m²) and included those areas where, based on preliminary observations, the lemurs spent the majority of their time.

Although the rate of interaction between two individuals can be compounded by the duration of each interaction, logistic considerations prevented consideration of interaction duration during this study. Additionally, because behaviors involving more than one individual were examined, problems of obtaining independent data (due to "cage effects," an interaction, or its effect on subsequent interactions) were assumed to be negligible (Martin and Bateson, 1986). Categories of interactions were established that would be applicable to inter- and intraspecific behaviors (Peireira et al., 1988). Interactions were scored from the perspective of the individual initiating the interaction. Even though an inter-

action, by definition, involves two individuals, a separate count was not established for the recipient's response to the interaction. Five different types of interactions were described during preliminary observations and used exclusively during subsequent observation periods.

Approach without response—an approach, within 2 m, is made by the initiator; this individual may approach more than one other individual if recipients are in close proximity (the interaction was scored only once on this occasion). No physical contact occurs during this interaction, but approaches may be within reaching distance of the recipient individual(s). No vocal communication occurs between individuals during this interaction.

Approach with aversion—an approach, within 2 m, by the initiator is met with avoidance behavior by the recipient (the latter moving away, usually rapidly, from the direction of approach). No physical contact occurs during this interaction. However, vocal communication may occur and is scored separately in its respective category.

Contact with aversion—contact by the initiator is met with an aversive response by the recipient. This aggressive behavior is usually interspecific and results in the recipient running away from the initiator. Physical contact must be made for an interaction to be scored in this category; vocal communication also may occur and is scored separately in its respective category. Examples include hitting, biting, and pulling.

Mutual contact—the initial contact is made by the initiator, and the recipient allows the contact to occur and may even reciprocate (in this instance, only one interaction is scored). This behavior is usually intraspecific and may result in extended periods of contact between individuals (scored as a single interaction). Examples include grooming, embracing, and mating.

Vocal communication—the initiator calls, and the recipient is the individual to whom the call is directed. Because the target of communication behaviors could not be reliably ascertained, any communication was scored as an intraspecific interaction. Examples include grunting, barking, and howling.

Preliminary analyses of rates of interaction revealed that the data violated standard assumptions for using parametric tests (Steel and Torrie, 1980). Nonparametric analyses, therefore, were used to analyze the data: Kolmogorov-Smirnov tests compared distribution rates of interaction over all observation periods to determine whether or not certain interactions occurred more often than others. Where more than one comparison was made for interactions performed by a single species, or between species, Bonferroni's adjustment factor was used to control for experiment-wise type I error (Zar, 1984). Kruskal-Wallis tests were used to ascertain any effect of sky conditions, mean species body mass, or residence time on the frequencies of interactions. Spearman's rank correlations (r_s) were calculated to determine relationships between air temperature and rates of interactions. Statistical significance was determined at $P \leq 0.05$ (with a Bonferroni adjustment where appropriate). Rates of either inter- or intraspecific interactions were not a function of the number of individuals representing each species (Kruskal-Wallis tests; $P = 0.178$ or 0.448 , respectively). Nonetheless, the number of each type of interaction for the number of individuals representing each species was standardized, thereby setting a uniform probability of encounter among all individuals for the species in the enclosure.

TABLE 2. Mean frequency ($\pm SE$) of interactions during 1 h for species of lemurs observed in the Madagascar exhibit at the Memphis Zoo and Aquarium, Memphis, Tennessee, between 24 September and 18 November 1995. Behaviors are described in text. Where mean totals are reported, the mean was obtained across individual observations (i.e., $n = 12$ for all mean totals). Different letters following values designate significant differences among behaviors performed within a single species ($P = 0.02$).

Behavior	Species			Mean for behavior
	<i>Lemur catta</i>	<i>Eulemur macaco macaco</i>	<i>Varecia variegata variegata</i>	
Intraspecific				
Approach with aversion	0.1 \pm 0.1 a	0.9 \pm 0.6 ab	1.5 \pm 0.5 a	0.8 \pm 0.3 a
Approach without response	4.2 \pm 0.8 a	1.6 \pm 0.7 ab	2.4 \pm 0.9 a	2.7 \pm 0.5 ab
Contact with aversion	0.1 \pm 0.1 a	0.1 \pm 0.1 a	1.2 \pm 0.7 a	0.4 \pm 0.3 a
Mutual contact	6.7 \pm 0.8 a	5.0 \pm 1.3 b	2.0 \pm 0.7 a	4.6 \pm 0.6 b
Vocal communication	0.0	0.2 \pm 0.1 a	11.8 \pm 6.0 a	4.0 \pm 2.2 ab
Intraspecific mean for species	11.0 \pm 1.4 ¹	7.8 \pm 2.0	18.8 \pm 7.5	37.6 \pm 8.1 ¹
Interspecific initiator mean for species	3.3 \pm 1.6 ¹	2.9 \pm 0.9	4.1 \pm 1.7	10.3 \pm 2.6 ¹

¹ Differences between frequency of total interspecific (as initiator) and total intraspecific interactions ($P = 0.03$).

RESULTS

Lemurs inhabiting the Madagascar exhibit at the Memphis Zoo and Aquarium were observed for 12 1-h periods. Total interactions between all individuals numbered between 16 and 133 during 1 h (mean $\pm SE = 47.8 \pm 9.4$). Many mutual contacts included grooming or resting with another individual; individual *L. catta* often rested against each other while basking in the sun. Only one incidence of mating (in *V. v. variegata*) was observed. Interspecific agonistic behaviors rarely involved any contact between individuals; physical contact occurred more frequently among intraspecific interactions of only *V. v. variegata*. All cases of contact with aversion involved a brief hitting action; retreat by the recipient was immediate, and pursuit by the initiator (if performed) did not lead to any subsequent contact. *L. catta* was the only species that did not vocally communicate during the observation periods.

Among intraspecific interactions performed by all individuals, mutual contact occurred more often than approach with aversion or contact with aversion (Kolmogorov-Smirnov test; $P = 0.01$; Table 2). After correcting for differences in the number of individuals representing each species, there was no difference in the frequency of any intraspecific behaviors between species (Kolmogorov-Smirnov tests; $P > 0.03$, not significant with Bonferroni's adjustment). Within species, only *E. m. macaco* exhibited intraspecific behaviors at frequencies that were statistically different. More mutual contact was performed by this species than either contact with aversion or communication (Kolmogorov-Smirnov tests; $P = 0.02$).

There was no difference in the frequencies of interspecific behaviors among any of the species (Kolmogorov-Smirnov tests; $P > 0.01$); some types of interspecific interactions were never observed. *L. catta* did not initiate any agonistic interactions (Fig. 1A) and exhibited mutual contact only towards *E. m. macaco*. No agonistic behavior was initiated by *E. m. macaco* towards *V. v. variegata*, and interspecific interactions were generally rare in the former species (Fig. 1B), as the two individuals spent much of their time resting or grooming while in mutual contact. *L. catta* and *E. m. macaco* appeared to initiate interactions more often

with each other than with the larger species. *V. v. variegata* never initiated mutual contact with either of the other species (Fig. 1C) and was the only species to initiate interspecific contact with aversion (including one instance of a physical blow).

Among general interaction categories for all species, intraspecific interactions occurred more frequently than interspecific interactions (Kolmogorov-Smirnov test; $P = 0.03$; Table 2). Within species, only *L. catta* performed more intraspecific than interspecific interactions (Kolmogorov-Smirnov test; $P = 0.03$). When adjusted for numbers of individuals representing each species, frequencies of either inter- or intraspecific interactions were not dependent upon the body size or the species' residence time (Kruskal-Wallis tests; $P > 0.05$).

Temperatures during observation periods ranged from 8 to 29°C, and sky conditions varied from overcast and raining to clear skies; most observation days had fair weather. Frequency of interaction was not a function of sky conditions (Spearman's correlation; $P > 0.05$), as all species appeared to perform behaviors regardless of the degree of cloud cover. More intraspecific interactions occurred with decreasing temperature (Spearman's $r_s = -0.712$; $P = 0.04$); however, this trend was probably due to *E. m. macaco* exhibiting a similar relationship (Spearman's $r_s = -0.707$; $P = 0.01$; Fig. 2). Frequency of intraspecific interactions was not a function of temperature in the other two species, nor was there any relationship between any single interaction type (either inter- or intraspecific) and temperature ($P > 0.05$).

DISCUSSION

Because the lemur species examined in this study occasionally or frequently live in a troop social structure (Tattersall, 1982), it is not surprising that, among the five described intraspecific interactions, mutual encounters occurred more frequently than agonistic encounters. If solitary social structures were more common among lemurs (e.g., mutual intraspecific contact occurring only during periods of mating receptivity), the frequency of agonistic encounters might equal or exceed that of mutual interactions reported here. Even within a troop, black lemurs often form pair-bonds (Colquhoun, 1993); this species exhibited a

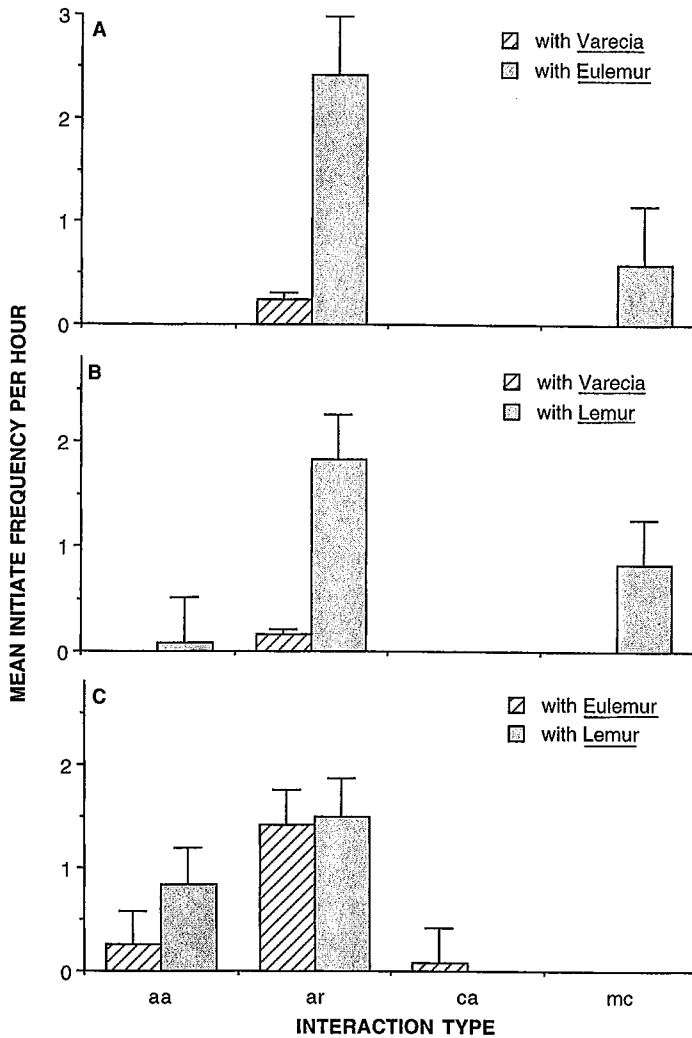


FIG. 1. Mean frequency (bars show SE; $n = 12$) of interspecific interactions (aa = approach with aversion; ar = approach without response; ca = contact with aversion; mc = mutual contact) during 1 h observation periods in the Madagascar exhibit at the Memphis Zoo and Aquarium, Memphis, Tennessee, between 24 September and 18 November 1995. Sections of the graph show interactions initiated by *Lemur catta* (A), *Eulemur macaco macaco* (B), and *Varecia variegata variegata* (C) towards the other two species in the exhibit.

higher frequency of mutual contacts than was noted for the other species. The absence of similar intraspecific trends in *V. v. variegata* may reflect their troops having a lower frequency of interindividual contacts (Tattersall, 1982). The absence of male *L. catta* in the enclosure prohibited the examination of pair formation in this species.

In spite of their relatively restricted quarters, interspecific interactions occurred less frequently than intraspecific interactions among lemurs in the enclosure. Additionally, agonistic encounters were rare, suggesting the feasibility of mixed-species exhibits. All species examined in this study, while not inclusively sympatric, maintain home ranges in their natural habitats that are larger than the area made available in the Madagascar exhibit (Tattersall, 1982; Colquhoun, 1993). As such, a high rate of interspecific interactions should be expected in space-limited enclosures typical of zoological parks. Increased aggression has

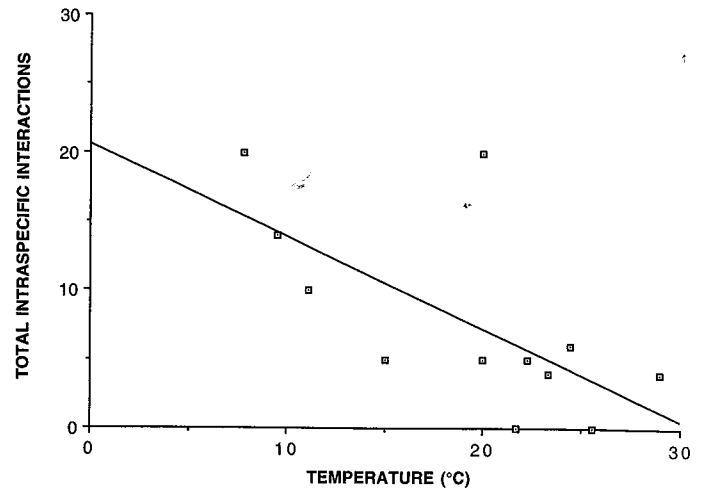


FIG. 2. Total number of intraspecific interactions performed by *Eulemur macaco macaco* as a function of temperature in the Madagascar exhibit at the Memphis Zoo and Aquarium, Memphis, Tennessee, between 24 September and 18 November 1995 ($r_s = -0.707$, $P = 0.01$).

been widely reported, especially following the introduction of non-resident members of several species, in natural settings (Southwick et al., 1974) and artificial enclosures (Bernstein et al., 1974; L. Taylor, pers. comm.).

The observed trend of increasing frequency of intraspecific interactions with decreasing temperature exhibited by *E. m. macaco* (Fig. 2) is suggestive of a behavioral mechanism to conserve body heat. Lemurs behaviorally thermoregulate either by moving from a shaded microhabitat into one of exposed sunlight or by increasing contact among individuals within the troop (Jolly, 1966; Morland, 1993). If the need to thermoregulate was responsible for the increased frequency of intraspecific interactions between black lemurs, mutual contacts should have exhibited a similar relationship. In other words, social thermoregulation requires a higher rate of mutual contact that was not observed in this study.

Two factors may account for the absence of reliable trends for interspecific encounters in this study. First, all species were recently introduced into the Madagascar exhibit; thus, little time had been available to members of any one species to establish territorial dominance (Sussman and Richard, 1974; Jolly et al., 1993). Second, all individuals were acclimatized to the Madagascar exhibit gradually without other species present (C. Brady, pers. comm.). Thus, individuals of all species were equally familiar with the enclosure and could avoid agonistic interactions through increased awareness of their surroundings and proximity to other individuals. Occasional "genital rubs" by *V. v. variegata* (stereotyped behavior indicating territory boundaries; Sussman and Richard, 1974) were ignored by members of other species that were observed within the areas delineated by the scent marks after their application. A practice of gradual introduction in an adequately-sized enclosure, allowing ample space for members of each species to exist relatively undisturbed, would appear to be a prerequisite for mixed-species exhibits.

This study provides baseline data necessary to establish trends in rates of interaction among and within the three species of lemurs (Barlow and Hersen, 1984). Continued monitoring of the Madagascar exhibit is advisable as relationships among pri-

mates may be influenced by the history of previous interactions (Quiatt and Reynolds, 1993). Recently, three red ruffed lemurs (*Varecia variegata rubra* E. Geoffroy 1812) were introduced into the Madagascar exhibit, representing the first attempt by any zoological park to maintain a mixed-species lemur exhibit housing four species (C. Philipp, pers. comm.). Comparing the types and frequencies of inter- and intraspecific interactions that occur following this introduction of *V. v. rubra* to the baseline data reported in this study may prevent unwanted aggression between species that could lead to injury to, or loss of, individuals in the zoo's captive breeding program.

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