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THE NATURE OF AGONISM AND DOMINANCE AND THEIR RELATIONSHIP TO SOCIAL GROOMING IN THE BROWN LEMUR, EULEMUR FULVUS

BY

RUBEN KAUFMAN

A thesis submitted to the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of
DOCTOR OF PHILOSOPHY

DEPARTMENT OF ANTHROPOLOGY

Edmonton, Alberta
Fall 1994

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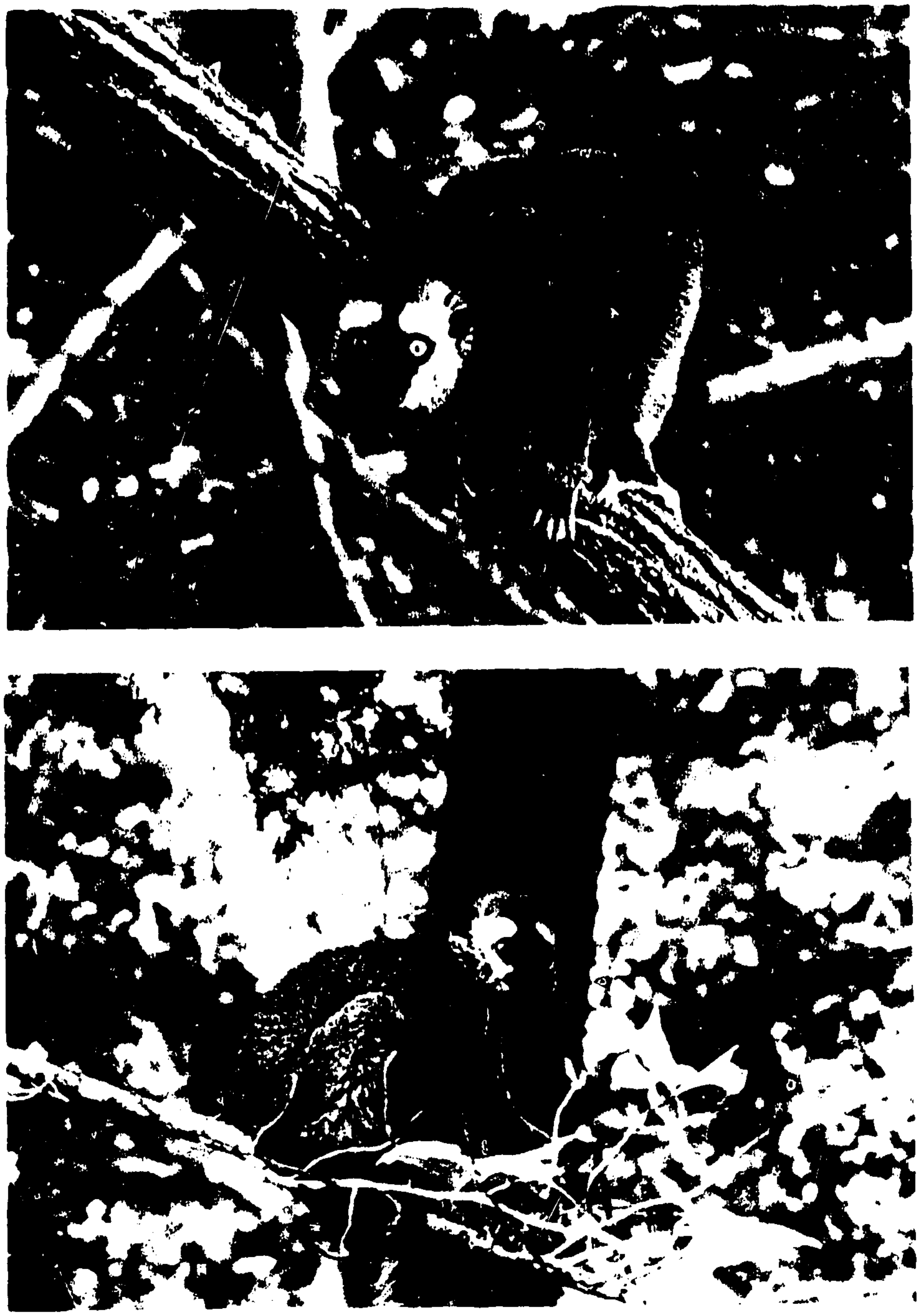
Eulemur fulvus rufus at the Duke University Primate Center:
above, 2 females and 2 males huddling;
below, 2 juvenile females and young adult male playing.



Eulemur fulvus rufus at the Duke University Primate Center:
above, female; below, male.

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled THE NATURE OF AGONISM AND DOMINANCE AND THEIR RELATIONSHIP TO SOCIAL GROOMING IN THE BROWN LEMUR, <u>EULEMUR FULVUS</u> submitted by RUBEN KAUFMAN in partial fulfullment of the requirements for the degree of DOCTOR OF PHILOSOPHY in ANTHROPOLOGY.

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Dr. P Willoughby

MARCH 11, 1994

To Pimento, who did her best to be a real brown lemur in an alien world, and to her family, friends, conspecifics, congeners, confamilials, etc. May she play forever in lemur paradise in the loving company of her fellows. And to all lemurs in Madagascar, which once was lemur paradise, and their relations who are now only ghosts. May their kind survive and flourish in the ages to come.

ABSTRACT

Agonistic behaviour in brown lemurs (Eulemur fulvus) was studied at Berenty, Madagascar and the Duke University Primate Center to answer questions arising from the work of other researchers regarding the frequency and intensity of aggression and the discernibility of dominance relationships.

Aggressive behaviour was found to be mild but not infrequent. Submissive responses to aggression were the exception rather than the rule. The direction of aggression was therefore used to determine dominance.

Unlike some other lemur species in which dominance has been documented, among brown lemurs there was no consistent dominance of females over males. The only consistency in intersexual dominance was that older animals dominated younger ones. Similarly, older animals received the majority of allogrooming in dyads with younger animals, even when dominance relationships did not exist.

Since female dominance has been hypothesized to be an adaptation of primates living in seasonal environments, in which there are unusually severe stresses on reproductive females, these findings about seniority, regardless of sex, as the key to dominance in brown lemurs pose a problem. However, the generalized and opportunistic nature of brown lemur habitat use may have freed this species from the constraints necessitating female dominance in others.

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I have not ceased to be amazed at the series of circumstances that gave me the opportunity to pursue academically my general fascination with natural history. For whatever has led me to this I will always be grateful, in spite of attendant difficulties and frustrations.

Any acknowledgments of the contributions of individuals to this work must begin with the lemurs themselves. They have been the raison d'etre for the entire adventure, and this kept me going through the times of drudgery. My appreciation of being in this world has been immeasurably enriched by the privilege of observing and delighting in their daily lives.

Those who have helped since the conclusion of the field research are many, and they have helped in various ways. Throughout this period my three cats have been my lifeline, and have been cherished company during those usual late night working hours as at all others. My friends Don Smith and Marcelle Gareau, my graduate student neighbours, fellow students (especially anthropology lab denizens) and family have been supportive in many ways, sometimes just by acknowledging a sigh of exhaustion.

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CHAPTER 1 INTRODUCTION: RESEARCH QUESTIONS AND THEORETICAL CONSIDERATIONS

RATIONALE:

QUESTIONS ARISING FROM PREVIOUS RESEARCH

Early field studies of Eulemur fulvus, the brown lemur (formerly Lemur fulvus: for nomenclature change see Simons and Rumpler 1988), concluded that agonism, i.e., social conflict behaviour, was rare and mild and that dominance relationships were not discernible. Brown lemurs were further described as spending much time in peaceful physical contact. Only one of these studies (Harrington 1975) focused on social behaviour, whereas in the others, conclusions regarding such behaviour were reached on the basis of ad libitum observation during otherwise systematic ecological study or surveys (Sussman 1975, 1977; Tattersall 1982).

Studies of social behaviour in captive E. fulvus were carried out at the Duke University Primate Center (DUPC) by Vick (1977) and Boskoff (1978) on animals in traditional caged runs, and by Colquhoun (1987) on semi-free-ranging animals in large forested enclosures. Vick and Boskoff observed intense and persistent agonistic behaviour during mating and birth seasons, and Colquhoun also observed similar agonism in a study during the mating season. Vick did not feel there were any behavioural patterns that could clearly be construed as constituting dominance relationships. Boskoff noted intrasexual dominance, but said that she could not detect intersexual dominance. Colquhoun, however, concluded that dominance was clearly an aspect of E. fulvus social life.

Vick and Conley (1976) distinguished the more noticeable, seasonal agonism from what they referred to as background agonism occurring year round: in contrast to background aggression, seasonal aggression frequently resulted in injury, sometimes severe. More recently, Vick and Pereira (1989) discussed seasonal aggression in lemurids in terms of what they called "episodic targeting aggression", in which an individual is targetted by one or more others until it no longer associates with the group, a phenomenon usually related to estrus cycling or births, and occurring when the group has reached a critical size - usually seven to nine individuals for brown lemurs (Harrington 1975; Sussman 1975; Tattersall 1977).

These results from the DUPC contrasted with the general conclusions from field studies mentioned above. Were agonism and dominance in this species essentially artifacts of captivity? In the field, Harrington (1975) saw two fights over access to an arboreal waterhole in which grappling animals fell from trees. He also noticed fresh wounds on some animals during mating season, but did not directly observe any physical conflicts at that time of year other than a single chase. It was thus not possible to know whether the wounds had been caused directly by aggression, or whether they had resulted from falls during chases, or else from some other accident.

It seemed unlikely to me that there would be no conflict whatsoever in free-ranging E. fulvus groups, even if overt, physical agonism were rare. According to classical Darwinian and current sociobiological theory, competition between individuals of a species is axiomatic, given differential reproductive success (Darwin 1859; and see for example Krebs and Davies 1981; Barash 1982); although Wilson (1975) states that, in many species in the animal kingdom, density-dependent controls prevent the population from reaching competitive levels.

It also seemed noteworthy that dominance relationships had not been reported for wild E. fulvus, considering that female dominance had been reported for a number of lemuriform species, and that this phenomenon had been explained quite plausibly as an adaptation to the seasonal environments of Madagascar, particularly given certain aspects of lemuriform physiology (Hrdy 1981; Jolly 1984).

There were therefore two bases for hypothesizing that agonism and dominance relationships would exist among free-ranging E. fulvus: the widespread occurrence of intraspecific competition in the animal kingdom - well documented for the order Primates (e.g., Holloway 1974; Walters and Seyfarth 1987; Silk 1987), including other lemuriform species (e.g., Jolly 1966; Pollock 1979) - and deduction from the Hrdy and Jolly hypotheses regarding female dominance in the infraorder Lemuriformes. Jolly further hypothesized that female dominance might occur through male deference to females with respect to resources, as well as through male submission to female aggression.

However, while competition implies agonism or conflict behaviour (Scott and Frederickson 1951), it does not follow that the form that agonism takes in a particular species must necessarily involve obvious aggression. It is possible that obvious physical aggression is what the earlier field researchers of E. fulvus had in mind in referring to this species as showing little agonism. If such aggression were rare, it would be difficult to detect any consistent dominance relationships. Dominance measured by other criteria, such as approach-avoidance behaviour, would be relatively difficult to measure, especially in a fairly cryptic, arboreal species such as E. fulvus.

Since, unlike previous field research, my study focused on agonism, I hypothesized that, even if obvious agonism mediated by physical contact were rare, I might nonetheless be able to detect agonism and dominance patterns in other forms. These could include supplantations with respect to food, water, and other physical resources; but I hypothesized that agonism might particularly involve supplantations with respect to social partners, considering that this has been said to be a species given to a high degree of affiliative physical contact behaviours (Harrington 1975; Vick and Conley 1976; Tattersall 1977). I also hypothesized that if dominance relationships existed, they might be reflected in the direction of allogrooming in dyads, because in many primate societies subordinants groom dominants more than vice versa (Walters and Seyfarth 1987; Rowell et al 1991).

The goals of my research were to answer the following questions:

1) Could agonism in this species be appropriately described as rare and mild, as had often been said?
2) If not, was agonism sufficiently frequent and clearcut to determine dominance relationships, said to be indiscernible by previous field researchers?
3) If dominance was discernible, what were the patterns - most importantly, did females dominate males as in a number of other lemur species?
4) If dominance patterns were discernible, were they related to patterns of allogrooming?

OVERVIEW OF DISSERTATION

Chapter 1: Statement of the research problem and review of the literature.

In this chapter I first discuss inconsistencies in the conclusions from previous researchers' work on brown lemurs which led to my formulation of the basic research questions for this dissertation. Literature on theoretical issues related to these questions is reviewed. This review includes the following topics: definition of terms such as aggression, agonism and dominance; discussion of controversies regarding the meaning and meaningfulness of the concept of dominance; and functional interpretations of the phenomenon of female dominance.

Chapter 2: a) Description of the natural history of the study species and of the study sites and groups.
b) Description of research methods.

Chapter 3: Nature, rates and contexts of agonism in E. fulvus

In this chapter I approach the question of whether E. fulvus agonism can in fact be appropriately characterized as rare and mild, as reported from earlier field studies. I present data on the nature and frequency of agonistic signals, on the contexts of agonistic interactions, and on the composition of agonistic dyads by age/sex class.

Chapter 4: Nature and patterns of dominance in E. fulvus

In this chapter I question whether dominance relationships in E. fulvus are in fact indiscernible, as reported from various field studies. I discuss the rationale for measuring dominance in terms of the direction of aggressive rather than submissive signals. I also address the question of the relationship of dominance to age and sex class.

Chapter 5: Dominance and social grooming in E. fulvus

Many studies of primates have concluded that unidirectional social grooming, or allogrooming, is generally directed to dominant animals by subordinate ones. The first question for this chapter is whether or not this holds true for E. fulvus. In dyads in which dominance was not measurable, I have looked for correlations between direction of unidirectional allogrooming and age and sex class of the individuals involved. My second question is whether mutual grooming (in which both animals groomed each other simultaneously) was more characteristic of egalitarian relationships lacking in dominance, and whether asymmetry in allogrooming (in which only one animal in a dyad was groomed at a time, with varying degrees of reciprocity or asymmetry in different dyads) was more characteristic of dyads with clear dominance or aggressive asymmetry.

Chapter 6: Conclusion

In this chapter I discuss the overall significance of patterns of agonism, dominance and social grooming in Eulemur fulvus.

THEORETICAL CONSIDERATIONS

(i) Defining Terms

Clear definitions of agonism, aggression and related terms are necessary before approaching the question of agonism in E. fulvus.

aggression: (the following definitions are not mutually exclusive)
1) behaviour involving assault or threat of assault that is physically or psychologically harmful to another individual (modified from Carthy and Ebling 1964; Southwick 1972; Hinde 1974; Karli 1991); or
2) self-assertive behaviour or display (i.e., threat signals, e.g., postures, sounds, odours, etc.) inducing physical withdrawal of another (Barnett 1968) related to establishing, maintaining or exercising priority of access to resources - food, water, space, or mates or other social partners - or to establishing or reinforcing dominance (modified from Hinde 1974; Bernstein 1981).

submission:
self-protective or deferential behaviour in response to aggression or potential aggression, acknowledging the superior agonistic status of another (modified from Hand 1986; Walters and Seyfarth 1987).

agonism:
either aggressive or submissive behaviour(s) in adaptation to a conflict or competitive situation (Scott and Frederickson 1951; Scott 1974).

dominance:
consistent winning, i.e., receiving and not giving submissive signals (including avoidance), or superior agonistic status as measured by consistently giving rather than receiving aggression, in repeated conflicts with a specific other individual, often directly related to priority of access to resources (modified from Hausfater 1975; Bernstein 1981; Hand 1986; Walters and Seyfarth 1987).

subordinance (also subordinacy, subordination):
the opposite of dominance, i.e., consistent losing, or consistent receiving rather than giving of aggression, in conflict with a specific other individual (modified from Chalmers 1979; Hand 1986).

The traditional ethological meaning of "aggression" is behaviour with the intent or threat to cause physical harm to another (Carthy and Ebling 1964; Southwick 1972; Hinde 1974). Primatologists have usually used the word aggression to describe all sorts of self-assertive behaviour that does not necessarily manifest an intent to injure. This is closer to the popular than the technical definition (Hinde 1974). Such behaviour includes displays; less obvious, less ritualized behaviours related to dominance; supplantations with respect to resources or social space; and territorial vocalizations.

Lorenz (1966) wrote that aggression is necessary if only the fittest are to survive, mate successfully, and carry on the species, even if aggression is mainly ritual and bluff rather than actual physical attack. He saw aggression as essential in establishing dominance relationships, which maintained order and stability in social groups. (Hinde, however, [1974] discussed how aggression can sometimes be dysfunctional. It can frighten away potential mates, result in injury to infants, consume otherwise valuable energy, or even cause harm to the aggressor.) In addition to this ultimate explanation, Lorenz also explained aggression in proximate terms as manifesting an innate need or drive to behave aggressively.

A radical change in focus regarding research on aggression in animal behaviour studies followed publication of E.O.Wilson's Sociobiology: the new synthesis in 1975. In the framework of neo-Darwinist evolutionary theory, the "Modern Synthesis" of the preceding 40 years - combining a functional interpretation of behaviour and other phenomena, in terms of their adaptive significance, with the principles of population genetics - Wilson (1975) argued that organisms are essentially DNA's way of producing more DNA, and that social and other behaviour must be understood in terms of its contribution to genetic fitness, i.e., the organism's success in replicating its genetic material in the next generation. Most biologists no longer believe that individuals are behaving for the good of the species: if they are behaving towards any general goal, it is their own reproductive success:

> ... self-sacrificing individuals, if they ever existed, would sooner or later be replaced by mutant types that behaved in ways that increased their fitness ... Therefore, the working hypothesis of the modern biologist is that an individual must resolve conflicts in ways that raise his or her reproductive success, regardless of the consequences this behaviour has for the population as a whole (Alcock 1989).

This theoretical shift in ethology in general is reflected historically in primatological studies. In 1974 Holloway's Primate Aggression, Territoriality, and Xenophobia was published, an edited volume of papers dealing with aggression. Much, though not all, of the material discussed in this book has to do with lab studies, or with often highly invasive experiments (e.g., lobotomies) conducted on otherwise semi-free-ranging animals. The emphasis since 1975 seems to reflect the influence of sociobiology in two ways.

First of all, the emphasis has been more on field studies. This is in keeping with the evolutionary approach of sociobiological explanation: the aim is to observe behaviour that is naturally occurring in order to understand its adaptive function.

Secondly, a focus on aggression per se - perhaps appropriate when it was still seen as the manifestation of a unitary drive or instinct - has been abandoned in favour of a more holistic approach which sees aggressive behaviour in terms of strategies, with evolutionary causes and adaptive consequences, that balance costs and benefits so as to ultimately maximize fitness, i.e., reproductive success (e.g., Silk 1987). This has in turn led to an increased emphasis on longterm studies, reflecting awareness of the fundamental importance of life histories in understanding such "strategies" (e.g., Silk 1987; Smuts 1987a, 1987b).

This change in focus has also meant that primate aggression is seen more in the context of dominance relationships. In some species, factors such as reconciliation and alliance formation are now seen as at least as important as aggression in determining the pattern of dominance relationship in a primate group (e.g., de Waal 1986). While still emphasizing the costs and benefits of particular aggressive behaviours, primatologists and other ethologists have emphasized that aggression is but one strategy for maximizing fitness, and that it must be examined alongside other kinds of influence, such as are wielded through affiliative behaviours (e.g., Smuts 1987a, 1987b), in order to understand the overall reproductive strategy of the actor. To understand the choice of one strategy over another, it is necessary to understand behaviours in context, and this calls for explanations of proximate as well as evolutionary causes of behaviour (Vehrencamp 1983; Hand 1986) .

With respect to primate behaviour, these kinds of considerations have been developed further by de Waal (1986), who said that aggression must be understood as one of several conflicting tendencies, including social attraction and cooperation, which are integrated into a cohesive system of social relationships through tolerance and reconciliation. This explanatory approach is distinctly proximate, and de Waal has stated that evolutionary explanations may be limited because they isolate aggression from its social context: insofar as aggression leads to conflict resolution, and insofar as the latter seems psychologically important to group members and thus contributes to group stability, then aggression can be seen as a constructive element in social groups (de Waal 1986, 1987, 1989). From this point of view, the distinction between group and individual selection is to some extent a false dichotomy (de Waal 1989).

Aggression is often discussed in relation to competition: the latter is a more inclusive phenomenon subsuming the former (e.g., Walters and Seyfarth 1987; de Waal 1987). According to Wilson:

> Competition ... means the active demand by two or more individuals of the same species (intraspecific competition) or members of two or more different species at the same trophic level (interspecific competition) for a common resource or requirement that is actually or potentially limiting (1975).

This includes both environmental resource competition, e.g., for food and shelter, and sexual competition. Competition can take the form of a scramble to gain first access to a resource, which is non-aggressive, or it can involve an aggressive contest.

Among social animals, most species engage in contest competition rather than scramble competition (Drickamer and Vessey 1982). In these cases, however, aggressive displays or threats are often used in place of physical aggression, and the limited resource is not fought over on each occasion (Walters and Seyfarth 1987). Furthermore, contest competition itself is not necessarily overtly aggressive. Based on the outcome of previous interactions involving aggression, a subordinate animal may avoid a dominant in an "approach-retreat" (or approach-avoid) interaction (Rowell 1966), or a dominant may supplant a subordinate from a mutually desired resource with only a mild threat.

The following are typical contexts for aggressive behaviour (after Hamburg 1973; Wilson 1975): dominance interactions (see below); competition for a valued resource in short supply; competition for mates; protection of infants; parental discipline; mother-offspring weaning conflict; meeting between unfamiliar animals, including territoriality - a related possibility is crowding, often resulting from human encroachment on natural habitat; strange behaviour by a familiar animal, e.g., due to sickness; and predator-prey relationships.

Walters and Seyfarth (1987) point out that most aggression in primate groups is not directly related to the acquisition of resources, but rather involves the establishment and maintenance of dominance relationships, which in turn affect resource access through such phenomena as approach-avoidance interactions, or competitive exclusion in which subordinates simply wait for dominants to finish with a desired resource before using it themselves.

Dominance can be defined as consistent winning of agonistic conflicts in a dyadic relationship, as determined by submissive signalling, including avoidance, on the part of the other individual (Hausfater 1975; Pereira et al 1990). In a species in which submissive signalling is rare, this definition is likely to be inadequate for delineating discrepancies in agonistic power in most dyads, and dominance can be defined in terms of the primary direction of aggressive signals, provided aggression is only infrequently responded to in kind. Either of these definitions is consistent with the notion of dominance as social power, influence or control, based on aggression or the potential for aggression.

Scott has used the term "agonism" for behaviour which is adaptive in a conflict situation between members of the same species. This usage excludes interspecific competition and predator-prey relationships (Scott and Frederickson 1951; Scott 1974).

Hand (1986) has more recently defined social conflict in proximate terms as incompatibility of motivational priorities between two or more individuals. Conflict situation behaviour or agonism includes defensive or appeasement behaviours such as fleeing or giving submissive vocalizations and gestures, as well as aggressive or self-assertive behaviours involving assault or threat. Both types of behaviours may even be manifested by the same individual in a single exchange or interaction. When agonism or conflict occurs between individuals in the same group, it is referred to as pertaining to dominance relations.

Andrew (1964) described aggressive signals of primates in general (with examples from both strepsirhine infraorders, lemuriforms and lorisiforms) from an evolutionary perspective, in a broader context of mammalian and other vertebrate aggressive signals. However, in studies of particular primate species, the repertoires of their aggressive signals have not necessarily been presented, even in discussions focusing on aggression (e.g., Holloway 1974). There have been studies which systematically describe aggressive signals (e.g., Hausfater 1975; Smuts 1985), but they are exceptional. Brown lemur aggressive signals were described by Vick and Conley (1976), as well as by Andrew (1964).

Aggression includes behaviours ranging from assault causing serious physical injury to threats involving no physical contact, although threats, if disregarded, may lead to physical aggression (Matthews 1964). Threats may be simple in form or may take the form of elaborate, ritualized displays (Barnett 1968; Walters and Seyfarth 1987). In many species, threats predominate over physical aggression (reviewed for cercopithecoids in Nagel and Kummer, 1974), whereas others are noted for a high rates of physical aggression (e.g., rhesus macaques, Macaca mulatta; de Waal 1989). The borderline between physical aggression and threats is not necessarily clear, because some aggressive physical contact, such as a light cuff, is probably too mild to cause physical discomfort, let alone pain or injury. The threat of harm is just as significant as inflicting physical damage, because in much aggression there is no physical contact, or only mild contact, yet threats -

which include displays and supplantation of another animal from a place, resource, or social partner - can ultimately induce both physical and psychological stress for the target animal (Karli 1991), resulting from exclusion from resources, adversely affecting its well-being and reproductive success (Barnett 1968; Marler 1976). Hinde (1970, cited in Hand 1986) says threats are typically used when the signaller is ambivalent or is inhibited from attacking. However, they might also function as a less energy-consuming form of aggression than physical assault.

Submissive behaviour is generally said to function to reduce the frequency or intensity of aggression (e.g., Walters and Seyfarth 1987). By signalling submissively, an individual acknowledges that it has lost a conflict, and thus halts further aggression (e.g., Hand 1986); or it acknowledges the agonistic superiority or status of another, thus preventing aggression in the first place.

Submissive signals in primates include fleeing, cowering or cringing, grimacing or grinning, and giving submissive vocalizations such as screams, squeals, or chatter (Andrew 1964; Hausfater 1975; Smuts 1985; de Waal 1987; Walters and Seyfarth 1987), and have been described among captive brown lemurs by Vick and Conley (1976). Various authors make separate use of the terms "submission" and "appeasement": Klein (1974), for instance, has reserved use of the term "appeasement" for "gestures facilitating or accompanying approach to a threatening animal". Others (e.g., Walters and Seyfarth 1987) do not clearly distinguish between the two terms. Hand (1986) argues that appeasement behaviour per se is not a status indicator, as it may involve reassurance-seeking on the part of a subordinate, reassurance-giving on the part of a dominant, or conciliation between animals of similar status. The occurrence of such inconsistencies in the literature has also been commented on by de Waal (1986).

Reconciliation, as opposed to conciliation or appeasement, is behaviour which involves making peace after an agonistic encounter; i.e., reconciliation behaviour is an attempt to restore social harmony. Study of this aspect of primate agonism-related behaviour has been pioneered by de Waal (1986, 1987, 1989).

In summary, submissive behaviour is a self-protective response to aggression, appeasement an attempt to reassure another of the lack of aggressive intent, and reconciliation an attempt to establish peace after a conflict.

Of course, aggression, including threats, need not be responded to submissively: it may also be responded to in kind. Finally, aggression may simply be ignored, or at least not responded to either aggressively or submissively.

(ii) The Meaning of Dominance

Dominance has been defined as social power, "...established through conflict or self-assertion or potential for 'aggression'. Likewise dominance is measured through studying the outcome of conflicts and/or conflict avoidance" (Bernstein 1981). When competitive interactions are predictable in terms of who does or does not gain or maintain access to a particular resource - be it food, water, space, or mates or other social partners, in terms of who signals submissively or avoids the other in the absence of immediate resource competition, or in terms of who typically gives rather than receives aggression, then one can speak of patterns of dominance (reviewed in Bernstein 1981).

Dominance has been variously defined, however, and the concept has provoked much argument. Its validity and utility have been questioned. Nevertheless, suggestions that it be abandoned as a useful construct in the study of behaviour have been characterized as throwing the baby out with the bathwater (Wade 1978; Bernstein 1981).

The concept of social dominance in the study of behaviour was first formulated in the early 1800s in the context of observations on bumblebees (Wilson 1975); but it did not make much of an impact until Schjelderup-Ebbe's discussion of pecking orders or linear hierarchies in domestic fowl in the 1920s (Gauthreaux 1978). Since the mid 1930s, numerous studies have shown the phenomenon of social dominance to be widespread throughout the animal kingdom (references in Gauthreaux 1978).

The concept of social dominance has changed since the 1930s from being largely descriptive, while assuming a given despotism in animals' social organization (Gauthreaux 1978), to being concerned more with function, the latter focusing most often on priority of access to resources (Bernstein 1970; Rowell 1974). Another proposed function of dominance is social control, although this has been dismissed by some as being a group selectionist argument (Fedigan 1982).

One of the more common criticisms has been that the concept of dominance is too multidimensional (e.g., Gartlan 1968; Syme 1974), with various measures of dominance having little correlation, sometimes not even being reliable between conspecific social groups (Bernstein 1970). Others (e.g. Richards 1974) have said that dominance still has conceptual value as an intervening variable, and have countered that various measures - priority, agonism, approach-avoidance, leadership, attention structure, reproductive success, direction of grooming, direction of mounts, direction of agonistic signals, etc. - have been shown to be correlated in some studies, although the patterns vary from species to species.

The point has been stressed that dominance is not a heritable quality of an individual, but a relationship between individuals, and that it can change (Bernstein 1981). As Hinde and Datta (1981) explained:

> the effect of experience in agonistic encounters (here, the independent variable) on the directionality of subsequent interactions (dependent variable) is to be understood in terms of an effect of the experience on "dominance" (intervening variable). The question of whether dominance exists is then put in perspective. It does not exist in a concrete data sense, but it may have usefulness as an explanatory concept (442).

Taking a somewhat different approach, Wade (1978) said that while dominance is not a unitary concept, this is no reason to reject it: this variability itself can prompt our questions and increase our understanding of the phenomenon. He argued that in fact there is a surprising extent of correlation between various measures of social behaviour and priority-of-access that has emerged from a variety of primate research.

Wade's (1978) comments largely take the form of a counterattack against Gartlan (1968) and Rowell (1974), who both questioned the existence of dominance in nature. Rowell (1974) suggested that dominance has no function because it is merely an artifact of captivity: hierarchies are actually "subordination hierarchies", the result of a naturally adaptive, individually variable (and perhaps genetically polymorphic) adrenal response to danger, which in the stressful conditions of captivity is overactivated in some individuals, who become the submissive or subordinate members of the group. However, Rowell did not explain why submissive signals should trigger aggressive responses in other individuals.

Rowell (1974) pointed out that when we speak of dominance (regardless of whether we feel it is natural or not) we are talking about the predictability of the outcome of competition within dyads. Bernstein (1981) emphasized the difference between dyadic interaction and dominance hierarchies. He pointed out that organizing relationships in a group into a linear, transitive hierarchy might mask certain triangular relationships (e.g., A dominates B, B dominates C, C dominates A) that in some instances result from coalitions of individuals. Bernstein said that even if the notion of hierarchy turns out to be irrelevant as a general principle of the organization of animal societies, "... dominance relations may still influence many aspects of social interaction within dyads, and this may have a profound influence on the organization of groups" (1981: 429).

(iii) Female Dominance, Reproductive Seasonality, Sexual Dimorphism and Sexual Selection

One of the purposes of this research was to determine whether or not E. fulvus conforms to the pattern of female dominance described for some other lemuriforms (Lemur catta: Jolly 1966; Indri indri: Pollock 1979; Propithecus verreauxi: Richard 1978; Phaner furcifer: Charles-Dominique and Petter 1980; Microcebus murinus: Perret 1982; Varecia variegata : Burton 1986; Foerg 1982,1985; Pereira et al 1988; Kaufman 1991), and until recently (Pereira et al 1990) thought to characterize all of the primates of Madagascar. In these species, female dominance has usually been said to take the form of female feeding priority (reviewed by Richard 1987).

A hypothesis to explain female dominance among lemurs and other primates (squirrel monkeys, Saimiri sciureus; and talapoin monkeys, Miopithecus talapoin) living in seasonal environments was developed by Hrdy (1981), and modified by Jolly (1984). The hypothesis rests on the premise that seasonality of resource availability such as occurs in Madagascar, and resultant reproductive seasonality, constitutes a special set of circumstances within the overall framework of sexual selection pressures, which themselves result ultimately from differential investment in offspring by females and males, as discussed in detail by Trivers (1972).

Trivers (1972), following Williams (1966) and Bateman (1948), stated that, because males are not as limited by the number of sperm they can produce as are females by the number of fertilized ova they can gestate and bear, females constitute a limiting resource for males. The parental investment of females far exceeds that of males, as the energy involved in making an ovum is so much greater than that required to manufacture a sperm cell. In the case of mammals this differential investment is particularly noteworthy.

> Once female mammals became committed to internal gestation and lactation, their parental investment was so great that the likelihood of evolving a social system in which the relative

> parental investment of males exceeded that of females and males became a limiting resource for females became exceedingly slim (Ralls 1976).

Therefore, males compete primarily for mates, whereas females compete primarily for food resources, the latter ultimately to ensure successful pregnancy and lactation.

Intramale competition can result in greater male variance in secondary sexual characteristics, and sexual dimorphism between males and females in characteristics such as size, weight and canine length. Sexual dimorphism often, but not always (Ralls 1976), results in male dominance over females, essentially as a side effect of intramale competition (Jolly 1984). However, female choice can decrease the disparity, because females may not necessarily choose to mate with the winners of intramale competition (reviewed in Fedigan 1983; Smuts 1987a). Ralls (1976) pointed out that the degree of sexual dimorphism in a species is the differential net result of various selection pressures, both natural and sexual, operating on females and males.

Hrdy (1981) suggested that lemuriforms, squirrel monkeys and talapoin monkeys are female-dominant and monomorphic because males in these species' seasonal environments can only afford to compete with each other, which entails gaining weight, during mating season. Jolly (1984), noting that mating season occurs during times of resource scarcity in a number of the above species, suggested that the focus should be on females rather than males: female dominance has evolved primarily in species for which seasonal resource scarcity and various physiological factors, such as high metabolic rates (in small-bodied species), constitute unusual energetic constraints for reproductive females. In the case of strepsirhines (lemuriforms and lorisiforms), Jolly also suggested as possible constraints less efficient placental nutrient transfer than that found in haplorhines (anthropoids and tarsiiforms), and relative altriciality and consequent faster postnatal growth. Richard and Nicoll (1987) further proposed that such energetic constraints may result partly from the need for seasonally folivorous primates with low basal metabolic rates to elevate these rates during gestation. Young et al (1990) stated more specifically that such species showed a high rate of prenatal maternal investment, as measured by prenatal weight gain of offspring.

As previously proposed by Petter-Rousseaux (1968; cited in Boskoff 1978) and Martin (1972), reproductive seasonality has been favoured because peak energy demands on the mother during later lactation, and the necessity for readily available food for newly weaned infants, require that these stages of reproduction and ontogeny take place during the wet season, when high quality food is more readily available. Female feeding priority has been favoured because energetic demands on reproductive females are also high during times of resource scarcity, which, for Malagasy primates in general, would include all of gestation and at least the earlier weeks of lactation (Jolly 1984). This situation can be seen as an extension of the constraints on pregnant and lactating females in traditionally male-dominant species, which result in the temporary dominance of these females over males (Ralls 1976). Kappeler (1990) has more recently shown that female dominance in L.catta is not restricted to the phenomenon of feeding priority. This is also the case for Varecia (Kaufman, unpub. data), and it may well turn out to be true for other lemur species.

According to Hrdy (1981), resource seasonality also theoretically limits energetically costly male-male competition to times of relative resource abundance, although Jones (1981) suggested that it may pay males in some species to compete in times of scarcity as well. If the Hrdy-Jolly hypothesis is correct, then reproductive seasonality in lemuriforms, aside from assuring that all females mate at the most opportune time in bioenergetic terms , might also function to minimize sexual selection pressures on males, and, indirectly, to limit male competition with females.

Thus, although the complexes of selective pressures operating on females and males are different, their respective adaptations are compatible, as of course they must be for any species to be viable. Hrdy (1981) and Jolly (1984) noted that there is little if any sexual dimorphism in lemuriform species: thus, males cannot outcompete females for resources, as may occur in larger anthropoid species, in which such competition might also be less harmful to reproductive females in terms of their energy budgets. Jolly (1984), following Hrdy (1981), pointed out that female dominance is also found in some haplorhine primate species, such as squirrel monkeys (Baldwin and Baldwin 1981), and talapoins (Rowell 1977), in which both sexes are constrained by small size and high metabolism. In those species male-male competition is very much seasonally restricted, reproductive demands on females are particularly heavy because of relatively high neonatal birth weights, and there is little if any sexual dimorphism. Jolly (1984) also cited data from other haplorhine primates, Himalayan langurs (Bishop 1979) and chacma baboons (Anderson 1982), which support the model that seasonal breeding and female dominance are adaptive responses to seasonal environmental stress. In those species, groups living at higher altitudes have "... greater female size with respect to males, seasonal reproduction, and relative tolerance (outside of peak mating periods) between males" (Jolly 1984: 212). In species in which there is not such strong ecological pressure on reproductive females, the effects of male-male competition tend to predominate. Sexual dimorphism, and, according to Hrdy and Jolly, male dominance over females, are more likely to occur under these circumstances.

However, even in the recently extinct subfossil lemurs, most of which were considerably larger than any extant species, there was apparently no significant dimorphism in body size (Gingerich and Ryan 1979), so it "... seems that prosimians have and had a radically different mode of ecological and social relations between the sexes from that of monkeys and apes" (Jolly 1984). Clutton-Brock and Harvey (1977) suggested that lemuriforms may differ from anthropoids in this respect largely as a result of phylogenetic inertia, with different sorts of adaptive "choices" having been made on their evolutionary paths.

Returning to the matter of the constraints that resource scarcity in the dry season could place on intramale competition, it appears to be the case that, in lemur species in which it has been observed, the mating season does result in a sudden increase in intramale competition. In P. verreauxi, the sifaka, in which agonism outside of the mating season is very rare, agonistic encounters at this time may result in severe injuries or even death; and the outcome of conflicts does not reflect pre-existing dominance hierarchies, which exist in this species with respect to feeding priority (Richard 1974, 1978). In L. catta, agonistic interactions do occur among males outside of the mating season, but not with the intensity shown during the mating season (Jolly 1966). The outcome of such interactions does not reflect pre-existing dominance relationships among males in the group. In summary, for male lemurs overall, extended harassment of consexuals outside of the mating season may simply be too costly, given resource seasonality and high metabolism; and the results of mating season agonistic interactions do not appear, in some species at any rate, to be predictable from intermale dominance relationships at other times of the year.

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CHAPTER 2 METHODS: STUDY SPECIES, SITES, GROUPS AND DATA COLLECTION

NATURAL HISTORY OF EULEMUR FULVUS

Eulemur fulvus, formerly called Lemur fulvus (for nomenclature change see Simons and Rumpler 1988), is one of five species of the genus Eulemur in the family Lemuridae. The seven subspecies of E. fulvus are distributed in all regions of Madagascar except for the arid and semi-arid south and southwest (Figs. 2.1 and 2.2). Tattersall has described this species as "... a series of closely related populations ..." with the subspecies recognized "... on the basis of certain modal types" (1982:52).

Adults of both sexes normally weigh about 2.5 kg, but weights as high as 4 kg have been reported (Tattersall 1982). Head and body length is usually about 400 cm, and tail length over 500 cm (Tattersall 1982). In most subspecies, including the two studied in my research, sexual dichromatism is marked. E. f. rufus have black muzzles, this colour extending up the centre of the face between the eyes, thinly surrounding the eyes, and then continuing up the centre of the forehead to meet the crown. Females are reddish-brown in body colour, with white around the black facial area, particularly over the eyes, and a grey to black crown. Males are grey-brown in body colour, with beige or grey around the central black facial area, and an orange or rust-coloured crown of fur longer than that on the tops of the heads of females. E. f. collaris females and males are grey-brown to dark brown. Females have a grey face, neck and crown and bushy, pale-orange cheek fur. Males are black in face, neck and crown, and their cheek fur is bushier than that of females, although similar in colour.

In both subspecies, both sexes have naked, wrinkled glandular skin in the circumanal area (Harrington 1974; Tattersall 1982). Both sexes scent-mark by rubbing the

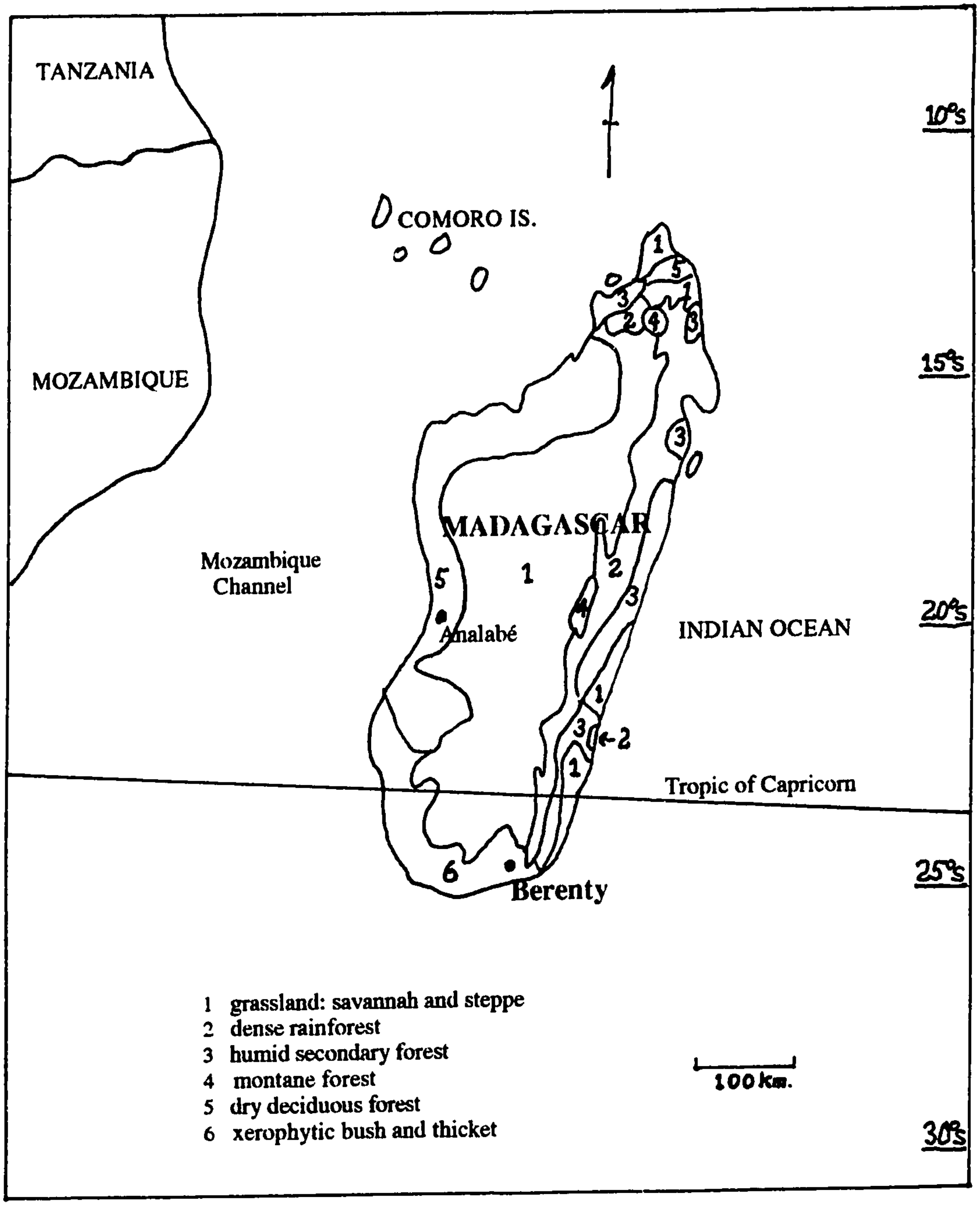
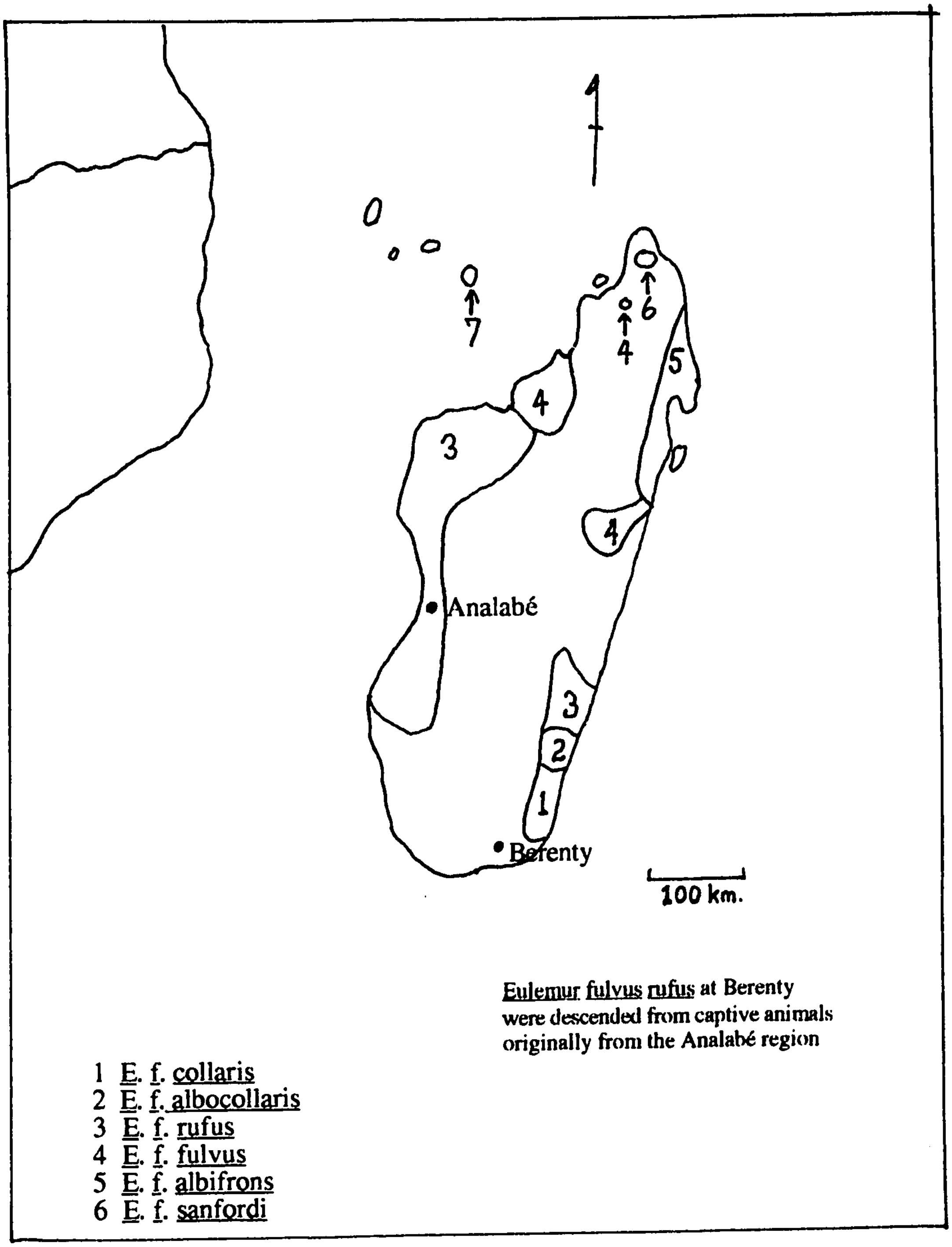


Fig. 2.1: Vegetational formations in Madagascar (modified after Tattersall 1982).



Eulemur fulvus rufus at Berenty were descended from captive animals originally from the Analabé region

Fig. 2.2: Distribution of the subspecies of Eulemur fulvus (modified after Tattersall 1982).

anogenital area on substrates (Harrington 1974; Chandler 1975; Vick and Conley 1976), depositing secretions of apocrine and sebaceous glands (Montagna 1962, cited in Harrington 1974), as well as, possibly, traces of urine and feces (Harrington 1974). The scrotal area of males is also a source of copious glandular secretions (Harrington 1974). Males anogenital-mark on females as well as on substrates (Harrington 1974; Chandler 1975; Vick and Conley 1976). They also rub their foreheads, sides of muzzles, chins and hands on substrates, but there are contradictions in the literature as to whether or not these areas are glandular (Andrew 1964; Rumpler and Oddou 1970, cited in Tattersall 1982; Chandler 1975; Vick and Conley 1976; Harrington 1974).

TABLE 2.1: ANNUAL REPRODUCTIVE CYCLE IN
<u>EULEMUR</u> <u>FULVUS</u> (after Boskoff 1978)

Reproductive season	Hemisphere	Months	Behaviours peaking at this time
Mating	Southern Northern	April-June Oct.-Dec.	Scent-marking and sniffing, copulation and aggression
Gestation	Southern Northern	June-Sept. Dec.-March	Grooming, and male-to-female sniffing of genitals
Birth	Southern Northern	Sept.-Oct. March-April	Aggression
Lactation	Southern Northern	Oct. -March. April-Sept.	Grooming, scent-marking, clasping, and mounting

Among other functions, scent-marking presumably co-ordinates sexual cycles between the sexes (Boskoff 1978; Table 2.1). Increased scrotal size in males precedes the first estrus period of the year by one to two months (Boskoff 1978). As in other lemurs, females are polyestrous, and a preliminary, anovulatory and non-receptive "pseudoestrous" has been noted in this species and Lemur catta (Boskoff 1978; Tattersall 1982), with males beginning to show sexual behaviour towards females at this time. Estrus itself is very brief, lasting from one to two days (Boskoff 1978). In Madagascar, a female brown lemur's first receptive ovulatory period is usually in April (Petter et al 1977), whereas the initial ovulatory estrus occurs during September or October in the northern hemisphere (Boskoff 1978). According to Boskoff (1978), estrus cycling, including female receptivity, occurs at 30 day intervals until July if conception does not occur, but cycles after December are probably anovulatory (Boskoff 1976, cited in Vick 1977). Gestation is normally 119 days (Boskoff 1978), and births in the wild are characteristically single (Tattersall 1982). Mating season for all lemur species is timed so that infants will be weaned when resources are most likely to be abundant in what are characteristically highly seasonal environments (Martin 1972; Jolly 1984).

E. fulvus normally live in multi-female, multi-male groups of from five to 12 individuals (Tattersall 1982). Sussman (1975) reported groups as large as 17 (including four infants); and solitary individuals, both juvenile and adult, have been seen at Ranomafana in the eastern rainforest (Meyers 1988) and at Berenty (pers.obs.).

E. fulvus are predominantly arboreal (Sussman 1975). Their locomotion is primarily quadrupedal walking, running, climbing and leaping; but they are capable of vertical clinging and leaping locomotion between narrow vertical substrates (per. obs.).

Brown lemurs have been reported to be both crepuscular (Harrington 1975; Sussman 1975), and diel or cathemeral (Tattersall 1982; Fleagle 1988) - the latter two terms meaning that they are alternately active and resting throughout the 24 hour day without respect to light cycles. I did not see or hear the Berenty brown lemurs active at night, but they foraged until an hour after sunset and were moving again at the first hint of light. Although they usually rested at midday, they were occasionally seen foraging in the heat of the day.

Brown lemurs were originally thought to be primarily folivorous, based on a study of dry forest E. f. rufus by Sussman (1975). However, more generalized herbivory was observed by Tattersall (1977) among E. f. mayottensis, and by Meyers (1988) among rainforest E. f. rufus. I observed the Berenty E. f. rufus eating insects, spiders, and spider web as well as leaves, buds, flowers, fruit, herbs, bark and fungi. I observed one instance of a brown lemur eating a gecko, which, because it barely moved when approached, was probably injured or sick. Omnivory in this species, including eating of large millipedes, has also been observed by O'Connor (pers.comm.) at Berenty. At the DUPC, brown lemurs have been known to catch and eat small birds accidentally trapped in enclosures.

AGE CLASSIFICATION USED IN THIS STUDY

For analytical and other methodological reasons, only two age classifications for individuals older than unweaned infants have been used in this study: juvenile and adult. In the case of females this was an obvious approach, as female brown lemurs can bear their first surviving offspring at two years of age. From weaning at four months until adulthood at conception of offspring, possibly as early as 20 months, females have been considered here to be juveniles. Although one could argue that there is a qualitative change throughout this period, ending in adolescence, this would seem to be of little practical value, at least for purposes of this study. Furthermore, such fine distinctions would have made behavioural sample sizes for much of the analysis too small for valid interpretation.

For males the situation is perhaps more complicated. Males do not look like adults, insofar as having fully descended testicles, until they are about four years old.

Nevertheless, males as young as 20 months were observed copulating extensively with receptive females. In some instances, such younger adult males were more sexually active and socially dominant than other older males. It therefore made sense, as in the case of females, to classify males as juveniles from weaning until the commencement of mating activity (although their fertility was not known). Furthermore, as in the case of females, finer distinctions would have resulted in sample sizes too small for meaningful attempts at interpretation of the data.

DESCRIPTION OF THE STUDY SITES, AND OF THE COMPOSITION, RANGES, ACTIVITY RHYTHM AND SUBSISTENCE ACTIVITY OF THE STUDY GROUPS

i) Berenty, Madagascar

The Berenty reserve is located in the semi-arid south of Madagascar, which consists mostly of xerophytic forest with strips of gallery forest. Neither *E. f. rufus*, nor any other *E. fulvus* subspecies, is indigenous to this region, although *E. f. rufus* are naturally distributed both in eastern rainforest and in western deciduous/gallery forest. The study animals are descended from captives originally taken from gallery forest in the deciduous forest zone of the central west coast of the country. These animals escaped from their cage during a cyclone in 1974, and established themselves as free-ranging animals in the 100 hectare private Berenty reserve: at the time of the study, the population numbered approximately 55 individuals in six social groups. The vegetation of this reserve, dominated by the kily tree, *Tamarindus indica*, has been described in detail elsewhere (e.g., Budnitz and Dainis 1975; Jolly 1966). The reserve is surrounded, where not bordered by the Mandrare River, by a vast sisal plantation. The other lemurs in the reserve are all indigenous: *L. catta*, ringtailed lemurs; *Propithecus verreauxi*, sifakas; *Lepilemur mustelinus*, sportive lemurs; and *Microcebus murinus*, mouselemurs.

After about two weeks of reconnaissance observations, I began my formal study of brown lemurs at Berenty on 22 Aug.1987, a couple of weeks before the first births occurred. The study continued until 26 Dec. 1987.

Of the six groups of E. f. rufus at Berenty, mean and modal size was seven individuals, with a range of five to 10. The sex ratio varied from .75 to 2.5 males per female. In each group, two or three infants were born between 22 Aug. and mid-October, with no mortality at the time the study was concluded late in December.

Focal data collection on the first group was begun before a second group was chosen. I originally considered a neighbouring group which became the second study group to be inappropriate, because at the beginning of the study it consisted of three E. f. rufus females and one E. f. collaris male, the latter being another escaped captive. Two other groups were easy to observe, but were in an area frequented by tourists, which disrupted their normal behaviour. The fifth and sixth groups had much of their ranges in an area including extensive patches of thorny vines, which made following their progressions impossible. The sixth group included E. f. rufus x E. f. collaris hybrid individuals and their infants.

The question of choosing another group was resolved when, on 29 September, three males left group 1, which had previously numbered 10 individuals (infants not included), and joined the three neighbouring females, which was presumably the reason for the disappearance from their presence of the E. f. collaris male. Because I had already collected a considerable amount of data on these three males, I decided to use this newly constituted group as group 2. Group 1 before the males' emigration I call group 1a, and after it group 1b. Berenty group compositions are given in Table 2.2.

Group 1a/b had a range of approximately 8.5 hectares (Fig.2.3), primarily in an area of gardens and orchards abandoned 15 to 20 years ago, but also including closed-canopy gallery forest dominated by the tamarind or kily tree. In addition to the kily tree, a

TABLE 2.2: BERENTY GROUP COMPOSITIONS

with estimated ages of individuals as of Sept. 30,'87

GROUP 1a: Aug. 17 - Sept. 29		GROUP 1b: Sept.30 - Dec.26	GROUP 2: Sept.30 - Dec.26
af 51	>>>>>>>>>>>>	af 51 (10 yrs.)	af 71 (7 yrs.)
af 52	>>>>>>>>>>>>	af 52 (5 yrs.)	af 72 (4 yrs.)
af 53	>>>>>>>>>>>>	af 53 (2 yrs.)	
jf 54	>>>>>>>>>>>>	jf 54 (1 yr.)	jf 73 (1 yr.)
am 55	>>>>>>>>>>>>	am 55 (7 yrs.)	
am 56	>>>>>>>>>>>>	am 56 (2 yrs.)	
am 58	>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>		am 58 (6 yrs.)
am 59	>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>>		am 59 (3 yrs.)
jm 57	>>>>>>>>>>>>	jm 57 (1 yr.)	
jm 50	>>>>>>>>>>>>>>>>>>>>	(1 yr.) >>>>>>>>>>>>>>>>>>>>>>>>>>>	?
		3 infants	2 infants

a=adult; j=juvenile;
f=female; m=male

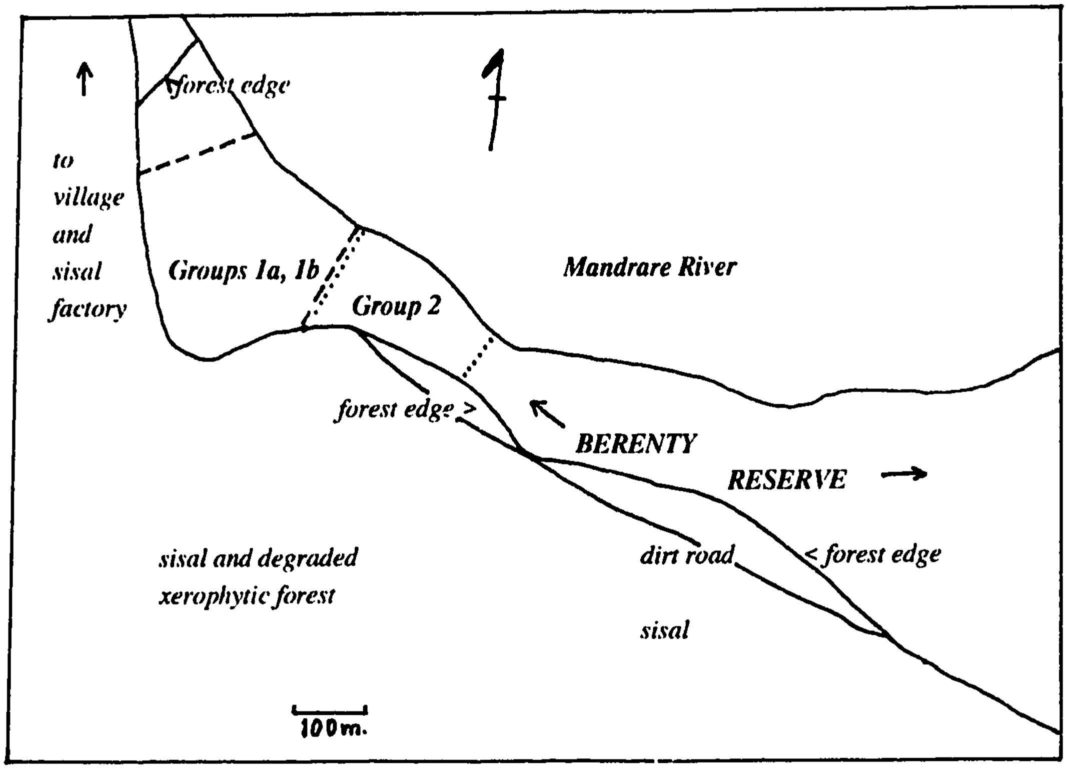


Fig. 2.3: Home ranges of the study groups in the Berenty Reserve

relative of acacias, of which the lemurs ate the pods and leaves, this area was dominated by the introduced trees Pithecolobium eduli, another acacia relative, of which lemurs ate the pods, and by a smaller tree, Cordia rothii, of which they ate the leaves and fruits. Group 2 had a range of 3.5 hectares (Fig.3), approximately half of which was in gallery forest similar to that described above, and half of which was in more open canopy forest mixed with brush and scrub vegetation (Budnitz and Dainis 1975).

The study animals spent most of their waking hours, and presumably their nighttime sleeping hours as well, in the trees at 5 to 25 m above the ground. Individual identification was not difficult. Sexual dichromatism in E. f. rufus is marked, and there are several aspects of individual pelage which can be unique, such as facial markings and tail thickness. During the dry winter and early spring (until late October), individuals could be readily identified even in the upper canopy. By November the foliage had begun to thicken considerably, but increased difficulty in identifying individuals was offset by relative ease in finding the study groups, as ranges shrank significantly with relative resource abundance, and movements became more predictable because the animals were now feeding extensively on fruits. Still, groups occasionally made "forays" far outside their normal ranges, and the hybrid group at this time moved more than 3 km from one end of the reserve to the other, establishing itself in a new range, largely in a part of group 1b's range which the latter had not used for several weeks.

The ranges of groups 1b and 2 overlapped slightly, and in this area intergroup agonistic encounters were frequent. Otherwise a common boundary was defended and regularly scent-marked.

The brown lemurs were active from approximately an hour before sunrise to an hour after sunset, with periods of activity and rest interspersed throughout the day. On cold days in winter (approximately 12°C) the animals spent most of the early morning in huddles of two or three individuals until as late as 0800 h. In late spring, when the temperature regularly exceeded 40°C, I observed them active as early as 0410 h over 150 m from their sleeping area. They characteristically had prolonged rest periods with only occasional movement from about 0900 h until 1530 h. One group was once observed foraging actively in a thunderstorm, and the onset of rain, a rare event, always seemed to cause the animals to move quickly to the upper canopy.

At dusk each group moved regularly to a small area of its range perhaps 40 m square: this was the only aspect of ranging that remained predictable throughout the study. Attempts to observe the animals at night were unsuccessful, as they were always foraging in the upper canopy when darkness fell, and a flashlight beam only lit up the lower branches which cast shadows beyond them. The first attempt to stay with a group after dark resulted in grunting vocalizations on their part until about 2000 h, at which time I left the area. These vocalizations always came from the same tree or two, and I believe they indicated tension at my presence rather than normal activity at this hour. Subsequent attempts to locate animals after dark were unsuccessful, although the groups were always last seen in the same small areas of their ranges. I succeeded in several, but not all, attempts to find the animals in their sleeping trees at the time they started moving and progressing in the morning. When I could not locate them there at this hour, I had no way of knowing whether they had moved just before dawn or earlier during the night. Progressions that were observed at dawn were very quiet. At dusk, however, the animals as a group frequently gave rasping vocalizations (similar to those given by individuals when they could not locate their groups) which were responded to in kind by neighbouring groups.

ii) Duke University Primate Center (DUPC)

I studied two groups of E. f. rufus and one group of E. f. collaris at the DUPC, Durham, North Carolina, U.S.A., for 7 months between Sept.1988 and Sept.1989: late Sept. to the end of Dec.1988; late Feb. to late June 1989; and late Aug. and early Sept.1989. Because the seasonal reproductive/behavioural changes are a response to changes in photoperiod (Boskoff 1978; Rasmussen 1985), the annual cycle in the northern hemisphere is 6 months out of synchrony with that in Madagascar. I thus began the DUPC portion of the research approximately 2 months prior to the beginning of the mating season, which lasted into January, 1989 for those females who did not conceive in November or December; the February to June portion covered the birth season, most births being in March and April; and the August-September 1989 portion, which I refer to as the weaning period, was late in what Boskoff (1978) called the lactation season.

Each of the study groups was semi-free-ranging in a forested enclosure surrounded by an electrified fence. The enclosures were 1.6, 3.5 and 5.8 ha in area, and the latter two shared a fence approximately 200 m in length, at which intergroup agonistic encounters occurred daily (Fig.2.4). The forest is dominated by loblolly pine trees, Pinus taeda, but also contains a number of deciduous species. The animals foraged on naturally occurring food resources, including leaves, buds, flowers, exudates, nuts and ants, and were also fed monkey chow and fruit daily, except during the summer months when fruit was only provided every second day. Fresh water was provided daily. Shelter in cold weather was availbable in heated nestboxes.

I have labelled the DUPC groups with letters, to avoid confusion with the numbered Berenty groups. Each of the two E. f. rufus groups, group RO and group HE, shared its enclosure with a group of ringtailed lemurs, L. catta, and ruffed lemurs, Varecia variegata. The E. f. collaris group, group CI, shared its enclosure with a group of sifakas, P. verreauxi . DUPC group compositions are presented in Table 2.3.

Each independent individual had a uniquely coloured collar and a uniquely coloured and shaped pendant. I was also able to recognize individuals on the same bases as at Berenty. The DUPC brown lemurs spent most of their waking hours active or resting on or near the ground, which made observation and recording of behaviour considerably easier than at Berenty.

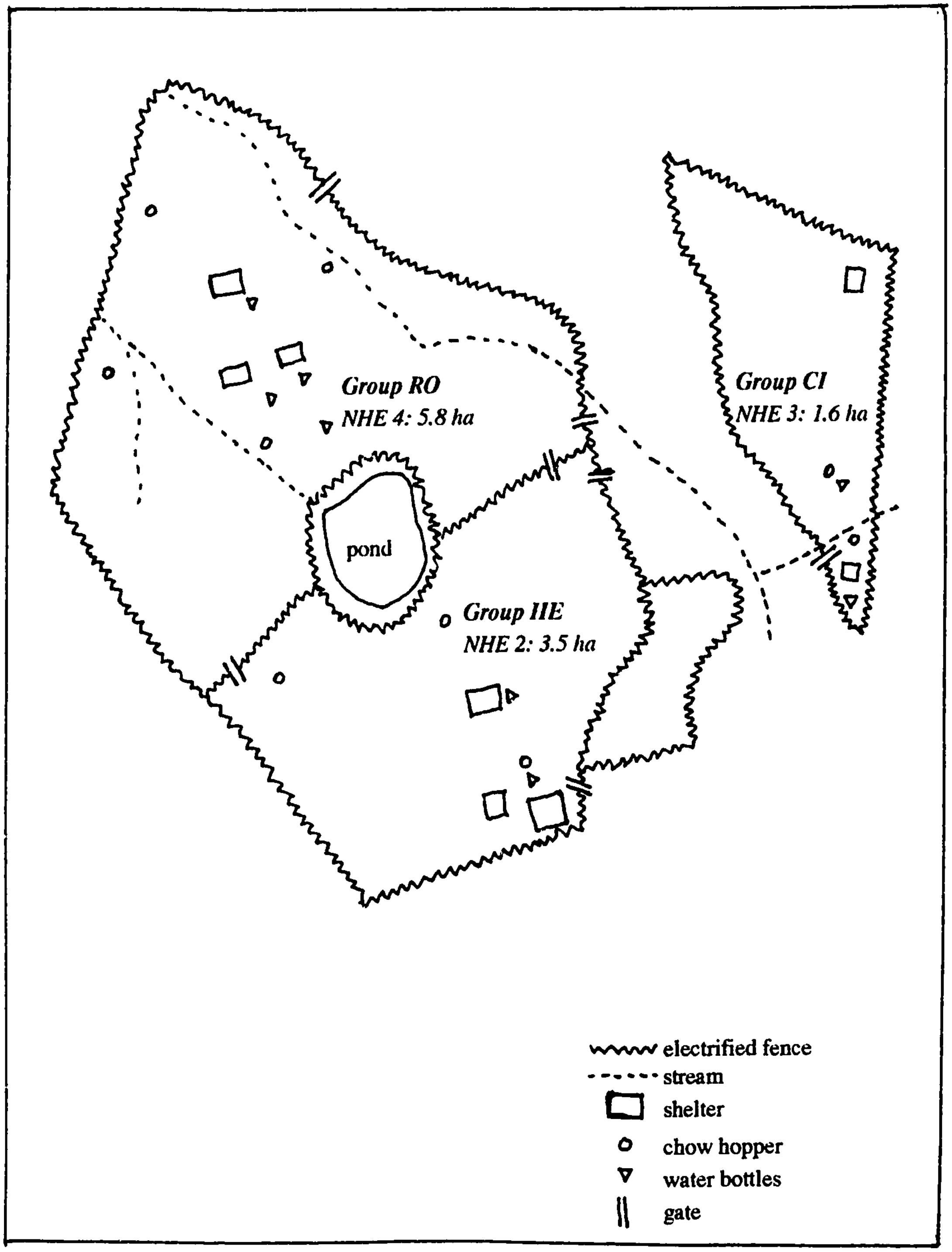


Fig. 2.4: Natural habitat enclosures (NHEs) at the DUPC which were inhabited by the study groups

TABLE 2.3: DUPC GROUP COMPOSITIONS

with known ages of individuals as of Mar. 30,'89 (midpoint of DUPC research)

GROUP HE	GROUP RO	GROUP CI
af 20 (17 yrs.)	af 40 (12 yrs.)	af 01 (6 yrs.)
af 21 (5 yrs.)	af 41 (6 yrs.)	af 02 (2 yrs.)
af 22 (3 yrs.)		
jf 23 (1 yr.)		
jf 24 (1 yr.)		
am 25 (9 yrs.)	am 42 (6 yrs.)	am 03 (5 yrs.)
am 26 (6 yrs.)	am 43 (3 yrs.)	am 04 (4 yrs.)
am 27 (6 yrs.)	am 44 (2 yrs.)	am 05 (4 yrs.)
am 28 (3 yrs.)		am 06 (3 yrs.)
am 29 (2 yrs.)		
		jm 07 (1 yr.)
2 infants	1 infant	2 infants

a=adult; j=juvenile;
f=female; m=male

The activity rhythm of the animals was similar to that of the Berenty groups. Observations of group locations at or after dusk and before and at dawn indicated that the animals were not active at night (or if they were, that they always returned before dawn to where they had been at dusk). Unlike the Berenty brown lemurs, they huddled below the canopy during rain.

Group HE lived for many years in an outdoor run before being transferred to the 3.5 ha enclosure, where they had lived since October 1986. All of these individuals except for adult male am25 were related to the oldest female, HE. When I began observations in September, 1988 group HE consisted of 10 individuals, five females and five males, including two juvenile females. In the spring of 1989, three infants were born, only two of which survived, and in June, a sexually-maturing female left the group, escaping from the enclosure.

Except for a mother and male offspring who had been separated for some time, Group RO comprised unrelated individuals. All individuals had been living in caged, outdoor runs, and they were released into the 5.8 ha enclosure at different times between August,1987 and April,1988. At the beginning of the study group RO consisted of five independent individuals, two adult females and three males of various ages, but all older than juveniles. Only one female had a surviving infant during the study, in the spring of 1989: it was driven from the group at the age of eight months by the unrelated adult female.

Group CI comprised individuals from two original groups, which had been living in separate caged outdoor runs, and which were released separately into a 1.6 ha fenced, forested enclosure in September, 1987. After various conflicts, including injuries necessitating removal of some individuals from the enclosure, these animals formed a single group, which had been intact for almost a year at the time my study began. This group consisted of seven individuals. Five were males, four of them brothers, and the fifth, a young juvenile, was the offspring of the oldest male and the older female from what was originally the other group. This female and her daughter both had surviving infants in the spring of 1989.

DATA COLLECTION

Agonism data were collected during focal animal observations and also by using the all-occurrences method (Altmann 1974). Data on affiliative behaviours were collected only during focal sessions. All-occurrences agonistic data were collected both on non-focal animals during focal sessions, and on all animals while focal sessions were not in progress (see Chapters 3, 4 and 5). Focal observations at Berenty totalled 107.83 hours (27 of which were carried out before the abovementioned departure of several males from Group 1a), and other observations about 130 hours. Focal observations at the DUPC totalled 311.67 hours and other observations about 150 hours - the former consisting of 116.17 hours during mating season, 162.33 hours during birth season, and 33.17 in the short follow-up season, which I hereafter refer to as the weaning season.

Focal sessions were 10 minutes in length, and individuals in each group were observed as focal animals on an approximately rotating basis, governed by the following principles:

1) Before each block of observations, morning or afternoon, on a particular group, a list was made of animals in the group on whom focal sessions needed to be conducted in order to balance the number of sessions for all individuals in the group.

2) Aside from the obvious basis of visibility, focal animals were also selected on the basis of activity; i.e., an animal engaged in social behaviour (e.g., grooming, play, huddling) was chosen over one engaged in some other activity (e.g., foraging, locomotion or self-grooming).

3) An animal involved in a continuation of an episode of huddling involving the previous focal animal was generally not chosen as the next focal animal if another, not so involved, but still involved in social behaviour, was scheduled for observation. Because grooming bouts very rarely lasted more than 10 minutes, this rule applied primarily to animals in huddles.

4) If it was appropriate, given the above, to chose a focal animal in the same huddle as the previous focal animal, an individual of the opposite sex and of a different age class was chosen whenever possible.

Observations were carried out using 7x24 binoculars when necessary; but usually (especially at the DUPC where the animals were more terrestrial in habit than at Berenty), it was possible to recognize individuals and behaviours without binoculars. Time was measured with a digital stopwatch. Data were recorded with pen and paper.

Raw data were later entered in transcribed form in MTS computer files. Files were manipulated for analysis using SPSS-X as well as MTS programmes on MTS. Except for the Pearson correlations in Chapter 5, which were carried out with SPSS-X, all statistical tests were non-parametric. The non-parametric tests were carried out with a pocket calculator, except for binomial tests, for which SPSS-X was used. An alpha level of .05 was used as a criterion for statistical significance.

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CHAPTER 3 NATURE AND PATTERNS OF AGONISTIC INTERACTIONS IN EULEMUR FULVUS

INTRODUCTION

The nature of agonistic behaviour was studied in two free-ranging and three semi-free-ranging groups of brown lemurs, Eulemur fulvus (Simons and Rumpler 1988) - formerly Lemur fulvus - in order to answer questions arising from previous research on this species. Those who had studied E. fulvus in the wild had remarked that agonism was typically both rare and mild, whereas much time was spent in peaceful physical contact (Harrington 1975; Petter et al 1977; Sussman 1977; Tattersall 1977). Studies in captivity all led to the conclusion that intense agonism occurred, but on a seasonal basis - related to births, mating, and sexual maturation of juveniles (Vick 1977; Boskoff 1978; Colquhoun 1987).

Of the field studies, only Harrington's (1975) focused on social behaviour. Sussman (1977) and Tattersall (1977) primarily studied E. fulvus ecology. Petter's pioneering survey of lemurs (1962) involved making "... brief records of the behavior and ecology of several species" (Tattersall 1982:17). Studies of social behaviour were conducted at the Duke University Primate Center (DUPC) by Vick (1977) and Boskoff (1978) on animals in caged runs, and by Colquhoun (1987) on semi-free-ranging animals.

Vick and Conley (1976) distinguished the more noticeable, seasonal agonism from what they referred to as "background agonism", occurring year round. In contrast to background agonism, seasonal agonism was likely to result in injury. Vick and Pereira (1989) have since discussed this seasonal agonism in lemurids in terms of what they call "episodic targeting aggression," during which an individual is targetted by one or more others until it no longer associates with the group, a phenomenon usually occurring when the group has reached a critical size. The critical size which they discovered in brown lemur groups at the DUPC is consistent with maximum group sizes of seven to nine individuals most commonly observed in naturally occurring groups (Harrington 1975; Sussman 1975; Tattersall 1977).

In the field, Harrington (1975) saw two conflicts in which grappling animals fell from trees. During the mating season, he observed one chase and noticed fresh "nicks" in the ears of some animals; but he did not see any physical conflicts at this time of year. It was thus not possible to know if the wounds resulted from another animal's aggression - either directly through bodily contact, or indirectly as a result of an accident while being chased or otherwise harassed - or if they resulted from some other accident. In light of the conflicting data on physical injury from captivity and the field, I hypothesized that persistent, intense and potentially injurious agonism in brown lemurs might essentially be an artifact of captivity.

The primary goals of my research were to determine 1) whether or not it was appropriate to characterize agonism as rare and mild in free-ranging E. fulvus, and 2) whether or not any patterns of dominance were discernible, as they had not been to previous field researchers. The second of these two matters is discussed in the following chapter. The first matter was paramount, because if agonism were rare and mild, it followed that it would be difficult to detect dominance relationships. My original plan was to conduct research at two sites in Madagascar. However, because arranging this proved impossible, I decided, after the Berenty research was concluded, to do a comparative study at the DUPC using the same methodology I had employed at Berenty.

My specific research questions were:

a) What kinds of signals were in the repertoire of E. fulvus agonistic behaviour, and in what proportions did the different types occur?

b) How frequent was agonism, and was there any significant seasonal variation?

c) Did the frequencies of agonistic dyad formation by age/sex class reflect group composition?

d) In what contexts did agonism occur, and were the different types of signals distributed randomly according to context?

METHODS

a) Natural history of the study species

E. fulvus (brown lemurs) normally live in multi-female, multi-male groups of from five to 12 individuals (Tattersall 1982). They are predominantly arboreal (Sussman 1975; Tattersall 1977; pers.obs.), and inhabit both dry forest and rainforest in Madagascar (Tattersall 1982). They have been reported to be either crepuscular (Harrington 1975; Sussman 1975) or diel, i.e., both diurnal and nocturnal (Tattersall 1979) - alternating several activity and rest periods in a 24 hour period.

Sussman (1975) found E. f. rufus in Madagascar dry forest to be primarily folivorous. More generalized herbivory was observed by Tattersall (1977) among E. f. mayottensis in the Comoro Islands, and by Meyers (1988) among E. f. rufus in rainforest habitat on Madagascar. The Berenty E. f. rufus that I studied were omnivorous, eating insects, spiders and other arthropods, as well as spider webs, leaves, buds, flowers, fruit, herbs, bark and fungi. This species thus appears to be generalized and opportunistic in diet.

b) Age classification used in this study

Individuals of both sexes have been classified as follows: infant, until weaning at four months; juvenile, from four to approximately 19 months, at which time both sexes can become sexually active and females can conceive; and adult, from approximately 19 months on.

c) Description of the study sites, and of the composition, ranges, activity rhythm and subsistence activity of the study groups

i) Berenty, Madagascar

E. fulvus is not indigenous to the semi-arid south of Madagascar where Berenty is located, which is the only forested region of Madagascar where brown lemurs are not naturally occurring. This region consists mostly of xerophytic forest with strips of gallery forest. The E. f. rufus (red-fronted or rufous lemurs) which I studied there were descended from captives taken in the early 1970s from gallery forest in the deciduous forest zone of the central west coast of the country. In 1987, when this research was carried out, there were approximately 55 brown lemurs in six social groups in the 100 ha Berenty reserve. The vegetation of this reserve, dominated by the kily tree, Tamarindus indica, has been described in detail elsewhere (e.g., Budnitz and Dainis 1975; Jolly 1966). A vast sisal plantation and the Mandrare River border the reserve and effectively render it a habitat island. The other lemurs in the reserve - Lemur catta, Propithecus verreauxi, Lepilemur mustelinus, and Microcebus murinus - are all indigenous.

After two weeks of reconnaissance observations, I began my formal study of brown lemurs at Berenty on 22 August, 1987, two weeks before the first births occurred. The study continued until 26 December, 1987.

Focal data collection on group 1a (Chapter 2, Table 2.2) was begun before a second group was chosen. On Sept.29, three males left group 1a, which had previously numbered 10 individuals (infants not included), and peacefully joined a neighbouring group of three females, two of them adults with newborn infants. I used this newly constituted group as the second group, group 2; and the remainder of group 1a became group 1b (Table 2.2).

Group 1a/b had a range of 8.5 hectares, and group 2 one of 3.5 hectares. The ranges of groups 1b and 2 overlapped slightly, and in this area intergroup agonistic encounters were frequent. Otherwise a common boundary was defended and regularly scent-marked.

E. f. rufus at Berenty were active from approximately an hour before sunrise to an hour after sunset, with periods of activity and rest interspersed throughout the day. The study animals spent most of their waking hours in the trees at five to 25 metres. Individual identification was not difficult. There is marked sexual dichromatism in *E. f. rufus* , and also variation in several aspects of individual pelage, such as facial markings and tail thickness.

ii) Duke University Primate Center (DUPC)

I studied two groups of *E. f. rufus* and one group of *E. f. collaris* (Chapter 2, Table 2.3) at the DUPC, Durham, North Carolina, U.S.A., for 7 months between September 1988 and September 1989: 30 September to 30 December, 1988; 26 February to 20 June, 1989; and 22 August to 6 September, 1989. Because the seasonal reproductive/behavioural changes are a response to changes in photoperiod (Boskoff 1978; Rasmussen 1985), the annual cycle in the northern hemisphere is six months out of phase with that in Madagascar. I thus began the DUPC portion of the research approximately two months prior to the beginning of the mating season; the February to June portion covered the birth season, most births being in March and April; and the August-September 1989 portion was during the late lactation period (Boskoff 1978), which I refer to as the weaning season.

Each of the study groups was semi-free-ranging in a multi-hectare forested enclosure surrounded by an electrified fence. The forest is dominated by loblolly pine trees, *Pinus taeda*, but also contains a number of deciduous species. The animals foraged on naturally occurring food resources, including leaves, nuts, buds, flowers, exudates, and ants, and they were also fed monkey chow and fruit daily, except during the summer months when fruit was only provided every second day. Fresh water was provided daily. Heated nestboxes provided shelter in cold weather.

I have labelled the DUPC groups with letters, to avoid confusion with the numbered Berenty groups. Each of the two E. f. rufus groups, group HE and group RO, shared its enclosure with a group of ringtailed lemurs, Lemur catta, and ruffed lemurs, Varecia variegata. The E. f. collaris group, group CI, shared its enclosure with a group of sifakas, Propithecus verreauxi.

Each independent individual had a collar with a uniquely coloured and shaped pendant. I was also able to recognize individuals on the basis of the same natural variation noted above in reference to the Berenty brown lemurs. Furthermore, the DUPC brown lemurs, whether active or at rest, spent most of their waking hours on or near the ground. This made observation and recording of behaviour considerably easier than at Berenty. The activity rhythm of the animals was similar to that of the Berenty groups.

Group HE had lived for many years in an outdoor run before being transferred to the 3.5 ha enclosure, where they had lived since October 1986. All of these individuals, except for the oldest male, am25, were related to the oldest female, af20.

Group RO comprised unrelated individuals, except for a mother and male offspring who had been separated for some time, and who had been living in caged, outdoor runs. The individuals in Group RO were released into a 5.8 ha enclosure, neighbouring that of Group HE, at different times between August,1987 and April,1988.

Group CI comprised individuals from two original groups, which had been living in separate caged outdoor runs, and which were released separately, in September, 1987, into a third fenced, forested 1.5 ha enclosure. After various conflicts, including injuries necessitating removal of some individuals from the enclosure by DUPC staff, these animals formed one group, which had been intact for almost a year at the time my study began.

d) Data collection

Data on agonistic interactions were collected during focal animal observations and also using the all-occurrences method (Altmann 1974). All-occurrences data were collected both on non-focal animals during focal sessions, and on all animals while focal sessions were not in progress. In the latter case, data were recorded in between focal sessions, during group progressions that began outside of focal sessions (in which case a session was not begun until the progression ceased), during estrus, during twilight observations (when the continuity of focal sessions was threatened by waning visibility), and during intergroup encounters (during which focal sessions were never initiated).

Focal observations at Berenty totalled 107.83 hours (27 of which comprised observations of Group 1a before the formation of Groups 1b and 2) and other observations about 130 hours. Focal observations at the DUPC totalled 311.67 hours and other observations about 150 hours - the former consisting of 116.17 hours during mating season , 162.33 hours during birth season, and 33.17 during the weaning season.

Focal sessions were 10 minutes in length, and individuals in each group were observed as focal animals on an approximately rotating basis (see Chapter 2 for details).

Agonistic behaviours occurring more than three seconds apart were recorded as separate events, during both focal and all-occurrences observations. Time was measured with a digital stopwatch. Data were recorded with pen and paper. I used 7x24 binoculars when necessary, but it was generally possible to recognize individuals and behaviours without them, especially at the DUPC where the animals were more terrestrial in habit than at Berenty.

e) Data analysis

Analysis of the proportions of different agonistic behaviours or "signals" at each site was based on the frequencies of signals initiating agonistic interactions. The frequencies do not apply to agonistic signals given in response to the initiating signal, with the exception of the category of "scuffles" or reciprocal aggression. In the event of reciprocal aggression, the specific signal initiating the agonistic exchange was not recorded; rather, the event was simply coded as reciprocal aggression. The rationale for this exception is that the reciprocity of aggression in such situations often appeared to be simultaneous, and furthermore that the antagonists were often giving different aggressive signals. Proportions of agonistic interactions involving submissive responses are discussed in Chapter 4.

For comparative analysis of the study groups, group rates of agonism were computed as the mean of individual hourly rates, taken solely from focal animal observations. For the DUPC groups, mean individual hourly rates of agonism for each group were computed separately for each season. For the Berenty data, mean individual hourly rates were computed for groups 1a, 1b, and 2: all of the Berenty data represent the birth season. Individual hourly rates of agonism represent agonism in which animals were involved regardless of the direction of aggressive and submissive signals.

All-occurrences data were used for comparison of rates of agonism during estrus, when focal animal data were not collected, with rates during those times of the mating season when females were not in estrus. They were also used for comparison with studies of other primates which employed this data collection method. In my study, differences between groups, or between seasons within groups, were examined for statistical significance using the Kruskal-Wallis one-way analysis of variance by ranks (Siegel and Castellan 1988). This test gives an identical result in a two-sample case to that of a rank sum or Wilcoxon-Mann-Whitney test (Welkowitz et al 1976).

Whether or not agonistic dyad combinations by age/sex class differed from expected frequencies, based on group compositions and the assumption that dyads of all age-sex compositions interacted at the same rate, was analysed with the chi-square single-sample goodness-of-fit test (Siegel and Castellan 1988). A chi-square test of association

(Siegel and Castellan 1988) was used to examine the relationship between category of agonistic interaction and context of agonism.

RESULTS

a) Proportions of different aggressive signals, unprovoked submission and reciprocal aggression

At Berenty, agonism was recorded 115 times during focal sampling, and 136 times during all-occurrences sampling, for a total of 251 agonistic events. At the DUPC, agonism was recorded 501 times during focal sampling, and 1086 times during all-occurrences sampling, for a total of 1587 agonistic events. A detailed listing of the frequencies of the different agonistic behaviours or "signals" initiating agonistic interactions, separated according to study site, is presented in Table 3.1. The similarity of the distribution of different signals at the two study sites was tested by applying the Kruskal-Wallis one-way analysis of variance by ranks to the percentages for the seven categories in Table 3.1. There was no significant difference between the sites in the proportions of different agonistic signals (H=0.1, df=1, p>0.7).

Agonistic signals were grouped into categories as indicated in Table 3.1 to facilitate analysis based on general types of agonistic interactions. "Threats" refers to interactions in which one animal indicated aggressive intent without physically contacting the recipient of the signal. Because of their high frequency, "cuffs" have not been lumped in with "other contact". They were the most frequent aggressive signal at both study sites. "Intervention" refers to all instances in which a third party became involved after the conflict had begun - either by threatening or physically contacting the original aggressor, or simply by acting as a buffer, without necessarily even looking at the original aggressor. All of the above terms

TABLE 3.1: FREQUENCIES OF THREATS AND PHYSICAL AGGRESSION INITIATING AGONISTIC INTERACTIONS, AND OF CHASES, THIRD PARTY INTERVENTION, UNPROVOKED SUBMISSION, AND RECIPROCAL AGGRESSION

		DUPC		BERENTY	
GENERAL CATEGORY	BEHAVIOUR	n	% of all agonism	n	% of all agonism
threats	feint	49		6	
	lunge	61		19	
	run at	136		9	
	chuffle (vocalization)	44		2	
	run at with chuffle	13		2	
	run at and tag	10		0	
	stare at	12		0	
	open-mouth threat	4		0	
	TOTAL	329	20.7	38	15.1
cuffs	TOTAL	552	34.8	116	46.2
contacts other than cuffs	tag (light cuff)	48		13	
	smack (hard cuff)	11		3	
	cuff/supplant	20		4	
	nip or nosepoke	95		5	
	multiple cuff	42		14	
	cuff/lunge	12		3	
	other combination	51		5	
	charge (contact)	5		0	
	bite	3		0	
	push	10		0	
	grab	16		0	
	pinch	2		0	
	respond to submission with aggression	2		0	
	TOTAL	317	20	47	18.7
chases	TOTAL	54	3.4	13	5.2
3rd party intervention	aggressive aid	43		3	
	buffer another	11		2	
	TOTAL	54	3.4	5	2
apparently unprovoked submissive signals	avoid	65		14	
	creep backwards toward	10		0	
	squeal	7		7	
	cringe / flinch	2		0	
	TOTAL	84	5.3	21	8.4
reciprocal aggression or "scuffles"	TOTAL	195	12.3	10	4
	GRAND TOTALS	1587		251	

refer to interactions in which the recipient - or, in the "intervention" cases, the original aggressor - responded either submissively or not at all. Thus, submissive signals occurred more frequently than indicated in Table 3.1 under "apparently unprovoked submissive signals"; that category includes only submissive signals which occurred in the apparent absence of aggression. Finally, "scuffles" refers to interactions in which aggression was responded to with aggression, in which cases I often could not tell which individual was the original aggressor.

Different agonistic behaviours were not equally obvious to the observer, and they can be roughly classified as either subtle or obvious, descriptions which crosscut the agonistic categories in Table 3.1: for example, threats could be subtle, as in the "feint" or "stare at", or obvious, as in the "run at". Subtle aggressive signals usually involved only arm and hand movement (e.g., "cuff", "grab"), or else movement of the upper body, but without spatial displacement of the animal with respect to the substrate (e.g., "nip"/"nosepoke"); and sometimes they involved virtually no movement (open-mouth threat, stare). The obvious aggressive behaviours that I observed involved spatial displacement of the aggressor with respect to the substrate (e.g., "cuff/supplant", "run at", "charge", "chase", "aggressive aid" and "buffer").

Cuffs, the most common aggressive behaviour, comprised 34.8% of all signals initiating agonistic encounters at the DUPC and 46.2% at Berenty. Other subtle signals accounted for 26.2% of initial agonistic signals at the DUPC and 27.1% at Berenty, bringing the percentage of aggressive signals (whether physical contacts or threats) involving little or no movement to 61% at the DUPC and 73.3% at Berenty.

All unprovoked submissive signals other than the squeal were subtle. They comprised 4.9% of agonism at the DUPC and 5.6% at Berenty, bringing the totals of subtle signals comprising aggression and unprovoked submission to 65.9% and 78.9% at the DUPC and Berenty respectively.

Obvious physical aggressive signals accounted for only 18.4% of all aggression at the DUPC, and 13.1% at Berenty. The remaining aggressive signal, the obvious, easy to localize chuffle vocalization, constituted 2.8% of aggression at the DUPC and 0.8% at Berenty, and the squeal accounted for 0.4% and 2.8% of agonism at these sites respectively, bringing the total of obvious aggressive and submissive signals to 21.6% at the DUPC and 16.7% at Berenty.

Reciprocal aggression was obvious, because it typically had a duration of several seconds. This agonism, comprising 12.3% of all conflict at the DUPC and 4% at Berenty, can be added to the other obvious behaviours , resulting in overall percentages of obvious agonistic events of 33.9% at the DUPC and 20.7% at Berenty.

b) Hourly rates of agonism in different groups and seasons

Mean individual hourly rates of agonism for each group in each season in which it was observed (Table 3.2) were computed from individual hourly rates based solely on focal animal data, and represent agonism in which animals were involved regardless of the direction of aggressive and submissive signals. These rates are hereafter referred to as focal agonism. For Berenty, the focal agonism median was 0.94 (range 0.67 - 1.37) and for the DUPC it was 1.56 (range 0.69-2.40).

With the exception of group CI in the birth season, all-occurrences hourly agonistic rates for each group were higher than the focal agonism rates (Table 3.3). For the all-occurrences rates, the median for Berenty was 1.1 with a range of 0.85 to 2.1, and the median for the DUPC was 2.35 with a range of from 1.23 to 4.16.

At the DUPC, no significant differences in focal agonism rates were found between groups within any season (mating season: H=1.7, df=2, p >.3; birth season: H=2.41, df=2, p =.3; weaning season: H=0.18, df=2, p >.99). At Berenty, seasonally equivalent to the birth season at the DUPC, the differences between groups in focal

TABLE 3.2: MEAN FOCAL INDIVIDUAL RATES OF AGONISM IN DUPC (BY SEASON) AND BERENTY GROUPS

SEASON	CI	HE	RO
mating	**0.69/hr.** range 0.18 - 1.64 n=26; hrs.=37.83	**1.17/hr.** range 0.20 - 2.52 n=61; hrs.=52.34	**0.96/hr.** range = 0.00 -1.65 n=25; hrs.=26.00
birth	**1.56/hr.** range 0.12 - 3.07 n=74; hrs.=47.33	**2.40/hr.** range = 1.50 - 4.04 n =187; hrs.=77.83	**1.80/hr.** range = 0.56 - 3.86 n=67; hrs.=37.17
weaning	**1.66/hr.** range 0.00 - 3.33 n=18; hrs.=10.83	**2.23/hr.** range = 0.75 - 8.55 n=32; hrs.=14.33	**1.38/hr.** range = 0.00 - 3.01 n=11; hrs.=8.00

	1a	1b	2
birth	**0.67/hr.** range = 0.32 - 1.60 n=18; hrs.=27.00	**1.37/hr.** range = 0.29 - 2.59 n=67; hrs.=48.83	**0.94/hr.** range = 0.45 - 1.46 n=30; hrs.=32.00

n is the total frequency of focal session agonism
for the group in that season

TABLE 3.3: COMPARISON OF HOURLY RATES OF AGONISM FROM FOCAL ANIMAL AND ALL-OCCURRENCES DATA

season	site	group	mean focal rate	all-occurrences *
mating	DUPC	CI	0.69	1.26
		HE	1.17	2.96
		RO	0.96	1.23
birth	DUPC	CI	1.56	1.3
		HE	2.4	3.54
		RO	1.8	2.54
	Berenty	1a	0.67	0.85
		1b	1.37	2.1
		2	0.94	1.1
weaning	DUPC	CI	1.66	2.22
		HE	2.23	4.16
		RO	1.38	2.35

* includes all occurrences during estrus (see Table 3.4)

agonism rates were also not significant (H=4.06, df=2, p >.1). However, focal agonism rates for this season were significantly higher at the DUPC than at Berenty (H=17.1, df=5, p <.01).

In all three DUPC groups focal agonism rates during the mating season were lower than those in the same groups during the birth season or the weaning season (Table 3.2). However, in only one group, HE, was the difference in focal agonism rates between seasons statistically significant, with the rate being highest in the birth season. (Kruskal-Wallis H=10.9, df=2, p <.001). (For group RO, H=0.85, df=2, p >.5.; for group CI, H=1.57, df=2, p > .3).

It seemed possible that focal rates during the mating season might have been artificially low because they did not include agonism occurring while females were in estrus. Although estrus lasts for just a few days, or even less than one day, during each mating season month (Vick 1977; Petter et al 1977; Boskoff 1978), depending upon the degree of synchrony between females in the group, agonism among males at these times is much more frequent than usual. Focal data were not collected during estrus at the DUPC because of the complexity of group dynamics and the high rate of interaction during these brief periods, further complicated by a much higher than usual degree of movement about the enclosures, and the fact that mating animals often hid from the view of others and the observer. Attempting to collect focal data under these conditions would have resulted in a lot of important interaction relevant to mating being missed.

I therefore computed all-occurrences of agonism during estrus separately from all-occurrences of agonism during the rest of the mating season (Table 3.4), to decide if not

TABLE 3.4: COMPARISON OF HOURLY RATES OF DUPC MATING SEASON AGONISM FROM ESTRUS AND NON-ESTRUS ALL-OCCURRENCES DATA COLLECTION

GROUP	GROUP RATE OF AGONISM: ESTRUS ALL OCCURRENCES	GROUP RATE OF AGONISM OTHER ALL OCCURRENCES
CI	6.80 / hr. n = 34; hours = 5	0.60 / hr. n = 25; hours = 42
HE	4.17 / hr. n = 150; hours = 36	2.38 / hr. n = 176; hours = 74
RO	12 events per hour n = 12; hours = 1	0.87 events per hour n = 26; hours = 30

having collected focal data during estrus might have artificially lowered the focal rates for this season. Two females in the DUPC study conceived in January and February of 1989, during which time I was not conducting observations. Rates of agonism during estrus are based on estrus in November and December.

The results suggest that, if I had collected focal data while females were in estrus, the mean focal rates for the mating season would have been higher. This is especially apparent in the case of group HE, which I sampled for 36 hours during estrus. During this time I observed 150 agonistic events for an hourly rate of 4.17, higher than the hourly rate of 2.38 recorded during 74 hours of all-occurrences sampling on this group outside of estrus. For group CI, the estrus all-occurrences hourly rate (6.8) represented a proportionately greater increase over the rate of other all-occurrences (0.6), but the sampling time of five hours was considerably less. A combination of synchrony of estrus in different groups and bad weather resulted in only one hour of such observation on group RO, during which I recorded 12 agonistic events. In group HE, a number of individual hours during estrus yielded similar frequencies, and in one particular hour-long stretch 23 agonistic events were recorded in this group.

Mean rates of focal aggression, rather than of all agonism, were computed separately for females and males in each group to determine whether or not one sex was more aggressive than the other, using data for agonism both within and between sexes, and for adults only. The results (Table 3.5) show that, out of 12 groups, counting each DUPC group in each season as a separate group, females had a higher mean rate in six groups and males had a higher mean rate in six groups.

TABLE 3.5: MEAN INDIVIDUAL HOURLY RATES OF AGGRESSION FOR FOCAL ANIMALS BY SEX

season	site	group	Females' rate	Males' rate
mating	DUPC	CI	0.19	0.47
		HE	1.01	0.67
		RO	0.55	0.9
birth	DUPC	CI	0.96	0.89
		HE	2.04	1.18
		RO	1.33	0.85
	Berenty	1a	0.36	0.57
		1b	0.66	2.59
		2	0.42	0.78
weaning	DUPC	CI	1.88	1.25
		HE	1.25	0.77
		RO	0.75	1.51

The sex showing the higher mean rate is underlined in each case.

c) Agonistic dyads by age/sex class

Only dyadic agonism is analysed in this section. Polyadic agonism, in which more than two individuals were involved from the start, constituted only 2% of agonistic interactions at Berenty and 2.7% at the DUPC. I distinguish this from agonistic aid situations, in which one animal intervened on another's behalf: such events have been analysed as separate dyadic interactions from those which stimulated them.

There were some seasonal differences in agonistic dyad composition by age/sex class within the three DUPC groups, which would be masked by lumping the relevant data for all DUPC seasons. For this part of the analysis, therefore, I compared seasons within the DUPC study, rather than lumping them, and because my research during the weaning season was relatively short, this season was not included in the dyad-composition analysis. Furthermore, only the birth season at the DUPC can be compared directly to the Berenty data, all of which is from the birth season. I describe only the adult combinations (Table 3.6), because all groups contained adults of both sexes, whereas only two Berenty groups (1a and 1b) contained juveniles of both sexes, and DUPC group RO contained no juveniles.

In the mating season at the DUPC, the frequency of conflict between adult males in all three groups was higher than expected based on group composition, and the frequency of conflict between adult males and adult females was lower than expected in all three groups. The frequency of conflict between adult females was virtually the same as expected in group HE, but lower than expected in the other two groups, CI and RO. CI and RO each contained only one adult female dyad, whereas HE contained three. However, only one of those three accounted for 93.3% of adult female vs. adult female conflicts in this group. (This dyad consisted of the oldest female, af20, and her granddaughter, af21. The third adult female was a young primiparous daughter of af20.)

TABLE 3.6: COMPARISON OF OBSERVED AND EXPECTED VALUES FOR AGONISTIC DYADS AS AGE/SEX CLASS COMBINATIONS

	DUPC GROUPS						BERENTY GROUPS					
MATING SEASON	**CI (n=65)**		**HE (n=278)**		**RO (n=63)**							
	E	**O**	**E**	**O**	**E**	**O**						
aF - aF	4.33	1	29.79	30	6.3	0						
aM - aM	26	41	99.29	154	18.9	32	no mating season observations					
aF - aM	34.67	23	148.9	94	37.8	31						
BIRTH SEASON	**CI (n=60)**		**HE (n=327)**		**RO (n=199)**		**1a (n=25)**		**1b (n=48)**		**2 (n=9)**	
	E	**O**	**E**	**O**	**E**	**O**	**E**	**O**	**E**	**O**	**E**	**O**
aF - aF	6	14	35.04	27	19.9	4	3.57	0	14.4	4	1.5	0
aM - aM	18	13	116.8	97	59.7	78	7.14	14	4.8	19	1.5	0
aF - aM	36	33	175.2	203	119.4	117	14.3	11	28.8	25	6	9

aF = adult female
aM = adult male

E = expected frequency
O = observed frequency

CHI-SQUARE TEST RESULTS

DUPC - Mating season:	Group CI:	χ^2 =15.91,	df=2,	p<.001*
	Group HE:	χ^2 =50.41,	df=2,	p<.001
	Group RO:	χ^2 =16.60,	df=2,	p<.001
DUPC - Birth season:	Group CI:	χ^2 =12.31,	df=2,	p<.01
	Group HE:	χ^2 = 9.61,	df=2,	p<.01
	Group RO:	χ^2 =18.36,	df=2,	p<.001
BERENTY - Birth Season:	Group 1a:	χ^2 =10.91,	df=2,	p<.01*
	Group 1b:	χ^2 =50.02,	df=2,	p<.001*
	Group 2 :	expected values violated χ^2 test assumptions.		

*For DUPC group CI in the mating season, and for Berenty groups 1a and 1b, the expected values resulted in marginal violation of the normal requirements for a chi-square test.

During the birth season, there were fewer consistent patterns across groups. Agonistic interactions among adults in Berenty group 2 were too infrequent to include this group in the chi-square analysis. Adult females and adult males were in conflict with each other slightly less often than expected in four of five groups, the exception being DUPC group HE, in which they were slightly more frequent than expected. Conflict among adult males was less frequent than expected in two groups, and more frequent than expected in the other three, DUPC group RO and Berenty groups 1a and 1b. Differences from expectation in the latter two groups were proportionately much greater than in RO, and were primarily the result of a high rate of aggression on the part of am55. Conflict among adult females was less frequent than expected in four of the five groups analysed here, the exception being DUPC group CI, in which the sole dyad for this combination was a mother-daughter pair, with the daughter, having her first infant, being responsible for 71% of the aggression in this dyad and 44% in the group as a whole (six individuals not including infants) during this season.

The binomial test was applied to the heterosexual dyad data for each group to determine whether or not one sex was significantly more aggressive than the other. Males were significantly more often the aggressors in three groups (1a, 1b and CI-mating-season) and females in two groups (HE-mating-season and RO-birth-season). Binomial test probablities are presented in Table 3.7.

d) Relationship between agonistic signals and contexts

A categorization of the contexts in which agonism occurred is given in table 3.8, based on frequencies of agonism from all-occurrences and focal data combined. Comparing the two study sites with the Kruskal-Wallis one-way analysis of variance by ranks, the overall proportions of contextual categories at each site were not found to be significantly different (H=0.06, df=1, p>0.8). For all interactions for which the context could be determined, access to huddles was the most frequently occurring context at both study

TABLE 3.7: BINOMIAL TEST PROBABILITIES FOR SEX DIFFERENCES IN AGGRESSION FREQUENCY IN ADULT HETEROSEXUAL DYADS

		Berenty groups			DUPC groups		
		1a	1b	2	CI	HE	RO
mating season							
	Females				1	46	13
	Males	no mating season observations			22	28	11
	p				≤.001	0.048	0.839
birth season							
	Females	1	5	2	20	81	62
	Males	10	20	7	10	81	28
	p	0.012	0.004	0.179	0.1	1	≤.001

sites, accounting for 27.1% and 30.7% of agonistic interactions at the DUPC and Berenty respectively. Access to food was the second most common context, accounting for 14.1% and 12.7 % of conflicts at the DUPC and Berenty respectively. Nevertheless, there are some obvious differences between sites for three categories (in addition, of course, to the fact that there were no mating season observations at Berenty and that the estrus category was therefore not applicable to the Berenty data). Grooming was recorded as the context 10.8% of the time at Berenty but only 1.2% of the time at the DUPC. Secondly, access to water was contested proportionately more often at Berenty (8% of all conflicts), than at the DUPC (2.8% of all conflicts). Finally, protection of infants was recorded more often at the DUPC.

The relationship between the categories of agonism (Table 3.1) and the contexts in which agonism occurred was analysed with the chi-square test of association for two independent samples (Siegel and Castellan 1988). The contexts were lumped into categories as follows, taking into account both similarity of context and low frequencies: access to resources, access to mates during estrus, access to or proximity in huddles, infant protection, other (known contexts of relatively low frequency) and undetermined. The

TABLE 3.8: FREQUENCIES AND PROPORTIONS OF CONTEXTS OF AGONISM

		DUPC		BERENTY	
CATEGORY	CONTEXT	n	%	n	%
resources	access to food	224	**14.1**	32	**12.7**
	access to water	44	**2.8**	20	**8**
estrus	access to mates	169	**10.6**	n/a	n/a
huddles	access to huddles	430	**27.1**	77	**30.7**
grooming	grooming	19	**1.2**	27	**10.8**
infants	protection of infants	103	**6.5**	6	**2.4**
aid	3rd party intervention	56	**3.5**	5	**2**
other	clasping	22	1.4	5	2
	scent-marking other's body	18	1.1	1	0.4
	mate-guarding during intergroup encounters	19	1.2	4	1.6
	play, play solicit	30	1.9	4	1.6
	redirected aggression	7	0.4	1	0.4
	weaning / infant carrying conflict	8	0.5	1	0.4
	access to sun or shade	4	0.3	0	0
	total of "other" contexts	108	**6.8**	16	**6.4**
undetermined	undetermined	434	**27.4**	68	**27.1**
	TOTAL	**1587**		**251**	

category "other" includes as contexts copulatory-like clasping of females by males outside of estrus, scent-marking of females by males, male guarding of females during intergroup encounters, play (turning into real aggression) or play solicitation, redirected aggression, mother-infant conflict (weaning or infant carrying), and access to sun or shade. Agonistic aid has not been included in the chi-square analysis of the relationship between signals and contexts, because agonism in the context of giving aid was itself recorded as aid, and it is thus not possible to characterize it in terms of threats, cuffs, etc.

The Berenty data (Table 3.9) did not allow legitimate use of a chi-square

TABLE 3.9: OBSERVED AND EXPECTED FREQUENCIES FOR CATEGORIES OF AGONISTIC SIGNALS ACCORDING TO CONTEXT: BERENTY

	threats		cuffs		other contact		chases		unprovoked submission		scuffles	
	E	O	E	O	E	O	E	O	E	O	E	O
resources	4	4	24.5	19	14.6	11	2.7	8	4	6	2.1	4
estrus	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
huddles	5.9	5	36.3	42	21.6	20	4.1	0	5.9	7	3.1	3
infant protection	0.5	0	2.8	3	1.7	3	0.3	0	0.5	0	0.2	0
other	2.9	1	17.9	26	10.7	8	2	2	2.9	0	1.5	1
undetermined	5.6	9	34.4	26	20.5	27	3.9	3	5.6	6	3	2

E is expected frequency; O is observed frequency.
In each case, the greater of the two is underlined.

analysis, even marginally, because over 50% of cells contained expected frequencies lower than five, and four of these were lower than one. Furthermore, no observed frequency deviated markedly from its expected value, so that it is not possible with the Berenty data to point to trends.

The result for the DUPC data was significant: $x^2 = 390.8$, df=25, p<.001 (Table 3.10). Chi-square single-sample goodness-of-fit tests were also carried out for the distribution of types of agonistic interaction in each context separately, to determine if only

TABLE 3.10: OBSERVED AND EXPECTED FREQUENCIES FOR CATEGORIES OF AGONISTIC SIGNALS ACCORDING TO CONTEXT: DUPC

	threats		cuffs		other contact		chases		unprovoked submission		scuffles	
	E	O	E	O	E	O	E	O	E	O	E	O
resources	45.7	30	96.8	121	66.9	61	9.3	13	15.1	11	34.2	32
estrus	28.5	86	60.3	12	41.7	28	5.8	13	9.4	16	21.3	12
huddles	73.1	14	154.9	203	107.1	144	14.9	3	24.2	19	54.8	46
infant protection	17.5	39	37.2	12	25.7	39	3.6	1	5.8	7	13.2	5
other	19.6	5	41.5	65	28.7	19	4	7	6.5	3	14.7	16
undetermined	75.6	86	160.3	138	110.9	90	15.4	16	25	30	56.7	84

E is expected frequency; O is observed frequency.
In each case, the greater of the two is underlined.

Overall $x^2 = 390.8$;
df = 25; p < .001.

one or at least not all of these were responsible for the significance in the two-sample test. In each case the result was significant with p <.001 (df=5). The x^2 values were as follows: for resources, 192.4; for estrus, 152.7; for huddles, 474.7; for infant protection, 87.3; for other, 141.8; and for undetermined 133.9.

These signals occurred more often than expected in the following contextual categories: in "resources", cuffs and chases; in "estrus", threats and unprovoked submission; in "huddles", cuffs and other contact; in "infant protection", threats, other contact and, to a lesser extent, unprovoked submission; in the category of "other" (i.e., contexts occurring relatively infrequently), cuffs, chases, and, to a lesser extent, scuffles; and in the "undetermined" category, threats, unprovoked submission, and scuffles.

DISCUSSION

a) The nature of agonistic signals

I propose as a likely reason for earlier descriptions of E. fulvus agonism as mild the subtle nature of the more common agonistic signals. The similarity of results from both study sites with respect to proportions of different signals overall strongly suggests that these are species-specific patterns. I also suggest that the rarity of either aggressive or submissive responses to aggression, and the rarity of wounding, are other possible reasons for the purported mildness of brown lemur agonism.

Cuffs and some other aggressive behaviours were typically carried out with little if any movement of any part of the animal other than its lower arm and hand, and it is possible that much of this subtle aggression was not detected by earlier field researchers, who were not focusing on agonistic behaviour. The same may apply to those signals which involved movement of at most the upper body without spatial displacement of the animal with respect to the substrate. Furthermore, aside from the squeal, a relatively rare event, most unprovoked submissive signals - avoiding, creeping backwards and cringing - were subtle. All subtle agonistic signals constituted 65.9% and 78.9% of all agonism at the DUPC and Berenty respectively. The considerably greater proportion of such signals could have contributed to the impression of other field researchers that agonisn in brown lemurs is mild.

The E. fulvus agonistic repertoire does not include obvious ssubmissive signalling in response to aggression, such as the combination of crouching, lowering of the head, grinning, and loud, prolonged, chatter-like vocalizations common among ringtailed lemurs and ruffed lemurs (pers. obs.), non-Eulemur species in the same family (Lemuridae), or, to give examples of anthropoid species in which agonism has been studied extensively, the fear grins and screaming of savannah baboons (e.g., Hausfater 1975), or the pant grunts and deep bowing movements of chimpanzees (e.g., de Waal 1989).

In response to aggression, submissive brown lemurs typically move quickly away from the aggressor, or turn aside. While rapid movement away from the aggressor is obvious when visibility is good, cowering or turning aside, if unaccompanied by a squeal vocalization, could go undetected by an observer, particularly in the wild where these animals are almost always arboreal. Moreover, submissive signals in response to aggression were observed in only 22.7% of agonistic interactions at Berenty and 25.4 % at the DUPC (see Chapter 4). Similarly, as discussed above, aggressive behaviour in response to aggression was also relatively rare, occurring in 4% of agonistic interactions at Berenty and 12.3% at the DUPC. Thus aggression was responded to agonistically only 26.7% of the time at Berenty and 37.7% of the time at the DUPC. I speculate that the usual lack of a submissive or aggressive response to aggression, combined with the fact that such submission as does occur is typically subtle, might have resulted in much aggression having been unrecognized as agonistic in nature by earlier field researchers, and in much aggression which was recognized as such being characterized as mild on the basis of the recipient's lack of response. If the recipient of aggression among brown lemurs most often does not respond either aggressively or submissively, how can we be sure that what looked like aggression was in fact aggression, and not overlook such situations? To make such judgments, it is necessary to know that on some occasions the same aggressive signal *is* responded to submissively or aggressively. Granted, this involves an assumption which may be erroneous - that brown lemurs are always communicating similar intentions to each other through what appear to a human observer to be similar actions.

The usual lack of a submissive or other response to aggression in brown lemurs does not lead to escalated aggression. This is interesting in light of the common notion that submission functions to deter an aggressor (e.g., Walters and Seyfarth 1987; Hand 1986). It is possible that among brown lemurs a non-response to aggression can perhaps be considered as a kind of passive aggression, in that the original recipient of aggression is signalling confidence by not responding submissively.

Alternatively, considering that submissive signals in some species can occasionally trigger aggression (e.g., savannah baboons: Rowell 1974, Smuts 1985; ruffed lemurs: pers. obs.), it is possible that non-reaction to aggression in brown lemurs has evolved as an alternative to overt submissiveness.

Finally, to return to the point about the subtlety of some submissive signals, it may be that the animals themselves perceive submissive responses to their aggression which human observers cannot normally detect. Andrew (1964) noticed that subordinate brown lemurs in captivity averted their eyes or turned away their heads when threatened by a dominant animal. It would be very difficult for an observer to detect such actions in a field situation, even if one were aware of their existence in the species' agonistic repertoire.

To summarize the above discussion, agonism in brown lemurs is mild, first of all, insofar as the majority of both aggressive and submissive signals are subtle, and secondly, insofar as recipients of aggression rarely respond either submissively or aggressively.

A third point regarding the question of mildness is the matter of the likelihood of wounding. The common phenomenon of serious, even fatal, injury in captivity related to "episodic targeting aggression" (Vick and Pereira 1989) may be an artifact of captivity, resulting when a normal process of peripheralization and/or emigration, which occurs without injury in the wild, is not able to run its natural course. The serious or fatal injuries that occurred in these circumstances at the DUPC involved animals in caged runs. During the course of my study, the only serious injuries that were suffered by study animals involved unnatural circumstances at the DUPC: in one case, an animal had his hand torn open during an intergroup encounter when he reached through a fence separating the groups; and in the second, a male who had been separating himself from the rest of the group in response to persistent aggression from the dominant male during mating season was wounded (again through fencing) when he was shut in a heated nestbox area with the rest of the group during cold weather.

I saw no wounds on brown lemurs at Berenty. I was not at Berenty during the mating season, the time of year when the most severe agonism has been observed in other lemur species (Jolly 1966, 1967; Richard 1974, 1978). However, I observed a lot of mating season agonism at the DUPC, and none of it resulted in wounding, except for the abovementioned instance of human intervention, which had the unfortunate consequence of preventing the ultimately wounded animal from distancing himself from his antagonist. The most intense aggression observed by Harrington (1975) during mating season consisted of a single chase, although nicks appeared in the ears of three of his study animals at this time. (He also on two occasions saw fighting animals "locked together and biting each other" [1975: 270] fall 5m from trees, but did not say that any wounds resulted from these conflicts, which occurred over access to an arboreal waterhole).

The most dramatically physical mating season agonism that I observed at the DUPC involved two males in group HE, am25 and the younger, more dominant male, am27. The former had mated in previous years with af20 and af21, but had been kept at a distance from them this season by persistent "run at" aggression from am27. During estrus, this escalated into an instance in which am2. charged am25 from over 15 metres away and made contact with him. The older male stood his ground and the two wrestled for barely more than a second before am27 walked slowly, limping slightly, in the direction from which he had come. His limp persisted only for a few minutes, and neither animal showed any sign of a wound.

In summary, I know of no conclusive evidence for serious wounding in free-ranging brown lemurs, in contrast to the very clear evidence from captive groups at the DUPC. In contrast to brown lemurs, wild ringtailed lemur and sifaka males engage in physical conflicts during mating season which result in bloodshed from lacerations caused by slashing with canines (Jolly 1966, 1967; Richard 1974, 1978). There is also a considerable body of evidence for serious wounding, typically effected by slashing or puncturing with canines, as being common in various anthropoid primate species. Much of this wounding occurs during male competition for access to estrous females (e.g., among howler monkeys, Sekulic 1983; among redtail monkeys, Cords 1984; among vervets, Henzi and Lucas 1980); and Wilson and Boelkins (1970) reported significantly more male deaths among rhesus macaques, as well as a peak in the frequency of wounds in males, during mating season. Dittus (1977) reported an increase in wounds to females as well as males during the mating season among toque macaques. Smuts (1985), discussing savannah baboons, described prolonged attacks by males on female "friends", resulting in wounding, when those females had harassed others who were also the males' "friends". She said that a female savannah baboon (<u>Papio</u> <u>cynocephalus</u>) can expect to sustain one serious physical injury per year inflicted by a male. Females at times of instability in the hierarchy have also been observed to inflict facial lacerations on each other (Smuts 1987).

Virtually all of the wounding in the abovementioned studies resulted from bites. Among the brown lemurs that I studied, I observed bites in only three out of 1587 agonistic interactions at the DUPC, and in none of the 251 at Berenty. Since my DUPC observations included two estrus periods during the mating season, it seems clear that the type of injurious aggression observed during mating season among ringtailed lemurs and sifakas, and some anthropoid primates, is not characteristic of brown lemurs. Similarly, although Colquhoun (1987) documented persistent chasing of *E. fulvus* individuals during mating season resulting in their expulsion from the group, he did not mention any wounding occurring as a result of this process.

b) Rates of agonism

The subtlety of *E. fulvus* agonistic signals discussed above could account not only for the earlier conclusions that agonism in this species was mild, but also, insofar as such subtlety may have resulted in much agonism being unnoticed, for the conclusions that it was rare as well. However, in earlier field studies, no quantitative definition of rarity was given. Considering that my study focused on agonism, some comparison of actual rates of agonism among *E. fulvus* with those of other species is warranted (Table 3.11). I computed rates of agonism for each of my study groups, as the mean of individual hourly rates from focal animal data, and for the group as a whole from all-occurrences data, to allow for comparison with other primate studies in which data were collected by one or the other of these methods (Table 3.3). Focal animal data probably provide a more reliable measure of rates of agonism than all-occurrences data collection. In the latter it is likely that some agonistic interactions in the group as a whole might be overlooked due to limits on the observer's ability to focus on all individuals at once, particularly in studying arboreal animals. For purposes of comparison with data on both free-ranging and semi-free-ranging primates from other studies, I here discuss data for each of my study sites separately.

The all-occurrences hourly rates of 0.85, 1.1 and 2.1 for Berenty groups 1a, 1b and 2 respectively are considerably higher than the figure of 0.1/hr given by Sussman (1975) or of 0.26/hr given by Harrington (1975) for their free-ranging groups of *E.f.rufus* and *E.f.fulvus*. I suspect that this is attributable primarily to differences in research focus. In Sussman's ecological study, rates of agonism were apparently based on all occurrences

TABLE 3.11: RATES OF AGONISM ACROSS SPECIES
AS MEAN FREQUENCY / INDIVIDUAL / HR. (FOCAL ANIMAL DATA)
OR MEAN FREQUENCY/GROUP/HR. (ALL OCCURRENCES DATA)

Species	Study	Data collection method	Habitat*	Group	Hourly rate**	
					focal animal	all-occurrences
Eulemur fulvus brown lemur	this study	both	f.r	1a	0.67	0.85
			f.r	1b	1.37	2.1
			f.r	2	0.94	1.1
			s.f.r.	CI	1.23	1.3
			s.f.r.	HE	1.94	3.54
			s.f.r.	RO	1.45	2.35
	Sussman 1975	all-occurrences?	f.r.			0.1
	Harrington 1975	all-occurrences	f.r.			0.26
Varecia variegata ruffed lemur	Kaufman 1991	focal animal	s.f.r.		1.49	
Propithecus verreauxi sifaka	Richard 1978	focal animal	f.r.	[illegible] groups: 0.25 - 0.44		
Cebus apella capuchin monkey	Rose 1992	focal animal	f.r.		0.89	
Ateles sp. spider monkey	Klein 1974	focal animal	zoo		0.1	
Alouatta sp. howler monkey	Klein 1974	all-occurrences ?				0.04
Papio cynocephalus savanah baboon	Hausfater 1975	focal animal	f.r.	females	1.8	
				males	4.89	
Macaca mulatta rhesus monkey	Drickamer 1975	all-occurrences	f.r.			6.25
	Teas et al 1982	all-occurrences	f.r.	females		1.6
				males		3.76

* f.r.=free-ranging; s.f.r.=semi-free-ranging **medians of seasonal rates were computed for DUPC groups

of agonism observed while primarily recording individual activity records at 5 minute intervals. Harrington recorded agonism in a study of social behaviour in general, using the all-occurrences method, in connection with research on scent-marking among captive animals. My study focused on agonistic behaviour, and it is probable that I was more attuned to the subtleties of such behaviour.

Richard (1978) recorded hourly rates of 0.25, 0.29, 0.42 and 0.44 through focal animal sampling on her four study groups of *P. verreauxi* in Madagascar. My lowest Berenty rate recorded by this method, 0.67, is half again as high as her highest rate. Sifakas, except for their abovementioned mating season violence, may be even more pacific than the oft-described peaceful brown lemurs. The median of 1.45 from focal data on the semi-free-ranging DUPC groups is very close to the hourly rate of 1.49 which I obtained in an earlier study of semi-free-ranging ruffed lemurs (*Varecia variegata*) at the DUPC, also based on focal animal sampling (Kaufman 1991).

Rose (1992), using focal animal sampling, recorded 0.89 agonistic events per individual per hour among capuchin monkeys (*Cebus apella*) in Costa Rican dry forest, a figure very close to my median of 0.94 from focal data for the Berenty groups. On the other hand, the rate of 0.04 agonistic events per hour given for howler monkeys (*Alouatta palliata*; Klein 1974) from data apparently collected on an all-occurrences basis - this was not explicitly stated - is far below my lowest all-occurrences rate from Berenty of 0.85.

Brown lemur agonism thus does not appear to be rare compared to some lemur and New World monkey species. However, the roughly comparable rates of *E. fulvus*, *Varecia*, and *Cebus* are far below those recorded in the field for males of some Old World monkey species. Hausfater (1975) recorded 4.89 agonistic interactions per hour for his focal male savannah baboons (*Papio cynocephalus*), and Teas et al (1982) observed 3.76 agonistic interactions per hour among rhesus (*Macaca mulatta*) males, collected on an all-occurrences basis. Teas' all-occurrences figure of 1.6 for rhesus females, and Hausfater's focal data rate of 1.8 for savannah baboon females, are much lower, and close to the brown lemur rates. I separated my rates for females and males (Table 3.4), and found that females were more involved in agonism in some groups, and males more so in others.

The highest rates quoted above are for male Old World monkeys. Since such open-country-dwelling, terrestrial, dimorphic species, in which the large males were probably favoured with observational bias by early primatologists (Smuts 1987), provided primatologists with much of their first information on aggression, this may account for anything lower than such rates being considered a manifestation of rarity of agonism. It is perhaps more accurate to characterize the males among these monkeys as showing an abundance of agonism, with the baseline of normal for pirmates being closer to the rates for brown lemurs or capuchin monkeys, or female baboons and macaques.

Although the E. fulvus focal agonism rates that I recorded at Berenty (from 0.67 to 1.37 events per focal animal hour), computed from birth season data, are almost entirely within the range of all the DUPC rates (from 0.69 to 2.40 events per focal animal hour), they are all below the DUPC birth season rates (Table [illegible]). There are two possible explanations for this. One is that the arboreality of the Berenty brown lemurs compared to the terrestriality of those at the DUPC resulted in observer bias favouring data collection at the DUPC. On the other hand, it may be that the more natural conditions at Berenty are a factor. The fact that animals there can emigrate to new groups, albeit within the confines of a 100 ha reserve that is a virtual ecological island, may take some social pressure off of the animals, whereas those at the DUPC, who could not at the time of my study move to other groups, may have experienced stress which translated into higher rates of agonism. Nevertheless, animals at the DUPC attempting to leave their enclosures were not deterred by the electrified fencing (pers. obs.; DUPC records). It may be, however, that social stresses had to build up to a level higher than in the wild before they would leave their natal groups.

The relatively high rates of all occurrences of estrus agonism compared to all occurrences of other agonism at the DUPC suggests that the focal rates for mating season would have been somewhat higher had focal sessions been carried out during estrus. Actually, because of the brevity of estrus, random focal sampling of all individuals in the group would probably not have resulted in much change in the focal rates for the season as a whole, as the high rates of estrus agonism typically involved only a few individuals in each group. However, if estrus among brown lemurs were not so brief and seasonally restricted, rates of agonism for this species might be considerably higher, as they are, particularly among males, in some Old World monkey species in which aggression peaks during the mating season.

c) Agonistic dyad combinations

For each of the combinations **af-af**, **am-am**, and **af-am** there are nine possible values in Table 3.6, because the three DUPC groups were analysed separately in two seasons, whereas the three Berenty groups were only observed during the birth season. Conflicts between adult females occurred more often than expected only twice out of nine times. In one of these instances, there is a plausible proximate explanation for this phenomenon: the female directing most of the aggression, af02 in group CI, was primiparous, and was exceedingly nervous for weeks after her infant's birth whenever her mother was nearby. In other groups, multiparous females with infants were not similarly aggressive towards other females. Primiparity is a more plausible explanation for af02's behaviour than fear of infanticidal intensions on her mother's part. If apprehension regarding infanticide were the reason for such aggressive behaviour, one would expect it to have been more pronounced where females were less closely related, which was not found to be the case.

Conflicts between adult males occurred more often than expected six out of nine times, including all three groups at the DUPC which were observed during mating season, at which time males competed for access to estrous females. Two of the remaining three instances of frequent aggression between males were in Berenty groups 1a and 1b, in which the dominant, older male was an extremely aggressive individual: even after two of his rivals left the group (1a), he continued his aggression against the younger remaining males (group 1b). In the sixth case, DUPC group RO in the birth season, the sexual maturation of the youngest male may have brought on much of the male-male conflict. However, males were in the late stages of sexual maturation in other DUPC groups at this time, without high levels of male-male aggression occurring.

Finally, with respect to female-male conflicts among adults, in only one of nine possibilities, HE group in the birth season, did these occur more frequently than expected. Most of this conflict involved af21, one of the same females involved in the higher than expected value for aggression between adult females in HE in the mating season. In the birth season, af21's young adult son became increasingly involved in supporting his mother against her female rival.

In summary, male-male agonism occurred during the mating season to a greater degree than expected, and conflict between adult females and adult males was relatively infrequent at any time. Particular dyadic combinations seem to be responsible for lack of consistency between groups as far as female-female agonism was concerned.

There was no consistent pattern as to which sex was more often the aggressor in adult heterosexual agonistic dyads. For example, during the mating season at the DUPC, males were found to be the aggressors significantly more often than females in group CI, but females were the aggressors significantly more often than males in group HE.

When significant differences were found in particular groups, they could sometimes be attributed to the behaviour of specific individuals within an age-sex class. For example, in Berenty groups 1a and 1b, the greater male aggressiveness consisted entirely of aggression by the oldest male, am55; and in CI during the mating season, the younger adult female af02, experiencing her first estrus, was the recipient of 21 out of 22 acts of aggression directed to adult females by adult males.

d) Relationship between agonistic interactions and contexts

Small sample sizes for Berenty prevented statistical or even descriptive analysis of the relationship between agonistic signals and context. For the DUPC data, it was shown that the type of agonistic interaction is not independent of the context.

Threats and unprovoked submission occurred more often than expected in the contexts of male competition over estrous females and mothers' protection of infants (and to a lesser degree in undetermined contexts). In other words, in the contexts of male competition for mates and mothers' protection of infants, a threat was usually sufficient to deter a competitor or potential aggressor; and sometimes not even that was necessary, as an animal would signal submissively in such contexts in the absence of threat, let alone physical aggression. The slightly greater than expected occurrence of unprovoked submission in undetermined contexts may be attributable to the fact that the submissive animal was responding merely to the presence of another who was usually dominant to it.

Cuffs, the most common aggressive behaviour, occurred more often than expected in relation to access to resources, access to or proximity in huddles, and "other" (i.e., relatively infrequent) contexts. However, other physical contact, although it occurred, as did cuffs, more often than expected in relation to huddles, was otherwise more frequent than expected only in the context of protection of infants. The most common signal in this category was the "nip" or "nosepoke."

Chases occurred more frequently than expected in relation to access to resources and to estrous females, and in the "other" category.

Finally, reciprocal aggression or "scuffles" occurred more often than expected only in undetermined contexts. This can be explained as a matter of observability. It is almost certain that I did not see every conflict that occurred in a group while I was observing the group or a focal individual in it. In the case of scuffles, I might have missed a conflict that became a scuffle if it had not became one: I saw the scuffle, but I did not see how or why it started, or, in other words, what the context was.

It is noteworthy, in the light of earlier discussion regarding the near absence of wounding in free- and semi-free-ranging brown lemurs, that all forms of physical aggression were less common than expected in the context of estrus, because this is the context in which violent aggression and wounding has been reported among ringtailed lemurs and normally peaceable sifakas.

The similarity of results from both study sites with respect to proportions of different contexts overall strongly suggest that these are species-specific patterns. There are, however, three contexts for which similarity between sites in their proportions is less marked than for most of the other contexts. Grooming was recorded as the context 10.8% of the time at Berenty but only 1.2% of the time at the DUPC. Eleven of 28 aggressive acts during grooming are attributable to the abovementioned irritable male, am55. However, the remaining grooming-context agonism at Berenty still accounts for 7.6% of all agonism at that site. This difference between sites remains unexplained. The second point of interest here is that access to water was contested proportionately more often at Berenty - 8% of the time as opposed to 2.8% at The DUPC. This makes sense, as water was frequently scarce at Berenty, whereas the DUPC animals were provisioned with it daily. Finally, protection of infants was recorded more often at the DUPC. This can perhaps be attributed to the fact that threats and unprovoked submission were the most likely agonistic signals in this context, and these behaviours are more difficult to see than are physical contacts and chases when animals, such as the Berenty lemurs, are usually up in trees.

The relationship between signal and context could not be compared between sites because of low expected frequencies at Berenty.

CONCLUSION

The primary goal in this paper has been to address questions regarding the nature and frequency (or rarity) of agonistic signals in E. fulvus. I found that agonism occurred frequently enough for me to be able to record most of the same signals at both study sites, and to compare the proportions of different signals and contexts, which were not significantly different at Berenty and at the DUPC.

E. fulvus have an extensive repertoire of aggressive signals. However, such signals do not consist of any elaborate, ritualized displays. Furthermore, submissive or aggressive signals in response to aggression are the exception rather than the rule. When submissive signals are given, they are typically very subtle: submissive vocalizations are essentially absent from E. fulvus' repertoire, except for the rarely given squeal. This lack of ritualization, and rarity of submission, along with an understatement or subtlety in style compared to other lemur species, and to many other primate species, as well as the extreme rarity of wounding, are likely reasons for earlier reports in the literature from the field as to the mildness and rarity of E. fulvus agonism.

If one measures mildness in terms of likelihood of injury as well as subtlety of execution - and the two may certainly be related - then it may well be that this species is characteristically mild as far as aggression goes. Captivity appears to have brought out an intensity of aggression rarely witnessed in the wild, likely resulting from the lack of natural escape routes. In terms of the usual subtlety of its expression, submissive behaviour in E. fulvus is mild as well.

Problems arise attempting to compare rates between studies of the same species because different researchers have employed differing observational or sampling methods in accordance with the particular goals of their studies. Furthermore, criteria for the recording of agonistic behaviours are not always explicitly stated in the literature. It may be that the subject matter itself imposes limits on studies comparing species, because agonistic and other behavioural repertoires are communication systems, or parts of such systems, which are essentially meaningful only on their own terms. Klein (1974) has suggested that attempting to compare rates across species is akin to comparing apples and oranges. I have nevertheless made some comparisons of rates and intensity of agonism for E. fulvus and other primate species, in order to put questions about rarity and mildness of agonism in perspective. I have concluded from these comparisons that brown lemur agonism is not rare, although it is mild in the senses of subtlety of execution and the rarity of wounding. This mildness or subtlety likely led earlier field researchers to overlook many occurrences of conflict.

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CHAPTER 4

NATURE AND PATTERNS OF DOMINANCE IN EULEMUR FULVUS

INTRODUCTION

Agonistic behaviour of brown lemurs, Eulemur fulvus (Simons and Rumpler 1988), formerly Lemur fulvus, was studied in two free-ranging and three semi-free-ranging groups in order to answer questions raised by contradictions in the literature regarding the frequency and intensity of agonism and the existence of dominance relations in this species. Earlier field researchers had generally concluded that agonism was rare and mild and that dominance relationships were indiscernible. Only one of these studies (Harrington 1975), however, focused on social behaviour. In one of the others, conclusions regarding such behaviour were reached on the basis of ad libitum observations made during a survey of various lemur species (Petter 1962), and the other two studies were essentially ecological in nature (Sussman 1975, 1977; Tattersall 1979).

Research on E. fulvus social behaviour in captivity was carried out at the Duke University Primate Center (DUPC) by Vick (1977) and Boskoff (1978), who studied animals in traditional caged runs and noted intense, persistent agonistic behaviour during mating and birth seasons, as well as during sexual maturation of juveniles. Colquhoun (1987) studied semi-free-ranging animals, and observed intense and persistent agonism during his study of reproductive behaviour. Vick could not discern any dominance relationships, but the other two authors concluded that dominance was clearly an aspect of E. fulvus social life.

These results from the DUPC contrast with the general conclusions from field studies. Was persistent, intense and potentially injurious agonism in this species essentially an artifact of captivity, and was dominance - reported only from captivity - therefore an epiphenomenon of unnatural conditions, as suggested by Rowell (1974)?

It is especially noteworthy that dominance relationships had not been reported for free-ranging E. fulvus, considering that female dominance had been reported for a number of lemuriform species, and that this phenomenon had been explained quite plausibly as an adaptation to the seasonal environments of Madagascar, particularly in relation to certain aspects of lemuriform physiology (Hrdy 1981; Jolly 1984. See Chapter 1). Nevertheless, if the lack of overt physical aggression is what the earlier field researchers of E. fulvus had in mind in referring to this species as showing little agonism, and if such aggression were very rare, it follows that it would be difficult to detect any consistent dominance relationships. Dominance measured by other criteria, such as approach-avoidance behaviour, would be relatively difficult to measure, especially in a fairly cryptic, arboreal species such as E. fulvus.

When dominance is measured according to the direction of agonistic signals, it can be defined as consistent winning in agonistic encounters within a dyad. However, what has been taken by primatologists to be indicative of consistent winning has varied. Essentially, the problem is whether submissive signals are necessary to indicate a loser, and therefore a winner, in an agonistic interaction (cf. Rowell 1974; Bernstein 1981) - i.e., for the interaction to be "decided" (e.g., Hausfater 1975; Smuts 1985) - or whether the direction of aggressive signals alone is a sufficient indicator of dominance. Walters and Seyfarth (1987) say, "Dominance is generally defined in terms of a consistent direction of aggressive behaviour between individuals ...", but they do not give references for this statement to make it clear whether or not anyone has in fact used aggressive signals alone for this purpose, when submissive signals are unclear or apparently non-existent. In fact, from the perspective of most primate species this may be a moot point, because submissive responses to aggression are the rule: for example, in Hausfater's (1975) study of savannah baboons, over 97% of aggressive acts elicited submissive responses. However, measuring dominance in terms of the direction of submissive signals may be inappropriate for a species in which submissive signals in response to aggression are the exception rather than the rule, which, from my preliminary observations, I observed to be the case for E. fulvus. If submissive responses do occur, but are not commonly detectable by human observers, then it would be neither productive nor valid, in attempting to describe dominance in this species in order to address important questions about lemurs in general, to say that dominance does not exist among these animals.

The first goal of my research regarding dominance was to determine whether or not agonism was sufficiently frequent to make it possible to delineate dominance relations. My second goal, if dominance relations could be discerned, was to delineate any apparent patterns. I expected to find some form of female dominance over males considering the plausibility of the Hrdy-Jolly hypothesis.

My specific research questions were:

1) Was dominance discernible in terms of significant asymmetry in the direction of aggressive signals within dyads? If so:
    a) How extensive was it in terms of the percentage of dyads in which it was observed?
    b) Were hierarchies discernible?
2) Were any age/sex patterns of dominance discernible?
3) Explicit submission (ES):
    a) What percentages of all agonistic interactions in the various groups involved submissive signalling in response to aggression?
    b) Did ES interactions occur more frequently in some contexts?
    c) Did agonistic interactions involve explicit submission more frequently than expected in response to particular aggressive signals?

METHODS

a) Natural history of the study species

E. fulvus (brown lemurs) normally live in multi-female, multi-male groups of from five to 12 individuals (Tattersall 1982). They inhabit both dry forest and rainforest in Madagascar, in both of which they are almost entirely arboreal (Sussman 1975; Tattersall 1979). Brown lemurs have been reported to be both crepuscular (Harrington 1975; Sussman 1975) and diel (Tattersall 1982), i.e., they are alternately active and resting throughout the 24 hour day without respect to light cycles.

Sussman (1975) discovered dry forest E. f. rufus to be predominantly folivorous. However, more generalized herbivory was observed by Tattersall (1977) among E. f. mayottensis, and by Meyers (1988) among rainforest E. f. rufus. At Berenty, E. f. rufus ate insects, spiders, and spider web as well as leaves, buds, flowers, fruit, herbs, bark and fungi (pers. obs.).

b) Age classification used in this study

Individuals of both sexes were classified as follows: infant (until weaning at four months); juvenile (from four to approximately 19 months, at which time both sexes become sexually active and females can conceive); and adult (from approximately 19 months on).

c) Description of the study sites, and of the composition, ranges, activity rhythm and subsistence activity of the study groups

i) Berenty, Madagascar

Although widespread in a variety of habitats in Madagascar, brown lemurs are not indigenous to the Berenty region in the semi-arid south of the country. This region consists of xerophytic forest with strips of gallery forest. The E. f. rufus study animals, "red-fronted" or "rufous" lemurs, were descended from captives taken in the early 1970s from gallery forest in the deciduous forest zone of the central west coast of Madagascar. In 1987 approximately 55 red-fronted lemurs in six social groups inhabited the 100 hectare Berenty reserve. The vegetation of this reserve, dominated by the kily tree, Tamarindus indica, has been described in detail elsewhere (e.g., Budnitz and Dainis 1975; Jolly 1966). The reserve is bordered on one side by the Mandrare river, and is otherwise surrounded by a vast sisal plantation. The other lemurs in the reserve - Lemur catta, Propithecus verreauxi, Lepilemur mustelinus, and Microcebus murinus - are all indigenous.

After two weeks of reconnaissance observations, my formal study of brown lemurs at Berenty began on 22 Aug., 1987, two weeks before the first births occurred. The study continued until 26 Dec., 1987. Focal data collection on group 1a was begun before a second group was chosen. On Sept.29, three males left group 1a (which had previously numbered 10 individuals, infants not included), and peacefully joined a neighbouring group of consisting of three females, two of them adults with newborn infants. I used this newly constituted group as my second group, group 2. The remainder of group 1a became group 1b. The home ranges of groups 1a/b and group 2 were 8.5 hectares and 3.5 hectares respectively.

The study animals spent most of their waking hours in the trees between 5 and 25 metres above ground. Because sexual dichromatism in this subspecies is marked, and since features of individual pelage such as facial markings and tail bushiness are usually unique in some way, individuals were readily identifiable in the dry season - at the beginning of the study - even when they were in the upper canopy. By November the foliage had begun to thicken considerably, but increased difficulty in identifying individuals was offset by relative ease in finding the study groups, whose movements became more predictable because the animals were now feeding extensively on localized fruit resources. Still, groups occasionally made day-long forays through the ranges of other groups. The ranges of groups 1b and 2 were slightly overlapping. In the shared area scent-marking occurred regularly and intergroup agonistic encounters were frequent. E. f. rufus at

Berenty were found to be active from approximately an hour before sunrise to an hour after sunset, with periods of activity and rest interspersed throughout the day.

ii) Duke University Primate Center (DUPC)

I studied two groups of *E. f. rufus* and one group of *E. f. collaris* at the DUPC, Durham, North Carolina, U.S.A., for 7 months between September 1988 and September 1989: late September to the end of December, 1988; late February to late June, 1989; and late August and early September, 1989. The annual cycle in the northern hemisphere is six months out of synchrony with that in Madagascar, because the seasonal reproductive/behavioural changes are a response to changes in photoperiod (Boskoff 1978; Rasmussen 1985). Thus the research at the DUPC was begun approximately two months before the beginning of the mating season, which lasted from November into January; the February to June portion covered the birth season, most births being in March and April; and the August-September 1989 portion was during the late lactation period (Boskoff 1978).

Each of the study groups was semi-free-ranging in a multi-hectare forested enclosure surrounded by an electrified fence. The forest is dominated by loblolly pine trees, *Pinus taeda*, but contains a number of deciduous species. The animals foraged on naturally occurring food resources, including leaves, buds, flowers, exudates, nuts and ants, and were also fed monkey chow and fruit daily, except during the summer months when they only received fruit every second day. Fresh water was provided daily. Shelter in cold weather was available in heated "nestboxes" at various locations in each enclosure in proximity to food and water. Each of the two *E. f. rufus* groups, group HE and group RO, shared its enclosure with a group of ringtailed lemurs, *L. catta*, and ruffed lemurs, *Varecia variegata*. The *E.f. collaris* group, group CI, shared its enclosure with a group of sifakas, *Propithecus verreauxi*.

Each independent individual had a unique combination of coloured collar and pendant, the latter also varying in shape. I was, however, able to recognize individuals on the same bases as at Berenty. Furthermore, the DUPC brown lemurs spent most of their waking hours active or resting on or near the ground, which made observation and recording of behaviour considerably easier than at Berenty. The activity rhythm of the animals was similar to that of the Berenty groups.

Group HE, consisting of 10 individuals - all but one of them (am25; see chapter 2, Table 2.2) related to the oldest female - had lived for many years in an outdoor run before being transferred to the 3.5 ha enclosure, where they had lived since October, 1986. Group RO was composed of a mother and son and three unrelated individuals, who had been living in different caged, outdoor runs, and who were released into a 5.8 ha enclosure neighbouring group HE at different times between August, 1987 and April, 1988. Group CI comprised individuals from two original groups, which had been living in separate caged outdoor runs, and which were released separately into a third fenced, forested 1.5 ha enclosure (not bordering either of the others) in September, 1987. After various conflicts, including injuries necessitating removal of some individuals from the enclosure, these animals formed one group, which had been intact for almost a year at the time I began my research at the DUPC.

d) Data collection

Data on agonism were collected during focal animal observations and also on an all-occurrences basis (Altmann 1974). All-occurrences data were collected both on non-focal animals during focal sessions, and on all animals while focal sessions were not in progress. In the latter case, this included between focal sessions, during group progressions that began outside of focal sessions (in which case a session was not begun until the progression ceased), during estrus, during twilight observations (when the continuity of focal sessions was threatened by waning visibility), and during intergroup encounters (during which focal sessions were never initiated).

Focal and all-occurrences observations totalled approximately 700 hours at both sites combined. Focal observations at Berenty totalled 107.83 hours and other observations about 130 hours. Focal observations at the DUPC totalled 311.67 hours and other observations about 150 hours – the former consisting of 116.17 hours during mating season, 162.33 hours during birth season, and 33.17 hours in the short follow-up season (at weaning time for most infants, and hereafter referred to as the weaning season).

Focal sessions were 10 minutes in length, and individuals in each group were observed as focal animals on a rotating basis. Agonistic behaviours occurring more than three seconds apart were recorded as separate events, during both focal and all-occurrences observations. Observations were carried out using 7x24 binoculars when necessary, primarily at Berenty. Time was measured with a digital stopwatch. Data were recorded with pen and paper.

e) Data analysis

In the majority (89.4%) of agonistic interactions, only one individual signalled aggressively. The aggressor in these interactions was considered to be the winner, regardless of whether or not the recipient responded submissively, with the exception that if both individuals were aggressive, one of them was considered the winner only if the other signalled submissively as well. (This occurred in only 9.7% of cases of reciprocal aggression). Dominance is defined here as consistent winning in agonistic interactions within a dyad. Most wins entailed aggression eliciting either no response or a submissive response. Very rarely, the winner was the recipient of "unprovoked" submissive signalling, i.e., when it had not signalled aggressively. Dominance was analysed in terms of the direction of aggressive signals, with the abovementioned qualifications, because submissive signals in response to aggression were the exception rather than the rule.

Interactions in which submissive signals were given I call explicit submission or ES interactions: they are a subset of all interactions used to measure dominance.

Aggressive signals and unprovoked submissive signals in E. fulvus are described in Appendix 1. Like unprovoked submissive signals, submissive signals in response to aggression include avoiding, cringing or flinching, and squealing; but submissive signals in response to aggression also include hurrying away. Squealing may occur in conjunction with other submissive signals in both provoked and unprovoked submission.

I used a quantitative criterion for defining dyadic dominance. To determine whether or not one individual could be said to have significantly dominated another, i.e., to have been the consistent winner, given the particular distribution of wins within each dyad, I applied the binomial test with an alpha level of .05. This criterion requires a minimum of six interactions for determinance of significance in a dyad.

An individual's aggressor percentage is the percentage of all agonism in which it was involved in which it was the sole aggressor, or, in the event of reciprocal aggression, the individual, if any, who did not signal submissively; and DS ratio is the ratio of dyads in which it was dominant to those in which it was subordinate.

The chi-square two-sample test (Siegel and Castellan 1988) was used to determine whether in some contexts ES interactions occurred more often than expected based on the overall proportion of ES agonism to all agonism. The same test was used to analyse whether or not the proportion of ES interactions varied significantly depending upon the particular aggressive signals initiating interactions. For both of these operations, the study sites were treated separately, but the data from all groups at each site were combined.

RESULTS

1) Nature and extent of dominance

Dominance in the sense of a linear hierarchy involving transitivity - in which each individual dominated all of those below it and was dominated by all of those above it - was not found in any of the study groups. This was not because of any instance of circularity - e.g., A dominated B, B dominated C, C dominated A - but because dominance, although it clearly existed in some dyads, was the exception rather than the rule. It was thus not possible to rank all individuals in a group in terms of their agonistic relationships with all other individuals. The orderings in the matrices constituting Tables 4.1 (Berenty) and 4.2 (DUPC) were therefore based on the percentage of each individual's conflicts which it won.

Furthermore, reversals within dyads (Tables 4.1 and 4.2) were not uncommon. There were 69 dyads, at both study sites combined, in which at least six agonistic interactions other than reciprocal aggression occurred (Table 4.3). In 28 of these, either the usual recipient of aggression was the aggressor/winner at least once (22 dyads), or else both individuals were equally often the aggressor (6 dyads). At least six ES interactions were observed in 25 dyads of the abovementioned 69 dyads (Table 4.4). In 14 of these, the usual aggressor/winner gave submissive signals in one or more conflicts, and in another both individuals were equally often submissive. Thus the dominant individual in a dyad was not necessarily the aggressor in all interactions, and in some dyads even gave explicit submissive signals on one or more occasions.

Lower rates of agonism and less observation time overall on the Berenty groups compared to the DUPC groups resulted in smaller samples of dyadic agonism at Berenty, and the binomial test could not be applied to most Berenty dyads because fewer than six agonistic interactions were observed in most of them. (At Berenty, where research was conducted only during the birth season, group rates of focal session agonism ranged from

TABLE 4.1: AGONISM MATRICES - BERENTY

GROUP 1a

All unidirectional aggression

Winner \ Loser	am 55	af 51	af 52	am 56	af 53	jf54	jm57	am 58	am 59	jm 50	Win%
am 55	*	1	5	1	4	17	8	3	4	2	94
af 51		*				3					75
af 52			*	1		1					40
am 56				*		1					33
af 53					*	1					20
jm 54						*					4
jf 57						1	*				10
am 58	2					1		*	1		57
am 59	1								*		17
jm 50						2	1			*	60

Shaded area includes interactions involving individuals not in group 1b.
"Win%" is percentage of all of its agonistic interactions won by this individual

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ES interactions only

Winner \ Loser	am 55	af 51	af 52	am 56	af 53	jm 54	jf 57	am 58	am 59	jm 50	Win%
am 55	*			1	2			3	3	2	79
af 51		*									n/a
af 52			*	1							100
am 56				*							0
af 53					*						0
jm 54						*					0
jf 57						1	*				100
am 58	2							*	1		50
am 59	1								*		20
jm 50										*	0

Shaded area includes interactions involving individuals not in group 1b.
"Win%" is percentage of its ES interactions won by this individual.

TABLE 4.1 cont'd: AGONISM MATRICES - BERENTY

GROUP 1b

All unidirectional aggression

	Loser							
Winner	am 55	af 52	af 51	af 53	am 56	jf 54	jm 57	Win%
am 55	*	1	4	13	18	29	22	99
af 52		*		1	1	1	2	83
af 51	1		*	3	1	1	8	76
af 53				*	2	9	3	42
am 56				2	*		1	12
jf 54						*	1	3
jm 57							*	0

"Win%" is percentage of all of its agonistic interactions won by this individual.

ES interactions only

	Loser							
Winner	am 55	af 52	af 51	af 53	am 56	jf 54	jm 57	Win%
am 55	*		2	3	7	8	5	96
af 52		*		1				50
af 51	1		*				1	100
af 53				*	1	1		29
am 56				1	*			11
jf 54						*		0
jm 57							*	0

"Win%" is percentage of its ES interactions won by this individual.

TABLE 4.1 cont'd: AGONISM MATRICES - BERENTY

GROUP 2

All unidirectional aggression

Winner	Loser am 58	am 59	af 71	af 72	jf 73	Win%
am 58	*		2	1	12	94
am 59		*	1	3	14	86
af 71		1	*		2	50
af 72	1			*	1	33
jf 73		2			*	6

"Win%" is percentage of all of its agonistic interactions won by this individual.

ES interactions only

Winner	Loser am 58	am 59	af 71	af 72	jf 73	Win%
am 58	*				1	100
am 59		*		1	2	100
af 71			*			n/a
af 72				*		0
jf 73					*	0

""Win%" is percentage of its ES interactions won by this individual.

TABLE 4.2: AGONISM MATRICES - DUPC

GROUP CI

All unidirectional aggression

Winner \ Loser	am 3	af 2	am 5	af 1	am 4	am 6	am 7	Win%
am 3	*	7	14	3	22	9	10	92
af 2	2	*	8	10		5	41	58
am 5		10	*			2	24	56
af 1		5	4	*		3	3	50
am 4	3	5			*	4	8	47
am 6	1	7	1	2	1	*	5	43
jm 7		13	1				*	13

"Win%" is percentage of all of its agonistic interactions won by this individual.

ES interactions only

Winner \ Loser	am 3	af 2	am 5	af 1	am 4	am 6	am 7	Win%
am 3	*	1	8	3	10	4	5	89
af 2		*	5	2			7	56
am 5		2	*			1	2	24
af 1		1	2	*				33
am 4	3	1			*	4		44
am 6	1	2	1	1		*	1	40
jm 7		4					*	21

"Win%" is percentage of its ES interactions won by this individual.

TABLE 4.2 cont'd.: AGONISM MATRICES - DUPC

GROUP IIE

All unidirectional aggression

Winner	Loser am27	af20	am26	af21	am29	am25	am28	af22	jf23	jf24	Win%
am 27	*	12	9	17	2	65	36	27	9	26	**94**
af 20	4	*	3	35	35	15	16		7	18	**80**
am 26	1	1	*	3	6	5	17	4	10	17	**80**
af 21	6	8	3	*	8	12	21	8	43	51	**67**
am 29		6		1	*		4	28	23	22	**55**
am 25	1	3	1	3	7	*	22	8	8	12	**36**
am 28		2		7	4	18	*	7	9	19	**35**
af 22		1		10	8	2	4	*	8	10	**34**
jf 23				1	1			2	*	11	**11**
jf 24				1	5		1		1	*	**4**

"Win%" is percentage of all of its agonistic interactions won by this individual.

ES interactions only

Winner	Loser am27	af20	am26	af21	am28	am29	am25	af22	jf23	jf24	Win%
am 27	*	1	4	5	2		18	14	2	15	**91**
af 20		*		14	3	12	4		1	3	**79**
am 26	1		*		2	4	1	1	2	5	**76**
af 21	4	3	1	*	1	1	1	5	20	23	**69**
am 28		1		3	*	1		2	1	8	**59**
am 29		3				*		6	6	6	**43**
am 25		2		1	3	1	*	3	4	5	**41**
af 22				2		1		*		1	**11**
jf 23									*	3	**8**
jf 24				1						*	**1**

"Win%" is percentage of [illegible] ES interactions won by this individual.

TABLE 4.2 cont'd.: AGONISM MATRICES - DUPC

GROUP RO

All unidirectional aggression

Winner \ **Loser**	am42	af41	af40	am44	am43	Win%
am 42	*	2	1	28	21	**80**
af 41	1	*	1	25	11	**68**
af 40	1	2	*	30	14	**64**
am 44	11	10	20	*	22	**37**
am 43		4	5	23	*	**32**

"Win%" is percentage ofall of its agonistic interactions won by this individual.

ES interactions only

Winner \ **Loser**	am42	af41	af40	am44	am43	Win%
am 42	*	1		1	9	**85**
af 41		*		1	5	**38**
af 40		2	*	10	2	**70**
am 44	2	6	4	*	6	**50**
am 43		1	2	6	*	**29**

"Wins%" is percentage of its ES interactions won by this individual.

TABLE 4.3: BINOMIAL TEST PROBABILITIES FOR DISTRIBUTION OF WINS IN ALL AGONISM IN DYADS WITH 6 OR MORE INTERACTIONS

sex com-bination	group	OLDER	% given if 50% or more	YOUNGER	% given if 50% or more	distribution of aggression	binomial test p
FEMALES	DUPC-HE	af20	81%	af21		35 - 8	<.001
		af21		af22	56%	10 - 8	0.815
		af20	100%	jf23		7 - 0	0.016
		af20	100%	jf24		18 - 0	<.001
		af21	98%	jf23		43 - 1	<.001
		af21	98%	jf24		51 - 1	<.001
		af22	80%	jf23		8 - 2	0.109
		af22	100%	jf24		10 - 0	0.002
		jf23	92%	jf24		11 - 1	0.006
	DUPC-CI	af01		af02	67%	10 - 5	0.302
	Ber 1b	af53	100%	jf54		9 - 0	0.004
MALES	DUPC-HE	am25		am26	83%	5 - 1	0.219
		am25		am27	98%	65 - 1	<.001
		am25	55%	am28	45%	22 - 18	0.635
		am25	100%	am29		7 - 0	0.016
		am26	100%	am28		17 - 0	<.001
		am26	100%	am29		6 - 0	0.031
	same age >	am27	90%	am26		9 - 1	0.022
		am27	100%	am28		36 - 0	<.001
		am28	50%	am29	50%	4 - 4	1
	DUPC-RO	am42	100%	am43		21 - 0	<.001
		am42	72%	am44		28 - 11	0.01
		am43	51%	am44	49%	23 - 22	1
	DUPC-CI	am03	88%	am04		22 - 3	<.001
		am03	100%	am05		14 - 0	<.001
		am03	90%	am06		9 - 1	0.022
		am03	100%	jm07		10 - 0	0.002
		am04	100%	jm07		8 - 0	0.008
		am05	96%	jm07		24 - 1	<.001

TABLE 4.3 cont'd: BINOMIAL TEST PROBABILITIES FOR DISTRIBUTION OF WINS IN ALL AGONISM IN DYADS WITH 6 OR MORE INTERACTIONS

sex combination	group	OLDER	% given if 50% or more	YOUNGER	% given if 50% or more	distribution of aggression	binomial test p
	Ber 1a	am55	100%	jm57		8 - 0	0.008
	Ber 1b	am55	100%	am56		18 - 0	<.001
		am55	100%	jm57		22 - 0	<.001
FEMALE-MALE	DUPC-HE	af20	83%	am25		15 - 3	0.008
		af20		am27	75%	4 - 12	0.077
		af20	89%	am28		16 - 2	0.001
		af20	85%	am29		35 - 6	<.001
		af21	75%	am28		21 - 7	0.014
		af21	89%	am29		8 - 1	0.039
	same age >	af22		am28	64%	4 - 7	0.549
		af22		am29	78%	28 - 8	0.002
		af21	80%	am25		12 - 3	0.035
		am26	50%	af21	50%	3 - 3	1
		am27	74%	af21		17 - 6	0.035
		am25	80%	af22		8 - 2	0.109
		am27	100%	af22		27 - 0	<.001
		am25	100%	jf23		8 - 0	0.008
		am26	100%	jf23		10 - 0	0.002
		am27	100%	jf23		9 - 0	0.004
		am28	100%	jf23		9 - 0	0.004
		am29	96%	jf23		23 - 1	<.001
		am25	100%	jf24		12 - 0	<.001
		am26	100%	jf24		17 - 0	<.001
		am27	100%	jf24		26 - 0	<.001
		am28	95%	jf24		19 - 1	<.001
		am29	81%	jf24		22 - 5	0.002

TABLE 4.3 cont'd: BINOMIAL TEST PROBABILITIES FOR DISTRIBUTION OF WINS IN ALL AGONISM IN DYADS WITH 6 OR MORE INTERACTIONS

sex combination	group	OLDER	% given if 50% or more	YOUNGER	% given if 50% or more	distribution of aggression	binomial test p
FEMALE-MALE	**DUPC-RO**	af40	74%	am43		14 - 5	0.064
		af40	60%	am44		30 - 20	0.203
		af41	73%	am43		11 - 4	0.119
		af41	71%	am44		25 - 10	0.018
	DUPC-CI	af02	76%	jm07		41 - 13	<.001
		am03	78%	af02		7 - 2	0.18
		am05	56%	af02		10 - 8	0.815
		am06	58%	af02		7 - 5	0.774
	Ber 1a	am55	100%	jf54		17 - 0	<.001
	Ber 1b	af51	100%	jm57		8 - 0	0.008
		am55	100%	af53		13 - 0	<.001
		am55	100%	jf54		29 - 0	<.001
	Ber 2	am58	100%	jf73		12 - 0	<.001
		am59	88%	jf73		14 - 2	0.004

TABLE 4.4: BINOMIAL TEST PROBABILITIES FOR DISTRIBUTION OF WINS IN ES INTERACTIONS IN DYADS WITH 6 OR MORE SUCH INTERACTIONS

SITE	GROUP	DOMINANT INDIVIDUAL	n of WINS	vs.	SUBORDINATE INDIVIDUAL	n of WINS	p value for dyad
BERENTY	1a	n/a			n/a		
	1b	am55	8		jf54	0	0.008
		am55	7		am56	0	0.016
	2	n/a			n/a		
DUPC	CI	af02	5		am05	2	0.453
		af02	7		jm07	4	0.549
		am03	10		am04	3	0.092
		am03	8		am05	0	0.008
	RO	af40	10		am44	4	0.061
		af41	5		am43	1	0.094
		am42	9		am43	0	0.002
		am43	6		am44	6	1
		am44	6		af41	1	0.055
	HE	af20	14		af21	3	0.013
		af20	12		am29	3	0.035
		af21	5		af22	2	0.453
		af21	20		jf23	0	< 0.001
		af21	23		jf24	1	< 0.001
		am27	14		af22	0	< 0.001
		am27	15		jf24	0	< 0.001
		am28	8		jf24	0	0.008
		am29	6		jf23	0	0.031
		am29	6		jf24	0	0.031

0.67 to 1.37 events per hour, significantly lower than range of 1.56 to 2.40 events per hour for the birth season at the DUPC; see chapter 3).

At Berenty, there was significant asymmetry, or dominance, in all 10 dyads with six or more agonistic events, and at the DUPC, in 42 out of the 59 dyads (Table 4.3). In one of the DUPC groups, RO, the majority of dyads with six or more agonistic events (four out of seven) did not show significant asymmetry: this was the only group in the study in which this was the case.

Fewer than six agonistic interactions were observed in 83 dyads (Appendix 2). Seventeen of these were in DUPC groups, including two dyads in which no agonism was observed, both involving am04, who was peripheralized from CI group during the mating season, and who was then, after three months of the study, permanently removed from the enclosure by DUPC staff. Of the other 66 dyads with fewer than six interactions, at Berenty, agonism was not observed at all in 31: however, 27 of these 31 were in group 1a, which was only intact for six weeks after the beginning of the study.

The individual in a dyad who won most ES interactions was almost always the same animal who was the usual winner overall (Tables 4.2, 4.3). Of the three exceptions to this – af02-am05 in group CI, af21-af22 in group HE, and am41-am44 in group RO – only in the last case was the asymmetry in overall wins statistically significant (Table 4.3); and in none of these three cases was there significant asymmetry in wins in ES interactions, although the p value for the am41-am44 dyad, .055, approached significance (Table 4.4). Measuring dominance in terms of the direction of aggression thus yielded a result similar to what would have been obtained if dominance had only been measured according to the direction of submissive signals in ES interactions. However, the direction of aggression measurement was advantageous in that it was based upon more extensive data.

In most dyads in which reciprocal aggression was observed (33 out of 47), it occurred fewer than four times. Four or more instances of reciprocal aggression were observed only in nine dyads in group HE, four in group RO, and in one dyad in group CI. These included instances in which one individual signalled submissively as well as aggressively (which happened 19 times in 195 instances of reciprocal aggression). Reciprocal aggression occurred over ten times in four dyads with measurable dominance and two without. In all six cases it involved young adult males with high aggressor frequencies but low aggressor percentages: am29 in HE, and am44 in RO.

2) Patterns of dominance: age and sex

For female-female combinations (Table 4.3), there was significant asymmetry in eight agonistic dyads. Older animals were dominant over younger ones in all of these eight cases.

For male-male combinations (Table 4.3), there was significant asymmetry in 16 dyads. One such dyad, am26-am27, involved animals of the same age. Older animals were dominant to younger ones in 14 of the other 15 dyads. The exception involved HE's male with the highest DS ratio, 6-year-old am27, dominating 9-year-old am25 .

For heterosexual combinations (Table 4.3), there was significant asymmetry in 27 dyads. The older animal, regardless of sex, was dominant in 25 of these 27 cases. Both exceptions occurred in DUPC group HE. In one, a 2-year-old male, am29, dominated a 3-year-old female, af22, who was the youngest of the three adult females in the group. In the other exceptional case, adult female af21 dominated the abovementioned 9-year-old male, am25.

Although dominance existed only dyadically, i.e., not as a hierarchy, and although the older animal was dominant in 47 out of 50 dyads of different age individuals, regardless of sex in heterosexual dyads, there were certain sex-related patterns in aspects of agonism related to dominance. When individuals in a group were ranked according to aggressor percentages and dominance/subordinance (DS) ratios (Tables 4.5, 4.6), both of which are measures of agonistic power within the group, the individual with both the highest aggressor percentage and the highest DS ratio in every group was an adult male. (In group 2, the younger adult male had the same DS ratio as the older one, but a lower aggressor percentage. Their DS ratios, 1-0, represented the only cases of dominance in the group: they both dominated the juvenile female.) In each group except HE, the male with the highest aggressor percentage and DS ratio was the oldest male in the group. In HE, the oldest male, am25, was, at nine years of age, physically past his prime. The next oldest males in HE, am27 and am26, were both six years old, and had the highest aggressor percentages at 94% and 80% respectively. (One female, af20, also had an aggressor percentage of 80%.) Am27, who had the highest DS ratio in the group, dominated both am26 and the older am25. There was no significant asymmetry in the direction of aggression between am26 and am25.

Except for the abovementioned case of group 2, the second-ranking individual in each group in terms of aggressor percentage was an adult female, but not always the oldest female. At the DUPC, these same females also had the second highest DS ratios in their groups, although in most groups this meant a ratio of either 1-0 (CI, RO and 1b) or 0-0 (1a and 2). In group HE, the highest ranking female, af20, had, as mentioned above, the same aggressor percentage as the second-ranking adult male, am26, but a higher DS ratio, 6-0 as compared to 4-1.

Only in CI and HE were there at least six agonistic interactions between the highest ranking male and the highest ranking female - using "rank" in the sense of aggressor percentage and DS ratio - and neither case involved significant agonistic asymmetry. The only cases of dominance of any male over any adult female were am27's dominance over af21 and af22 in HE, and, at Berenty, am55's dominance over af53. Af21 was the only multiparous female of these three. The other two gave birth for the first time during the course of the study. Five of the eight cases of female dominance over adult males involved

TABLE 4.5: INDIVIDUAL ALL AGONISM AND ES WINS PERCENTAGES AND DOMINANCE/SUBORDINANCE RATIOS: BERENTY

GROUP 1a

	all unidirectional aggression			dominance		ES interactions only			
I.D.	total N	aggressor / wins n	aggressor / wins %	dyads dom.	dyads sub.	total ESn	ES wins n	wins as % of ES	ESn as % of total N
af 51	4	3	75	0	0	0	0	n/a	0
af 52	7	2	29	0	0	1	1	100	14
af 53	5	1	20	0	0	2	0	0	40
jf 54	28	1	3	0	1	1	0	0	4
am 55	48	45	94	2	0	14	11	79	29
am 56	3	1	33	0	0	2	0	0	67
jm 57	10	0	0	0	1	1	1	100	10
am 58	7	4	57	0	0	6	3	50	86
am 59	6	1	17	0	0	5	1	20	83
jm 50	5	3	60	0	0	2	0	0	40

TOTAL ESn = 27.6% of total N

GROUP 1b

	all unidirectional aggression			dominance		ES interactions only			
I.D.	total N	aggressor n	aggressor %	dyads dom.	dyads sub.	total ESn	aggressor n	aggressor %	ESn as % of total N
af 51	18	14	78	1	0	4	2	50	22
af 52	6	5	83	0	0	1	1	100	17
af 53	33	14	42	1	1	7	2	29	21
jf 54	41	1	2	0	2	9	0	0	22
am 55	88	87	99	4	0	26	25	96	30
am 56	25	3	12	0	1	9	1	11	36
jm 57	37	0	0	0	2	6	0	0	16

TOTAL ESn = 25.0% of total N

GROUP 2

	all unidirectional aggression			dominance		ES interactions only			
I.D.	total N	aggressor n	aggressor %	dyads dom.	dyads sub.	total ESn	aggressor n	aggressor %	ESn as % of total N
af 71	6	3	50	0	0	0	0	0	0
af 72	6	2	33	0	0	1	0	0	17
jf 73	31	2	6	0	2	3	0	0	10
am 58	16	15	94	1	0	1	2	100	6
am 59	21	18	86	1	0	3	3	100	14

TOTAL ESn = 10.0% of total N

TABLE 4.6: INDIVIDUAL ALL AGONISM AND ES WINS PERCENTAGES AND DOMINANCE/SUBORDINANCE RATIOS: DUPC

GROUP CI

	all unidirectional aggression			dominance		ES interactions only			
I.D.	total N	aggressor / wins n	aggressor / wins %	dyads dom.	dyads sub.	total ESn	ES wins n	wins as % of ES	ESn as % of total N
af 01	30	15	50	0	0	9	3	33	30
af 02	112	65	58	1	0	25	14	56	22
am 03	71	65	92	4	0	35	31	89	49
am 04	43	20	47	1	1	18	8	44	42
am 05	64	36	56	1	1	21	5	24	33
am 06	40	17	43	0	1	15	6	40	38
jm 07	104	14	13	0	4	19	4	21	18

total ESn = 30.6% of total N

GROUP IIE

	all unidirectional aggression			dominance		ES interactions only			
I.D.	total N	aggressor / wins n	aggressor / wins %	dyads dom.	dyads sub.	total ESn	ES wins n	wins as % of ES	ESn as % of total N
af 20	161	129	80	6	0	47	37	79	29
af 21	236	160	69	5	2	85	59	69	37
af 22	125	45	35	2	1	35	4	11	28
jf 23	132	15	11	1	7	39	3	8	30
jf 24	192	7	4	0	9	70	1	1	36
am 25	181	64	35	3	3	44	20	45	24
am 26	80	64	80	4	1	21	16	76	26
am 27	214	202	94	7	0	67	61	91	31
am 28	186	65	35	2	4	27	16	59	15
am 29	154	81	53	2	5	41	21	51	27

total ESn = 28.7% of total N

GROUP RO

	all unidirectional aggression			dominance		ES interactions only			
I.D.	total N	aggressor / wins n	aggressor / wins %	dyads dom.	dyads sub.	total ESn	ES wins n	wins as % of ES	ESn as % of total N
af 40	73	46	63	0	0	20	14	70	27
af 41	52	37	71	1	0	16	6	38	31
am 42	65	52	80	2	0	13	11	85	20
am 43	99	32	32	0	1	31	9	29	31
am 44	165	60	36	0	2	36	18	50	22

total ESn = 25.6% of total N

younger adult males, while two consisted of af20 and af21 dominating the 9-year-old male, am25, in group HE, and one involved af22 and am29, both of whom were two-year-olds.

With the exception of group RO, the individuals in each group with the lowest aggressor percentages and DS ratios were juveniles. In RO, in which there was no juvenile, the youngest male had the lowest DS ratio and the second lowest aggressor percentage, while the middle in age of the three males had the second lowest DS ratio and the lowest aggressor percentage.

3) Explicit submission (ES)

a) Extent of ES interactions

Submissive signals in response to aggression were observed in only 22.7% of all agonistic interactions at Berenty and 25.4% of all agonistic interactions at the DUPC. Although rates of agonism were lower at Berenty, in groups 1a and 1b the proportions of interactions involving explicit submission to all agonistic interactions were similar to those in the DUPC groups (Table 4.7). This was not the case for Berenty group 2, for which I had the smallest sample of all agonism of all the study groups. In group 2, with ten possible agonistic dyads, I observed only four interactions involving explicit submission (Table 4.2), representing only three dyads. Interactions involving explicit submission constituted two and a half times as much of all agonism (25.6%) in DUPC group RO as in the similarly sized (5 individuals) Berenty group 2 (10%), and nine of the ten RO dyads were characterized by interactions involving explicit submission.

While the proportion of all conflicts in DUPC group HE involving explicit submission was similar to those in all other groups except Berenty group 2 (Table 4.7), agonism was most frequent in group HE, as reflected in relatively high mean hourly rates of focal session agonism in every season (chapter 3); and dominance was thus recorded in proportionately more dyads in this group than in any of the other study groups (Table 4.7). In no group was explicit submission observed in all of the dyads in which agonism was observed.

TABLE 4.7: INTERGROUP COMPARISON OF PROPORTIONS OF POSSIBLE DYADS SHOWING AGONISM, ES INTERACTIONS AND DOMINANCE

Group	Size	Focal observation hrs.	Rate and n of focal agonism*	n of all agonism	Possible dyads	Dyads showing agonism		Dyads showing ES		ES as % of all agonism	Dyads showing dominance	
BERENTY						n	%	n	%		n	%
1a	10	27	0.67/hr (n=18)	62	45	19	42	8	18	27%	2	4
1b	7	48.83	1.37/hr (n=67)	124	21	19	90	9	43	25%	6	29
2	5	32	0.94/hr (n=30)	40	10	8	80	3	30	10%	2	20
DUPC						n	%	n	%		n	%
He	10	144.5	1.94/hr (n=280)	841	45	45	100	41	84	28%	32	71
Ro	5	71.17	1.45/hr (n=103)	232	10	10	100	9	90	25%	3	30
Ci	7	96	1.23/hr (n=118)	233	21	19	90	16	76	30%	7	33

*For each group at the DUPC, data from all seasons were combined.

b) ES interactions and contexts of agonism

The percentages of all interactions involving explicit submission in each context is given in Table 4.8. For purposes of statistical analysis, contexts other than "access to or proximity in huddles" were lumped into more inclusive categories: "resources" includes "food" and "water"; and "other" comprises all remaining contexts listed in Table 4.8, with the exceptions that for the DUPC data "infant protection" and "access to mates" (during estrus - not observed at Berenty) were treated independently . (The expected value for "infant protection" did not permit it being treated independently for the Berenty data.)

As indicated in Tables 4.9 (Berenty) and 4.10 (DUPC), the overall distribution of ES interactions across contextual categories was significantly different from expected values based on overall proportion of ES interactions in relation to all agonism at each site (Berenty: $x^2 = 11.7$, df=2, $p < .01$; DUPC: $x^2 = 21.4$, df=4, $p < .001$). At both Berenty and the DUPC, ES interactions occurred more often than expected in the context of access to physical resources, and less often than expected in the context of access to or proximity in huddles and in the "other" category. At the DUPC, interactions also involved explicit submission more often than expected in the contexts of access to mates during estrus (essentially male-male competition) and of protection of infants.

Percentages of ES interactions in particular contexts were in some cases quite similar at both study sites, and in other cases quite different (Table 4.8). In the latter cases, however, the frequency on which at least one of the compared percentages was based tended to be low (less than 10), especially for the Berenty data.

c) Relation of occurrence of explicit submission to particular aggressive signals

The proportions of ES interactions to all agonistic interactions according to the nature of the agonistic signal which initiated the interaction is given in Table 4.11. For

TABLE 4.8: PROPORTIONS OF AGONISM INVOLVING EXPLICIT SUBMISSION ACCORDING TO CONTEXT

	BERENTY			DUPC		
CONTEXT	total frequency	ES frequency	ES %	total frequency	ES frequency	ES %
food	32	10	31%	224	78	35%
water	20	11	55%	44	15	34%
access to or proximity in huddles	68	12	18%	430	85	20%
grooming	27	0	0%	19	0	0%
scent-marking	1	1	100%	4	0	0%
play	4	0	0%	30	6	20%
non-estrus sexual	5	0	0%	36	5	14%
estrus: male-male conflict	n/a	n/a	n/a	169	49	29%
intergroup mate-guarding by males	4	2	50%	19	4	21%
mother's protection of infants	6	0	0%	103	28	27%
weaning conflict	n/a	n/a	n/a	8	5	63%
agonistic aid	5	1	20%	56	14	25%
other	70	18	26%	281	76	27%
undetermined	9	2	22%	164	40	24%
TOTAL	251	57	23%	1587	405	26%

TABLE 4.9: OBSERVED AND EXPECTED FREQUENCIES FOR DISTRIBUTION OF ES INTERACTIONS ACCORDING TO CONTEXT: BERENTY

	resources		huddles		other	
	E	O	E	O	E	O
ES	11.8	21	15.4	12	29.7	24
OTHER	40.2	31	52.6	56	101.3	107

The greater value in each E/O comparison is underlined.

TABLE 4.10: OBSERVED AND EXPECTED FREQUENCIES FOR DISTRIBUTION OF ES INTERACTIONS ACCORDING TO CONTEXT: DUPC

	resources		huddles		mates		infants		other	
	E	O	E	O	E	O	E	O	E	O
ES	68.3	93	109.6	85	43.1	49	26.3	28	157.8	150
OTHER	199.7	175	320.4	345	125.9	120	76.7	75	461.2	469

The greater value in each E/O comparison is underlined.

TABLE 4.11: PROPORTIONS OF AGONISM INVOLVING EXPLICIT SUBMISSION ACCORDING TO SIGNAL

	BERENTY			DUPC		
SIGNAL	total frequency	ES frequency	ES %	total frequency	ES frequency	ES %
cuff	116	4	3%	552	91	16%
physical other than cuff	61	21	34%	371	118	32%
threat	38	8	21%	329	77	23%
agonistic aid	5	1	20%	54	16	30%
scuffle	10	1	10%	195	17	9%
submissive signal only (or first)	21	21	100%	86	86	100%
TOTAL	251	56	22%	1587	405	26%

purposes of statistical analysis, "cuffs" were retained as a separate category due to their high frequency, but most of the signals listed in Chapter 3 were combined into one of the more inclusive categories of "physical aggression" (other than cuffs, and including chases), "threats", and, for the DUPC data, "reciprocal aggression" and "agonistic aid". The latter two categories were combined for the Berenty data due to low expected frequencies. Strictly speaking, neither "agonistic aid" nor "reciprocal aggression" constitutes a type of signal as such: in the former case, however, I considered that intervention itself constituted a kind of metasignal to both parties already involved, regardless of whether it involved a cuff, a lunge, etc.; and in the latter, I typically did not observe the specific signal that began a bout of reciprocal aggression. All signals constituting submission in the absence of, or preceding, apparent aggression by the other individual were not included in this analysis, because interactions in which they occurred were all ES interactions by definition.

As indicated in Tables 4.12 and 4.13, the proportions of agonistic interactions which involved explicit submission varied significantly according to the type of aggressive signal category (Berenty: $x^2 = 30.8$, df=3, $p < .001$; DUPC: $x^2 = 53.8$, df=4, $p < .001$). At both study sites agonistic interactions involved explicit submission less frequently than expected in response to a cuff, and more often than expected in response both to other kinds of physical aggression and to threats. At the DUPC, interactions involved explicit submission less often than expected during reciprocal aggression - in which one both individuals were aggressive but in which one of them also signalled submissively - and more often than expected as a consequence of agonistic aid. Expected values for most Berenty categories were quite low; and the Berenty data, despite lumping of "reciprocal aggression" and "agonistic aid", actually fall short of meeting the assumptions for a chi-square test (Siegel and Castellan 1988).

TABLE 4.12: OBSERVED AND EXPECTED FREQUENCIES FOR DISTRIBUTION OF ES INTERACTIONS ACCORDING TO INITIATING SIGNAL: BERENTY

	cuffs		other physical		threats		reciprocal aggression and aid	
	E	O	E	O	E	O	E	O
ES	17.7	4	9.3	21	5.8	8	2.3	2
OTHER	51.7	40	52.2	30	98.3	112	12.7	13

TABLE 4.13: OBSERVED AND EXPECTED FREQUENCIES FOR DISTRIBUTION OF ES INTERACTIONS ACCORDING TO INITIATING SIGNAL: DUPC

	cuffs		other physical		threats		reciprocal aggression		aid	
	E	O	E	O	E	O	E	O	E	O
ES	117.3	91	78.8	118	70	77	41.4	17	11.5	16
OTHER	434.7	461	292.2	253	259.1	252	153.6	178	42.5	38

DISCUSSION

1) Nature and extent of dominance

Dominance in E. fulvus was found to be a phenomenon characterizing particular dyads, but not a system organizing the entire group. Although individuals could be ordered in terms of their percentages of all conflicts won - the conventional system, and one which minimizes reversals in a group with a transitive, linear hierarchy (Lehner 1979) - this did not result in rank orders in which each individual dominated all those below it and was dominated by all those above it. This was not because of circularity in this respect, but because agonism between two individuals was often too rare, or involved too much symmetry in the direction of aggression, for it to be said that dominance existed.

The fact that hierarchies did not were not recognizable does not mean that animals could not have had a sense of each others' dominance or subordinance in terms of their tendency to win or lose conflicts with various group members, or to put it another way, of their position in the group. An anecdotal event which suggests awareness of these relationships involves af21 in group HE. This female, the multiparous granddaughter of af20, had for several weeks been a focus of attention among males after she had an infant. A younger adult female, af22, af20's daughter, had an infant at about the same time, but it soon disappeared. When af20 finally had an infant, the males suddenly shifted their attention to her, and af21 became distinctly peripheral, socially and spatially, to the rest of group HE. She gradually worked her way back in, but to do so she started by affiliating with jf24, clearly the most subordinate individual in the group, who was dominated - in the statistical sense used in this paper - by everyone in the group.

To understand fully the dynamics of dominance in any group, it would be necessary to analyze all of the social relationships in detail, which is beyond the scope of this paper. However, different individuals may have different social styles, or be exercising different options in their relationships. For example, am27 and am26 were the same age.

They had, respectively, the highest aggressor percentage and a tie for the second highest in their group. However, the raw frequency of aggression for the most dominant individual, am27, was over two and a half times that for am26. These two individuals apparently had an understanding: am26, who was subordinate to am27, was free to affiliate and mate with af22 without interference from am27; but am26 in turn had little to do with af20 and af21, both of whom am27 also tried to keep away from am25, who had once been the sole reproductive male in the group (DUPC records). (Am25 did not try to affiliate with af22, who was his daughter). Most of am27's aggression was directed towards am25.

The differing proportions of dyads in which dominance was recorded in different groups were partly related to differences in sampling time. Due to the application of focal animal sampling to groups of different sizes, and because data on agonism were also collected on an all-occurrences basis while focal sampling was in progress, differing amounts of time spent observing different groups resulted in a bias favouring the recording of sufficient agonistic interaction to document dominance in larger groups (Table 4.7).

However, lower focal rates of agonism in the Berenty groups, compared with those for the DUPC groups, suggest that there is more to the matter than sampling. The question then becomes whether the differing rates of agonism reflect differences in observability - the Berenty brown lemurs being almost completely arboreal, and those at the DUPC, at least during the daylight hours, almost completely terrestrial - or whether higher rates of agonism and more common occurrence of dominance are in fact functions of captivity in an environment where the animals are semi-free-ranging rather than free-ranging.

Because the ranges of the Berenty groups were small and the reserve itself was a virtual island, not permitting emigration outside of it, there may have been spatial constraints on the animals at Berenty not unlike those on semi-free-ranging lemurs at the DUPC, although probably to a lesser degree. To address properly the question of observability versus environmental effects would require data from another field site that is more natural than Berenty in terms of size and emigration possibilities. On the other hand, the higher rates of agonism and resultant higher frequency of dominance at the DUPC may have resulted less from the effects of the two environments on the animals than from differing observation conditions.

However, the fact that Overdorff (Pereira et al 1990) recorded submissive as well as aggressive signals among wild E. f. rufus in the Madagascar rainforest indicates that, among brown lemurs, the social behaviour on which dyadic dominance is based - whether defined on the basis of aggressive or submissive signals - is not strictly a function of captivity, nor of arguably unnatural constraints, such as at Berenty, on otherwise free-ranging groups.

2) Patterns of dominance: age and sex

The data clearly indicate that females do not always dominate males in E. fulvus as they do in L. catta (Pereira et al 1990; Kappeler 1990), V. variegata (Kaufman 1991), I. indri (Pollock 1979), and perhaps some other lemuroid species (Richard 1987). Furthermore, in female-dominant species such as V. variegata, infant females may even dominate older males (Kaufman 1991). In this study of E. fulvus, no infant or juvenile dominated an older individual. ES interactions between the most dominant (in both aggressor percentage and DS ratio senses) females and the most dominant males were typically few in number, and dominance did not exist in any such dyad.

Since females do not dominate males in E. fulvus, then either the Hrdy-Jolly hypothesis for the evolution of female dominance among lemuriforms based on energetic constraints related primarily to resource seasonality is invalid, or else there must be a reason why such constraints are not operative for this particular species. Evidence suggestive of the latter possibility is that this species is very generalized in diet and habitat. As discussed in a previous section of this chapter, brown lemurs have been discovered to be opportunistic omnivores, and they inhabit both rainforest and dry forest on Madagascar. It seems likely that they can adapt readily to a range of environmental conditions which may be more limiting for some other lemuriform species, although research on the diets of various populations of other species would be necessary to substantiate the notion that they are less generalized and opportunistic than E. fulvus.

3) ES interactions

It has been said that the general function of submission in agonistic interactions is to deter aggression (e.g., Walters and Seyfarth 1987; Hand 1986). However, as mentioned in Chapter 3, the usual lack of a submissive response to aggression in brown lemurs does not lead to further aggression on the part of the original aggressor. Assuming that the deterrence idea is a valid generalization about the function of submission, the usual lack of obvious submission and of resulting continued aggression in E. fulvus agonistic interactions needs to be explained.

It seems unlikely that the reason is because a non-response to aggression may be a kind of passive aggression. When non-responses were analysed as losses, the results regarding dominance within dyads were consistent with those for ES interactions alone. Moreover, what appears to a human observer to be a lack of submissive response to aggression may be otherwise to a brown lemur. Observing captive brown lemurs at close range, Andrew (1964) noticed that subordinates sometimes merely averted their eyes in response to a threat from a dominant animal. This suggests that considering apparent non-responses to aggression as implicit submission is justified, and that measuring dominance in E. fulvus in terms of the direction of aggressive signals is appropriate.

Evidence that submissive signals in some species occasionally trigger aggression (e.g., savannah baboons: Smuts 1985; ruffed lemurs: pers. obs.) challenges the idea that submission necessarily has a deterrent function. It is possible that non-reaction to aggression in brown lemurs has evolved as a way of reducing the risk of encouraging further aggression. However, since brown lemur aggression is extremely unlikely to result in wounding under natural or semi-natural conditions, the risk entailed in encouraging further aggression through submission would probably be low. It seems more likely that the lack of obvious submissive signals reflects the mild nature of aggression. Elaborate or emphatic submissive responses to aggression may simply be unnecessary as a deterrent to further aggression in a species in which aggression itself is typically mild; and if there is a chance that submission could itself aggravate an aggressor, subtle submission may be an optimal solution for a subordinate individual.

The fact that ES interactions occurred less often than expected in the context of access to huddles, and less often than expected in response to cuffs, is consistent with the finding presented in chapter 3, that cuffs occurred disproportionately often in the context of access to, or proximity in, huddles. Because cuffs are the most common aggressive signal in E. fulvus, and because submissive signals are uncommon in response to this type of aggression, then it is not difficult to understand why previous field researchers found dominance relationships to be indiscernible.

CONCLUSION

Conclusions from earlier studies to the effect that dominance was not discernible in E. fulvus likely stemmed from the mildness of most aggression and the lack of obvious submissive responses to most aggression, the same phenomena which led to the notion that agonism was rare, which was discussed in Chapter 3. If it was hard to detect agonism when it occurred, it follows that it would be difficult or impossible to discern dominance relationships.

In this study, focusing on agonism, and using a statistical criterion for measuring dominance, I recorded dyadic dominance at both the DUPC and Berenty, but did not discover linear hierarchies. I have suggested lower rates of agonism and relatively difficult observation conditions at Berenty as reasons for the relative rarity of recorded dominance at Berenty compared to the DUPC. It is understandable from these data why earlier field researchers - who, except for one case (Harrington 1975), were not focusing on social behaviour, and in that one not focusing on agonism - concluded that dominance relationships did not exist in E. fulvus, whereas two of the three DUPC researchers concluded differently.

Most importantly, with respect to prevalent notions about the universality of female dominance in lemuriforms, and explanations for the evolution of female dominance in these and other primates, I discovered that brown lemurs are neither female dominant nor male dominant. Dominance is specific to particular dyads: in some heterosexual dyads females dominate males, and in others males dominate females. The most important factor for predicting dominance in any dyad, heterosexual or isosexual, is age: in dyads in which dominance is measurable, the older individual is usually the dominant one. Since the Hrdy-Jolly hypothesis for the evolution of female dominance in lemuriforms and other primates rests on the idea that females are highly constrained energetically with respect to reproduction in these species, partly because they live in very seasonal environments, I have suggested that brown lemurs, living in a variety of habitats and being dietary generalists and opportunists, may be less constrained than other lemurs in this respect, thus obviating the need for female dominance.

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CHAPTER 5

DOMINANCE AND SOCIAL GROOMING IN EULEMUR FULVUS

INTRODUCTION

Social behaviour of brown lemurs, Eulemur fulvus (Simons and Rumpler 1988), formerly Lemur fulvus, was studied in two free-ranging and three semi-free-ranging groups, in order to answer questions raised by contradictions in the literature regarding the frequency and intensity of agonism and the existence of dominance relations in this species. Research was conducted on affiliative as well as agonistic behaviour, so that dominance patterns, if discernible, could be examined for their possible relationship to other aspects of social behaviour. Because of a common, although not universal, finding in primate research that the usual direction of allogrooming is from subordinates to dominants (reviewed in Walters and Seyfarth 1987; Rowell et al 1991), I recorded and analysed social grooming behaviour in particular for its possible relationship to agonism and to any patterns of dominance that I might discern.

Earlier field studies of E. fulvus (Harrington 1975; Sussman 1975, 1977; Tattersall 1979) all concluded that agonism was rare and mild, and that dominance relationships could not be discerned. However, research carried out on captive (Vick and Conley 1976; Vick 1977; Boskoff 1978) and semi-free-ranging (Colquhoun 1987) brown lemurs at the Duke University Primate Center (DUPC) led to different conclusions from the above. All of the latter researchers documented agonism in detail, and Boskoff and Colquhoun concluded that dominance relationships existed.

I observed a variety of agonistic behaviours among free-ranging brown lemurs at the Berenty Reserve in Madagascar and semi-free-ranging animals at the DUPC, and documented dominance relationships at both sites to an extent that I was able to conclude that the basic rule of dominance was that older animals dominated younger ones (see Chapter 4). I discovered no systematic dominance of females over males, nor vice versa. This was significant given that dominance of females over males was reported from field studies for a number of lemuriform species (reviewed in Richard 1987), and that this phenomenon, unusual among primates, was explained as an adaptation to the seasonal environments of Madagascar, particularly in relation to certain aspects of lemuriform physiology (Hrdy 1981; Jolly 1984). I concluded that the generalized dietary habits of this species and its adaptation to a variety of habitats in Madagascar suggested that it was not as constrained as were other lemuriforms by the environmental factors discussed by Hrdy and Jolly, and that this may have obviated the need for female dominance.

Having documented that dominance relationships existed, and that older animals as a rule dominated younger ones, my goal was to examine possible relationships between dominance patterns and social grooming patterns.

My specific research questions were:

1) In dyads with both dominance and significant asymmetry in the direction of allogrooming, was the dominant individual usually the primary recipient of allogrooming?
2) Was there any pattern to the primary direction of allogrooming with respect to age and sex?
3) Was simultaneous mutual grooming more characteristic of dyads in which there was not significant asymmetry in the direction of aggression, or in which aggression was rare?

METHODS

a) Natural history of the study species

E. fulvus live in multi-female, multi-male groups of from five to 12 individuals (Tattersall 1982). They inhabit both dry forest and rainforest in Madagascar, in both of which they are almost entirely arboreal (Sussman 1975; Tattersall 1979). Brown lemurs have been reported to be both crepuscular (Harrington 1975; Sussman 1975) and diel, i.e., alternately active and resting throughout the 24 hour day without respect to light cycles (Tattersall 1982).

Sussman (1975) found E. f. rufus at his dry forest research site to be predominantly folivorous. However, more generalized herbivory was observed by Tattersall (1977) among E. f. mayottensis, and by Meyers (1988) among rainforest E. f. rufus. At Berenty, E. f. rufus eat insects, spiders and other arthropods, as well as leaves, buds, flowers, fruit, herbs, bark, fungi and spider webs (pers. obs.).

b) Age classification used in this study

Individuals of both sexes were classified as follows: infant (until weaning at four months); juvenile (from four to approximately 19 months, at which time both sexes can become sexually active and females can conceive); and adult (from approximately 19 months on). Group composition and ages of individuals are presented in Tables 2.2 and 2.3, Chapter 2.

c) Description of the study sites, and of the composition, ranges, activity rhythm and subsistence activity of the study groups

i) Berenty, Madagascar

Although widespread in a variety of habitats in Madagascar, brown lemurs are not indigenous to the Berenty region in the semi-arid south of the country. This region consists of xerophytic forest with strips of gallery forest. The E. f. rufus study animals, "red-fronted" (Tattersall 1982) or "rufous" (Overdorff 1992) lemurs, were descended from captives taken in the early 1970s from gallery forest in the deciduous forest zone of the central west coast of Madagascar. In 1987 approximately 55 rufous lemurs in six social groups inhabited the 100 hectare Berenty reserve. The vegetation of this reserve, dominated by the kily tree, Tamarindus indica, has been described in detail elsewhere (e.g., Budnitz and Dainis 1975; Jolly 1966). The reserve is bordered on one side by the Mandrare River, and is otherwise surrounded by a huge sisal plantation. The other lemurs in the reserve - Lemur catta, Propithecus verreauxi, Lepilemur mustelinus, and Microcebus murinus - are all indigenous.

After two weeks of reconnaissance observations, my formal study of brown lemurs at Berenty began on 22 August, 1987, two weeks before the first births occurred. The study continued until 26 December, 1987. Focal data collection on group 1a was begun before a second group was chosen. On 29 September, three males left group 1a (which had previously numbered 10 individuals, infants not included), and peacefully joined a neighbouring group of consisting of three females, two of them adults with newborn infants. I used this newly constituted group as my second group, group 2. The remainder of group 1a became group 1b. Group 1a/b ranged over 8.5 hectares, and group 2 over 3.5 hectares.

The study animals spent most of their waking hours in the trees at heights of from 5 to 25 metres. Because sexual dichromatism in this subspecies is marked, and since features of individual pelage such as facial markings and tail bushiness were usually unique in some way, individuals were readily identifiable in the dry season - at the beginning of the study - even when they were in the upper canopy. By November the foliage had begun to thicken considerably, but increased difficulty in identifying individuals was offset by relative ease in finding the study groups, whose movements became more predictable because the animals were now feeding extensively on fruits. Still, groups occasionally made day-long "forays" through the ranges of other groups. The ranges of groups 1b and 2 were slightly overlapping, and in this shared area intergroup agonistic encounters were frequent. Otherwise a common boundary was defended and regularly scent-marked. E. f. rufus at Berenty were found to be active from approximately an hour before sunrise to an hour after sunset, with periods of activity and rest interspersed throughout the day.

ii) Duke University Primate Center (DUPC)

I studied two groups of E. f. rufus and one group of E. f. collaris at the DUPC, Durham, North Carolina, U.S.A., for 7 months between September, 1988 and September, 1989: 30 September to 30 December, 1988; 26 February to 20 June, 1989; and 22 August to 6 September, 1989. The annual cycle in the northern hemisphere is six months out of phase with that in Madagascar, because the seasonal reproductive/behavioural changes are a response to changes in photoperiod (Boskoff 1978; Rasmussen 1985). The DUPC portion of the research was therefore begun approximately two months before the beginning of the mating season, which lasted from November into January; the February to June portion covered the birth season, most births being in March and April; and the August-September 1989 portion was during the late lactation or weaning period (Boskoff 1978).

Each of the study groups was semi-free-ranging in a multi-hectare forested enclosure surrounded by an electrified fence. The forest is dominated by loblolly pine trees, Pinus taeda, but also contains a number of deciduous species. The animals foraged on naturally occurring food resources, including leaves, nuts, buds, flowers, exudates, and ants, and were also fed monkey chow and fruit daily, except during the summer months when fruit was only provided every second day. Fresh water was provided daily. Heated nestboxes provided shelter in cold weather.

Each of the two E. f. rufus groups, group HE and group RO, shared its enclosure with a group of ringtailed lemurs, Lemur catta, and ruffed lemurs, Varecia variegata. The

E.f. collaris group, group CI, shared its enclosure with a group of sifakas, Propithecus verreauxi.

Each independent individual had a unique combination of coloured collar and pendant, the latter also varying in shape. I was, however, able to recognize individuals on the same bases as at Berenty. Furthermore, the DUPC brown lemurs spent most of their waking hours active or resting on or near the ground, which made observation and recording of behaviour considerably easier than at Berenty. The activity rhythm of the animals was similar to that of the Berenty groups.

Group HE, consisting of 10 individuals - all but one of them (am25; see chapter 2, Table 2.2) related to the oldest female - had lived for many years in an outdoor run before being transferred to the 3.5 ha enclosure, where they had lived since October, 1986. Group RO was composed of a mother and son and three unrelated individuals, who had been living in different caged, outdoor runs, and who were released into a 5.8 ha enclosure neighbouring group HE at different times between August, 1987 and April, 1988. Group CI comprised individuals from two original groups, which had been living in separate caged outdoor runs, and which were released separately into a third fenced, forested 1.5 ha enclosure (not bordering either of the others) in September, 1987. After various conflicts, including injuries necessitating removal of some individuals from the enclosure, these animals formed one group, which had been intact for almost a year at the time my study began.

d) Data collection

Because of their durational rather than instantaneous nature, social grooming data were recorded only from observations on focal animals (Altmann 1974). Focal sessions were 10 minutes in length, and individuals in each group were observed as focal animals on a rotating basis. Social grooming was recorded as either "allogrooming" or "mutual grooming". In allogrooming, the behaviour at any point in time was unidirectional, but during entire interactions was frequently reciprocal, often with several alternating unidirectional segments. Mutual grooming consisted of the same behaviour as allogrooming, i.e., combing the other animal's fur with the toothcomb, or licking the other animal's muzzle or anogenital region; but in mutual grooming both animals did this simultaneously. In allogrooming, unidirectional segments of less than 3 seconds were not recorded. Thus, if two animals allogroomed each other with rapid directional changes, consisting of segments of less than 3 seconds each, it was recorded as "alternate grooming" and lumped with mutual grooming for later analysis.

Focal and all occurrences observations totalled approximately 700 hours at both sites combined. Focal observations at Berenty totalled 107.83 hours and other observations about 130 hours. Focal observations at the DUPC totalled 311.67 hours and other observations about 150 hours - the former consisting of 116.17 hours during mating season, 162.33 hours during the birth season, and 33.17 hours in the short follow-up season (at weaning time for most infants).

Observations were carried out using 7x24 binoculars when necessary, primarily at Berenty. Time was measured with a digital stopwatch. Data were recorded with pen and paper.

e) Data analysis

I used the binomial test to determine whether dominance existed in agonistic dyads by computing the probability of the distribution of wins in each dyad. This test accounts for the actual frequencies involved in a particular proportion, thus necessitating the six event minimum for a probability of less than .05. Because this test determines the probability of the frequencies of discrete events, it cannot be used for durational data. It was therefore problematical to determine both a minimal dyadic duration of allogrooming and a minimal degree of asymmetry for consideration of a dyad in the analysis.

I devised a solution based on a similar rationale to the binomial test: the same proportion has a lower probability as the sample size of the behaviour increases. I therefore needed criteria for significant asymmetry which were increasingly conservative for dyads with longer durations of allogrooming, as well as a minimum amount of allogrooming for consideration of a dyad for such analysis. Since the mean unidirectional segment of allogrooming was approximately 30 seconds, I decided to use 3 minutes as a minimum for inclusion in the analysis, because at six times 30 seconds it was consistent with the six event minimum for agonism, and also resulted in approximately the same number of dyads to consider. For directional asymmetry of allogrooming in a dyad to be considered significant, I decided that any dyad with less than 6 minutes of allogrooming had to have an asymmetry of at least 96%-4%, any with 6 to 11.9 minutes an asymmetry of at least 86%-14%, any with 12-17.9 minutes an asymmetry of at least 76%-24%, and any with 18 minutes or more an asymmetry of at least 66%-34%. The 96%-4% criterion for dyads of less than 6 minutes may be relatively more stringent than the others; but if it is, that would compensate for possible sampling error in dyads with shorter allogrooming durations.

RESULTS

1) Dominance and the direction of allogrooming.

At least 3 minutes of allogrooming was recorded in 62 of a possible 152 dyads at both study sites (76 possible at each site; Table 5.1). Twenty of these 62 dyads were at Berenty, and 42 were at the DUPC. Fourteen of the Berenty dyads met the criteria for significant asymmetry, as did 20 of the DUPC dyads, for a total of 34 significantly asymmetrical allogrooming dyads (Table 5.1). Only seventeen of these 34 dyads also involved agonistic dominance (Chapter 4), and in all 17 dyads the agonistically dominant individual was the primary recipient of allogrooming (Table 5.2).

TABLE 5.1: ALLOGROOMING GIVEN AND RECEIVED IN ALL DYADS IN WHICH IT TOTALLED 3 MINUTES OR MORE

sex combination	group	older	% rec'd if 50% or more	* if significant asymmetry	younger	% rec'd if 50% or more	total minutes
FEMALES	DUPC- HE	af20	100%	*	af22		5.3
		af20	80%	*	jf23		23
		af20	83%		jf24		3.4
		af22		*	jf24	73%	20.5
	DUPC- RO	af40	81%	*	af41		18.6
	DUPC- CI	af01	76%		af02		4.4
	Ber.- 1a	af51	81%		jf54		3.7
		af52	100%	*	jf54		4.8
	Ber.- 1b	af52	95%		jf54		5.4
	Ber.- 2	af72	100%	*	jf73		5.2
MALES	DUPC- HE	am25			am26	66%	3.8
		am25		*	am27	100%	5.2
		am26	72%		am28		9.8
		am26	89%	*	am29		6.5
	DUPC- RO	am42	91%	*	am43		11.1
		am42	100%	*	am44		4.2
		am43	50%		am44	50%	5.1
	DUPC- CI	am03	94%	*	am05		13.6
		am03	89%	*	am06		8.4
		am03			jm07	59%	13
		am05	65%		am06		6.3
		am06			jm07	70%	4.9
	Ber.- 1a	am55	100%	*	jm60		8.3
	same age >	am56	90%		am59		4.2
		am58	98%	*	am59		8.6
	Ber.- 1b	am55	100%	*	am56		3.3
		am55	100%	*	jm57		3.1
		am56	67%		jm57		5.6
	Ber.- 2	am58	92%		am59		4.9

TABLE 5.1: ALLOGROOMING GIVEN AND RECEIVED IN ALL DYADS IN WHICH IT TOTALLED 3 MINUTES OR MORE (cont'd)

sex combination	group	older	% rec'd if 50% or more	* if significant asymmetry	younger	% rec'd if 50% or more	total minutes
HETERO - SEXUAL	DUPC- HE	af20	100%	*	am26		3.6
		af20			am27	83%	4.2
		af21	100%	*	am28		17.5
		af21	58%		am29		3.3
	same age >	af22	89%	*	am28		6.1
		am25		*	af21	98%	22.7
		am27			af21	58%	4.8
		am26	71%		af22		8.2
		am27	97%	*	af22		16.1
		am27	85%	*	jf23		19.3
		am26	60%		jf24		6.1
		am27	65%		jf24		3.5
	DUPC- RO	af40			am42	66%	12.1
		af40	82%	*	am43		15.2
		am42			af41	63%	13.9
		af41	71%		mf43		11.5
		af41	75%		am44		12.7
	DUPC-CI	af01	99%	*	am03		8.3
		af01	84%		am05		4.3
		af01	100%	*	jm07		3.5
		af02	73%		jm07		6.9
		am03			af02	64%	8.4
		am05			af02	66%	9.7
		am06		*	af02	98%	6.1
	Ber 1a	am59		*	af53	100%	15
	Ber 1b	am51	95%	*	am56		8
		am51	93%	*	jm57		8.9
		am55	90%	*	af53		7
		af53	100%	*	jm57		5.2
		am55	100%	*	jf54		5.3
		am56	98%	*	jf54		6.8
	Ber 2	af72	100%	*	am59		3.2
		am58	83%		jf73		4.5

TABLE 5.2: DIRECTION OF AGGRESSION AND ALLOGROOMING IN DYADS IN WHICH THERE WERE AT LEAST 6 AGONISTIC EVENTS AND 3 MINUTES OF ALLOGROOMING

sex combination	group	older	agg'sor % if 50 or more	gr.rec'd % if 50 or more	**if significant asymmetry in aggression & allogrooming	younger	agg'sor % if 50 or more	gr.rec'd % if 50 or more
FEMALES	DUPC-HE	af20	100%	80%	**	jf23		
		af20	100%	83%		jf24		
		af22	100%	73%	**	jf24		
	DUPC-CI	af01				af02	67%	76%
MALES	DUPC-HE	am25				am26	83%	66%
		am25				am27	98%	100%
		am26	100%	72%	**	am28		
		am26	100%	89%	**	am29		
	DUPC-RO	am42	100%	91%	**	am43		
		am42	72%	100%	**	am44		
		am43	51%	50%		am44		50%
	DUPC-CI	am03	100%	94%	**	am05		
		am03	90%	89%	**	am06		
		am03	100%			jm07		59%
	Ber - 1b	am55	100%	100%	**	am56		
		am55	100%	100%	**	jm57		

TABLE 5.2: DIRECTION OF AGGRESSION AND ALLOGROOMING IN DYADS IN WHICH THERE WERE AT LEAST 6 AGONISTIC EVENTS AND 3 MINUTES OF ALLOGROOMING (cont'd)

sex combination	group	older	agg'sor % if 50 or more	gr.rec'd % if 50 or more	**if significant asymmetry in aggression & allogrooming	younger	agg'sor % if 50 or more	gr.rec'd % if 50 or more
HETERO-SEXUAL	DUPC-HE	af20		83%		am27	75%	
		af21	75%	100%	**	am28		
		af21	89%	58%		am29		
		af22		89%		am28	64%	
		am25			**	af21	80%	98%
		am27	74%	58%		af21		
		am27	100%	97%	**	af22		
		am27	100%	85%	**	jf23		
		am26	100%	60%		jf24		
		am27	100%	65%		jf24		
	DUPC-RO	af40	74%	82%		am43		
		af41	73%	71%		am43		
		af41	71%	75%		am44		
	DUPC-CI	af02	76%			jm07		73%
		am03	78%			af02		64%
		am05	56%			af02		66%
		am06	58%			af02		98%
	Ber 1b	af51	100%	93%	**	jm57		
		am55	100%	90%	**	af53		
		am55	100%	100%	**	jf54		
	Ber 2	am58	100%	83%		jf73		

2) Relationship of direction of allogrooming to age and sex

For female-female combinations (Table 5.1), there was significantly asymmetrical allogrooming in six dyads, and in all six the primary recipient was the older female.

For male-male combinations (Table 5.1), there was significantly asymmetrical allogrooming in ten dyads, and in nine of these ten the primary recipient was the older male. In the exceptional case, am25, the 9-year-old male in group HE, who was physically past his prime, was the donor of 100% of the 5.2 minutes of allogrooming with 6-year-old am27, who agonistically dominated am25.

For heterosexual combinations (Table 5.1), there was significantly asymmetrical allogrooming in 18 dyads, 17 of which involved individuals of different ages. In 14 of these 17 the primary recipient was the older individual, regardless of sex. The three exceptions comprised the following dyads (Table 5.1):

a) am25 and af21 in DUPC group HE. In this case, the younger animal, a 5-year-old female, received 98% of 22.7 minutes of allogrooming with the abovementioned 9-year-old male.

b) am06 and af02 in DUPC group CI. In this case, the younger animal, a nulliparous/primiparous female, received 98% of 6.1 minutes of allogrooming with a young adult male.

c) am59 and af53 in Berenty group 1a. In this case, the younger animal, a primiparous female, received 100% of 15 minutes of allogrooming with a young adult male who was one of the three males to leave the group shortly thereafter.

3) Mutual grooming

In addition to allogrooming, in which grooming in a dyad was unidirectional at any one point in time, animals also engaged in mutual grooming, i.e., they groomed each other simultaneously. Mutual grooming comprised 26.6%, by duration, of all social grooming at both study sites. The percentages of all focal animal observation time in each group consisting of mutual grooming ranged from 0.63% to 2.45%, whereas those for allogrooming ranged from 2.43% to 6.63% (Table 5.3). (Mutual grooming durations for

TABLE 5.3: PERCENTAGES OF ALL FOCAL OBSERVATION HOURS IN EACH GROUP ACCOUNTED FOR BY ALLOGROOMING AND BY MUTUAL GROOMING

Group	Number of individuals	Focal observation hours (FO)	Allogrooming as % of FO hrs.	Allogrooming as min./hr.	Mutual grooming as % of FO hrs.	Mutual grooming as min./hr.
BERENTY						
1a	10	27	6.63%	3.98	0.63%	0.38
1b	7	48.83	4.93%	2.8	1.61%	0.97
2	5	32	2.43%	1.46	1.13%	0.68
DUPC						
CI	7	96	3.74%	2.24	1.38%	0.83
HE	10	144.5	4.93%	2.96	1.75%	1.05
RO	5	71.17	4.98%	2.99	2.45%	1.47

all dyads, as well as allogrooming duration and asymmetry and aggression frequency and asymmetry, are presented in Appendix 2).

For all dyads with three or more minutes of mutual grooming (Table 5.4), correlations were run for each group between duration of mutual grooming on the one hand and duration of allogrooming and frequency of aggression on the other. Groups 1a and 2 at Berenty were not analysed, because the former contained no dyads with more than three minutes of mutual grooming, and the latter included only three such dyads. Data from group 1a were not lumped with those from dyads which also existed in 1b because the differences in group composition may have affected the relevant behaviours in each group. The only significant correlation was for the relationship between durations of mutual grooming and of allogrooming in group CI (r = .5581, n=13, p=.047) (Table 5.5).

Furthermore, there did not appear to be any relationship between the duration of mutual grooming and the asymmetry of either allogrooming or aggression. Extensive mutual grooming was recorded in dyads both with and without dominance: it occurred in high-frequency, significantly asymmetrical agonistic dyads; in high-frequency, symmetrical agonistic dyads; in low-frequency, significantly asymmetrical agonistic dyads; and in low-frequency, symmetrical agonistic dyads (Table 5.4). Similarly, extensive mutual grooming was recorded in dyads both with and without significant allogrooming asymmetry. The occurrence of extensive mutual grooming in some dyads in which there was significant asymmetry in the direction of allogrooming indicates that the simultaneous reciprocity of mutual grooming is not necessarily a correlate of highly symmetrical or reciprocal allogrooming relationships (Table 5.4).

TABLE 5.4: RELATIONSHIP OF MUTUAL GROOMING DURATIONS TO DURATION AND ASYMMETRY OF ALLOGROOMING AND FREQUENCY AND ASYMMETRY OF AGGRESSION

I.D.#1	I.D.#2	mutual grooming (minutes)	allo-grooming (minutes)	% of allogrooming received by primary recipient underlined if significant	frequency of aggression	% of aggression directed by primary aggressor underlined if significant
af01	af02	3.6	4.4	76%	15	67%
am03	am05	9.5	13.6	94%	14	100%
am03	am06	9.6	8.4	89%	10	90%
am03	jm07	5.2	13	59%	10	100%
am04	am06	4.9	1.9	82%	5	80%
am05	am06	7.9	6.3	65%	3	67%
am06	jm07	3.5	4.9	70%	5	100%
af01	am03	3.9	8.3	99%	3	100%
af01	jm07	3	3.5	100%	3	100%
am04	af02	3	1.1	100%	5	100%
am05	af02	4.3	9.7	66%	18	56%
am06	af02	5.5	6.1	98%	12	58%
af02	jm07	5.5	6.9	73%	54	76%
af20	af22	5.3	5.3	100%	1	100%
af20	jf23	17.6	23	80%	7	100%
af21	jf23	3	1.4	100%	44	98%
af22	jf23	16.8	2	56%	10	80%
af22	jf24	4.3	20.5	73%	10	100%
jf23	jf24	10.3	0.75	56%	12	92%
am26	af22	4.8	8.2	71%	4	100%
am27	af22	7.2	16.1	97%	27	100%
af22	am28	4.1	6.1	89%	11	64%
am25	am27	17.5	5.2	100%	66	98%
am25	am29	5.6	0.2	100%	7	100%
am26	am28	7.2	9.8	72%	17	100%
af20	am25	3.5	1.1	50%	18	83%
am25	af21	13.7	22.7	98%	15	80%
am27	af21	3.7	4.8	58%	23	74%
am27	jf23	9.4	19.3	85%	9	100%

TABLE 5.4: RELATIONSHIP OF MUTUAL GROOMING DURATIONS TO DURATION AND ASYMMETRY OF ALLOGROOMING AND FREQUENCY AND ASYMMETRY OF AGGRESSION (cont'd)

I.D.#1	I.D.#2	mutual grooming (minutes)	allo-grooming (minutes)	% of allogrooming received by primary recipient outlined if significant	frequency of aggression	% of aggression directed by primary aggressor outlined if significant
af40	af41	4.1	18.6	81%	3	67%
am42	am43	15.4	11.1	91%	21	100%
am43	am44	12.8	5.1	50%	45	61%
af40	am42	31.6	12.1	66%	2	each 50%
af40	am43	17	15.2	82%	19	74%
am42	af41	7.6	13.9	63%	3	67%
af41	am43	7.8	11.5	71%	15	73%
af41	am44	6.6	12.7	75%	35	71%
af52	jf54	5.2	5.4	95%	1	100%
am55	jm57	3	3.1	100%	22	100%
am56	jm57	3.1	5.6	67%	1	100%
af51	jm57	6.4	8.9	93%	8	100%
am55	af52	3.8	0.2	100%	1	100%
af52	am56	6.6	0.5	83%	1	100%
af52	jm57	4.1	0.8	100%	2	100%
af53	jm57	3.6	5.2	100%	3	100%
am55	jf54	5.3	5.3	100%	29	100%
af71	af72	8.9	1.5	60%	0	n/a
af71	jf73	5.8	2.3	100%	2	100%
af72	am59	4.2	3.2	100%	3	100%

TABLE 5.5: PEARSON CORRELATIONS BETWEEN MUTUAL GROOMING AND ALLOGROOMING DURATIONS AND MUTUAL GROOMING DURATIONS AND FREQUENCY OF AGGRESSION

Group	Mutual grooming durations and allogrooming durations	Mutual grooming durations and frequency of aggression
CI	r=.5581 n=13 p=.047	r=.0820 n=13 p=.79
HE	r=.2998 n=16 p=.259	r=.1954 n=16 p=.468
RO	r= -.2368 n=8 p=.572	r= -.1752 n=8 p=.678
Ib	r=.1880 n=9 p=.628	r= -.0168 n=9 p=.966

DISCUSSION

1) Dominance and the direction of allogrooming

In the 17 dyads with both dominance and significant asymmetry in the direction of allogrooming, all of the dominant individuals received the majority of allogrooming. The phenomenon of dominants receiving more overall allogrooming than subordinates has been documented in several species (reviewed in Walters and Seyfarth 1987), and it has been documented in others that the dominant individual in a dyad typically receives more grooming from the subordinate than vice versa (e.g., capuchins: Robinson and Janson 1987; vervets: Seyfarth 1980; chimpanzees: Simpson 1973).

Seyfarth (1977) proposed a model for such distribution of grooming in relation to dominance. He suggested that, through allogrooming, lower-ranking animals attempt to manipulate higher-ranking ones into alliances that will enable the lower-ranking animals to have reliable agonistic support and better access to food resources. Because of competition to groom higher-ranking animals, those closest in rank to the desirable grooming partner are most successful in efforts to groom it. This social dynamic operates at all levels of the hierarchy, and, as a consequence, individuals primarily groom others of similar rank. This model was developed to explain patterns of grooming in vervet monkeys, among which individuals within a group are, in typical cercopithecine fashion, ranked hierarchically.

Seyfarth's model has been supported by the results of studies on some species (reviewed in Gouzoules and Gouzoules 1987), but it has been shown not to apply in other species in which rank appeared not to function as a grooming attractant (reviewed in Walters and Seyfarth 1987). Some researchers have further argued that when the possible effects of kinship are accounted for, considering that female rank is determined by matrilineal kinship among cercopithecines, the effect of rank in grooming can be shown to be less universal than that of kinship (Walters and Seyfarth 1987).

Nevertheless, the model helped to focus attention on the fact that, in many species, dominants are groomed more by subordinates than vice versa. I have therefore looked at the relationship between dominance and the primary direction of allogrooming in dyads, even though brown lemurs do not form hierarchies, in contrast to species on which Seyfarth's model was based (see Chapter 4). My findings indicate that, in E. fulvus, when a dominance relationship is identifiable in a dyad, subordinates do groom dominants more than vice versa. Probably because brown lemur groups are small and non-hierarchical compared to those of most cercopithecines, and perhaps because social grooming constitutes a small percentage of animals' waking hours, competition to groom dominants did not appear to be a factor in the agonistic and allogrooming relationships of the study groups. (Competition in other areas was apparent at times, especially among adult males attempting to huddle with adult females).

Among brown lemurs the motivation to groom may be similar in part to that discussed by Seyfarth, i.e., to obtain agonistic support and access to resources; but it may be that subordinates groom dominants more than vice versa and receive certain benefits from affiliating with them (if in fact they do, a matter which has not been analysed in this paper) because both are aspects of a more overriding relationship, such as kinship. I did not know the degrees of relatedness of animals in the Berenty study groups; but in two groups at the DUPC, CI and HE, most animals were so closely related to each other that the effects of kinship would be difficult to discern. In group RO, on the other hand, the only kin were a mother and adult son, and there was nothing in the nature of their agonism, allogrooming [illegible] grooming to indicate that this had any effect on their relationship. The mother's [illegible] and mutual grooming relationships with all three males were similar in [illegible] there was no significant asymmetry in allogrooming in any of these dyads. In group HE, the oldest female had a very antagonistic relationship, involving 43 agonistic interactions, with her adult granddaughter, whom she dominated, whereas she had only one agonistic interaction with her adult daughter. The former pair were never observed mutual grooming, and only allogroomed for 1.2 minutes, while the latter were involved in each for over five minutes. However, the oldest female and her adult granddaughter competed for the attentions of the most dominant male, whereas the adult daughter and another adult male affiliated almost exclusively with each other.

It may be that the question of the relative effects of kinship and dominance with respect to allogrooming is more appropriately explored in large, hierarchical groups of Old World monkeys than in small non-hierarchical groups such as those of brown lemurs. Furthermore, preliminary data on group transfer indicate than in E. fulvus both sexes emigrate from their natal groups (Meyers 1988; pers. obs.), so that kinship is not likely to have evolved as an important factor determining the social relationships of adults unless peers emigrate together, as is common among other seasonally breeding primates (Pusey and Packer 1987). The notion that subordinates groom dominants for agonistic and foraging benefits can be seen as both a functional-evolutionary and a proximate explanation for the primary direction of allogrooming. On the proximate level, it may also be that, in small groups, individuals have psychological needs for harmonious relationships with all of their groupmates (cf de Waal 1989), in which case allogrooming may be functioning as appeasement behaviour. I have not, however, analysed allogrooming in terms of its temporal relation to agonism, and so can only speculate regarding the reconcilation possibility.

2) Relationship of agonism and allogrooming to age and sex

The older animal in an agonistic dyad was almost always the primary aggressor, and, where asymmetry was significant, it was thus the dominant animal (Chapter 4). The older animal was also usually the primary recipient of allogrooming in allogrooming dyads. However, in group HE, the 6-year-old male (am27) who dominated the 9-year-old male (am25) also received 100% of the 5.2 minutes of allogrooming between the two of them; and the 5-year-old adult female (af21) who also dominated the 9-year-old male received 98% of 22.7 minutes of allogrooming with him. Thus some of the allogrooming exceptions correlate with agonism exceptions.

Two younger females other than af21 also received a significant majority of allogrooming in heterosexual dyads with older males. In one of these dyads (am59-af53) there was no agonism, and in the other (am06-af02) there was no dominance, with aggression by both parties approximately equal. However, there may also be a trend for males to give more grooming than they receive in dyads with females in which they also give more aggression than they receive. For instance, the oldest male in group CI had three agonistic interactions with the oldest female, in all of which she signalled submissively, yet he gave her 99% of 8.3 minutes of allogrooming. Similarly, in group HE, am27, although he significantly dominated af21, received from her only 42% of 4.8 minutes of allogrooming. There were no comparable instances of females who were more aggressive to male dyad partners who also gave them more allogrooming than they received from them.

Similarly, adults who significantly dominated juveniles often received far less than a significantly asymmetrical amount of allogrooming in return, and at times the juvenile received the majority of allogrooming, although never to the point of significant asymmetry.

Whether an animal was dominant or subordinate and received more allogrooming than it gave in a dyad or vice versa are related factors which are independently correlated with the relative ages of the individuals. The fact that, in the 17 dyads in the study with significant asymmetry in both agonism and allogrooming, each had the same individual as the primary aggressor and the primary grooming recipient does not mean that one of these variables is dependent upon the other. Allogrooming of significant asymmetry occurred in dyads without significant agonistic asymmetry, i.e., dominance, and the direction of allogrooming asymmetry cannot therefore have been determined by dominance. In these cases, as in dyads with dominance, the older individual was as a rule the primary recipient. The dominant individual in a dyad does not receive more grooming because it is more aggressive, and the subordinate does not groom more because it is subordinate. Age seems to be the independent variable determining both dominance and the primary direction of allogrooming.

3) Mutual grooming

Mutual grooming appeared to be a different kind of grooming from allogrooming in that it was not simply simultaneously reciprocal allogrooming and thus an extension of highly symmetrical allogrooming relationships. This is attested to by the usual difference in an individual's primary partners for each type of social grooming. The duration of individuals' mutual grooming with specific individuals did not show any pattern of relationship to the duration or asymmetry of allogrooming with those same individuals.

Mutual grooming and allogrooming may have different social functions in the short or proximate term. I speculate that mutual grooming may be a means whereby non-agonistic social relationships are being affirmed, at least temporarily as a kind of truce, in which even a clearly dominant individual may reciprocate in full, whereas allogrooming may have more to do with appeasement and Seyfarthian manipulation. Further analysis is necessary to see if mutual grooming or allogrooming preferences are systematically related to huddling preferences, and whether the huddling partner preferences are in turn characteristic of relationships which are low in agonism.

4) Possible reasons for differences between study sites in sample sizes and directional asymmetries

It is probable that more 3-minute-minimum allogrooming dyads were recorded at the DUPC than at Berenty primarily because of the greater number of focal sessions per individual at the DUPC (Table 5.3). These sampling differences could also account for the fact that a greater proportion of both agonistic and allogrooming dyads were significantly asymmetrical at Berenty than at the DUPC, considering that the likelihood of observing reciprocity in a symmetrical dyad is greater the longer the dyad is observed (cf Rowell et al 1991).

However, the possibility that uniqueness of social relationships in different groups may play a role in the degree of asymmetry in dyads cannot be ruled out. In group RO at the DUPC, four out of seven dyads with at least six agonistic interactions did not show significant agonistic asymmetry, and only one of nine dyads with at least 3 minutes of allogrooming was significantly asymmetrical. Furthermore, RO was distinct from the other similarly sampled DUPC groups in that only one of its 10 dyads had less than 3 minutes of allogrooming. The mean focal hourly rate of allogrooming in this group was about twice that in the same sized Berenty group, 2.99 as opposed to 1.46 minutes per focal hour.

CONCLUSIONS

The importance of the concept of dominance has been said by some to lie at least partly in the predictive value of dominance with respect to other social variables. In this sense dominance has been referred to as an intervening variable (Hinde 1978, 1983). From an adaptationist perspective, the overriding function of dominance is its contribution to reproductive success. Other correlates of dominance presumably reflect this, in that they also contribute to the same end, or at least show that other individuals are attempting to share in the benefits of dominance by affiliating with dominant individuals. The notion that subordinates groom dominants more than vice-versa is taken to be an indication of the latter point.

However, as discussed above, a number of studies have either shown that allogrooming does not follow this pattern in all species, or that subordinates, although they may be grooming dominants more than vice-versa, are not necessarily competing with each other to share in some supposed benefits, as has been suggested by Seyfarth (1977). I have shown that subordinate brown lemurs do groom dominants more than vice versa. Inasmuch as this has to do with dominance, I have argued that the phenomenon may have proximate as well as ultimate causes. Subordinates may be appeasing dominants for reasons of social harmony in a small group, as well as for reasons of competition with other animals. However, since only 17 dyads involved both dominance and significant allogrooming asymmetry, whereas dominance occurred in another 35 dyads (Chapter 4, Table 4.4) and significant allogrooming asymmetry in another 17 (Table 5.2), the primary direction of allogrooming was not determined by dominance. Because the direction of asymmetry of allogrooming, as well as dominance, could almost always be predicted by knowing the relative ages of the individuals in a dyad, I have concluded that age is the independent variable determining both of these phenomena. Dominance in brown lemurs is thus not an intervening variable, at least as far as allogrooming is concerned.

Some have argued that dominance must be an intervening variable to be a useful concept (reviewed in Bernstein 1981). However, as de Waal (1987) has said, dominance relationships exist in spite of arguments about the validity of dominance as an explanatory model for social behaviour. Delineating these relationships in brown lemurs has been important with regard to theories about dominance in lemurs and other primates in general, insofar as I discovered that systematic female dominance does not characterize this species (Chapter 4). The independence of social grooming from dominance relationships in this species necessitates asking new questions of a proximate as well as ultimate nature to explain allogrooming and mutual grooming. This does not mean that social grooming and dominance relationships are unrelated. The bonds formed and reinforced by social grooming can influence or reflect other behaviours, such as mating preferences, and can therefore have as much to do with social power in a group as do dominance relationships.

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CHAPTER 6

CONCLUSION: OVERVIEW AND SIGNIFICANCE OF PATTERNS OF AGONISM, DOMINANCE AND SOCIAL GROOMING IN BROWN LEMURS, EULEMUR FULVUS

I have argued that E. fulvus agonistic behaviour is subtle: it is typically both mild in physical intensity and lacking in ritualized displays and obvious submissive signals such as loud vocalizations. In these respects brown lemurs differ from some other lemuriform species as well as various anthropoid primates (Chapters 3 and 4).

Why and how such a species style might have evolved is a matter about which we can only speculate. Was it a more adaptive alternative in the niche of ancestral brown lemurs, or the Eulemur genus in general, than, for example, the more explicit agonism of the confamilial ringtailed lemurs (Lemur catta) or ruffed lemurs (Varecia variegata)? Comparative research on the nature of agonism in a wide variety of lemuriforms could disclose whether E. fulvus' subtle agonistic style is characteristic of the entire Eulemur genus and whether such an agonistic style distinguishes this genus from other lemurids and other families of lemuriforms. If this turns out to be the case, then one may argue that phylogenetic inertia is a factor determining the nature of agonism in brown lemurs. Attempting to speculate on the current adaptive value of subtlety may then be a meaningless exercise. As long as this style is not maladaptive, it could remain in the repertoire of this lineage in spite of subsequent environmental departures from ecological conditions in which this pattern first arose.

I have said that, while it makes sense to characterize this species agonism as mild in comparison with some other primates, this mildness likely led earlier field researchers to say that it was rare as well. I have discussed comparative data to support my contention that brown lemur agonism is not rare (Chapter 3). If comparing frequency and intensity of agonism across species is akin to comparing apples and oranges, this does not mean that we should avoid such comparisons. What it does mean is that it is necessary to state the criteria for characterizations of frequency and intensity more clearly than has often been the case in primate studies (Chapter 3).

Earlier field researchers of brown lemurs (Sussman 1975, 1977; Harrington 1975; Tattersall 1977,1979) could not discern dominance relationships in this species, whereas two of three researchers of brown lemurs at the DUPC (Vick 1977; Boskoff 1978; Colquhoun 1987) did report dominance, one for captive animals and another for a semi-free-ranging group. I have argued that there are several possible reasons as to why dominance had not been apparent in the field. First, earlier observers did not focus on agonism, although one (Harrington 1975) was studying social behaviour in general. Second, the subtlety of E. fulvus agonism, including the rarity of obvious submissive signals, likely resulted in much agonism going undetected by the researchers; and if agonism was often undetected, then it follows that it would be hard to discern dominance relationships. Third, naturally occurring brown lemurs are typically arboreal (unlike those semi-free-ranging at the DUPC who spend most of their active time on the ground) and are thus harder to observe. Finally, captive and semi-free-ranging animals may be stressed due to inability to emigrate, and this may result in increased frequency and intensity of agonism, making dominance easier to detect than in the wild.

In addition to the above considerations, the following factors make the picture of dominance in brown lemurs different from that in species in which dominance has been most thoroughly researched (see Chapter 4): 1) dominance in brown lemurs has to be recorded primarily in terms of the direction of aggression, given the rarity of submissive behaviour; 2) reversals of the direction of aggression within dyads are common; and 3) hierarchies apparently do not exist in E. fulvus. The last point deserves mention because, although the distinction between dominance hierarchies and dominance in dyads has been made clear by various authors (e.g., Hinde 1978; Bernstein 1981), those who study social behaviour in primates still often treat the absence of hierarchies as meaning that dominance does not exist (e.g., Robinson and Janson 1987; Struhsaker and Leyland 1987).

Perhaps the most significant conclusion from this study in terms of implications for lemur and primate studies in general is the discovery that females do not systematically dominate males among brown lemurs as they do in some other lemuriforms, and as they have often been assumed to do in all lemur species. I have suggested that this does not warrant rejection of the Hrdy-Jolly hypothesis for the evolution of female dominance, because brown lemurs may be sufficiently generalized in diet that reproductive females are not as energetically constrained as are those in at least some related species. Research on other species is necessary to further test the Hrdy-Jolly hypothesis.

In brown lemur dyads with measurable dominance, the older animal is almost always the dominant one (Chapter 4), but there is a suggestion that males past their physical prime may decline in dominance (Chapter 4). This phenomenon has been documented in male chimpanzees, among whom age is said to be "... the single best predictor of dominance rank" (Nishida and Haraiwa-Hasegawa 1987): older males dominate younger ones, except for males past their prime, who fall in rank. However, the question of the relationship between age and dominance has not been widely addressed in the primate literature, judging from a fairly recent and comprehensive volume on primate social systems and behaviour (Smuts et al 1987).

Making sense of the role, if any, of age in dominance relationships in different species would entail the inclusion of factors such as type of mating system and identity of emigrating sex. For instance, among callitrichids, the oldest female and male in an extended-family monogamous group dominate their offspring and suppress the reproductive activity of offspring (reviewed in Fedigan 1982). This is clearly adaptive in these species in which females typically bear twins and need help from mates and older offspring in caring for infants. In ruffed lemurs, however, a species in which young are left in a birth nest or parked on branches or in forks of trees while the mother forages, maturing female offspring have been observed to become dominant over their mothers, at least in captivity (Foerg 1982). Since both sexes, apparently, emigrate in brown lemurs (Meyers 1988; pers obs.), dominance of older individuals in this species may be the proximate cause of younger subordinates leaving their natal groups.

Age also determines the primary direction of grooming in brown lemurs, with the older animal in a dyad typically receiving the majority of allogrooming (Chapter 5). Allogrooming was focused on here as a potential correlate of dominance because such a relationship is frequently referred to in the primate literature. Dominance, while correlated with the direction of allogrooming in brown lemurs, cannot be said to determine it, because allogrooming of significant asymmetry was observed in many dyads in which dominance could not be discerned.

Some primatologists have argued that dominance must have predictive value for other behavioural variables if it is to be a meaningful concept, and they have suggested that species specificity regarding which variables can be predicted by dominance undermines the validity of the dominance concept (reviewed in Bernstein 1981). de Waal (1989) disagrees, saying dominance as an agonistic phenomenon exists whether or not it is correlated with other variables. He even suggests resurrecting the notion of dominance drive (1987), which is consistent with his emphasis on proximate as well as ultimate explanations for behavioural phenomena. Rejecting the dominance concept because of species differences and lack of consistent correlations between dominance and other variables has been likened to throwing out the baby with the bathwater (Bernstein 1981).

Although it is not a reflection of dominance relationships, social grooming in E. fulvus may be related to social power in the sense of non-agonistic influence. I have discussed a tendency for males who dominate certain females to nonetheless receive from them less allogrooming than they give to them. This suggests that females, as a more limiting factor for males in terms of reproduction than vice versa (Trivers 1972), are exercising social power over males. On a more complex level, females may in turn benefit in conflicts with other individuals from the agonistic power of those males who affiliate with them for grooming, huddling (not examined here) and reproduction. I observed numerous instances of a male being aggressive toward another with whom he normally had a friendly relationship when a female with whom the first male was sitting threatened the second male. When a male was sitting with a female who was nervous or threatening at the proximity of a second male, the first male would often be aggressive toward the second, even if the males normally had a strong affiliative relationship with each other.

The phenomenon of simultaneous mutual grooming is noteworthy because it comprised about a quarter of social grooming time overall, and because it has not been reported for anthropoid primate species. Mutual grooming is common in other lemur species, e.g., ringtailed and ruffed lemurs (pers. obs.). It is also part of the social repertoire of some other mammalian species as diverse as peccaries (Sowls 1984) and dwarf mongooses (Rasa 1984). Perhaps simultaneous mutual grooming is a retention of an ancestral mammalian behaviour. In more proximate terms, it might also be more easily carried out by mouth-grooming animals (prosimians and members of other mammalian orders) than by hand-grooming ones (anthropoid primates), at least on parts of the body which such animals are incapable of reaching for self-grooming.

As different from other primates as prosimians may be in some respects, and as much as this may have to do with being primitive in the strict sense of retaining and manifesting ancestral characteristics, it is important to stress the relatively recent realization in primatology that prosimians are not unintelligent animals lacking the complexities of social organization and behaviour known to exist among so-called "higher" primates. Within the prosimian suborder, there is as much variation in niche, morphological adaptations, and social organization as among anthropoid primates (Tattersall 1982). There is a corresponding degree of variation in prosimian social behaviour, as exemplified by the unexpected finding in the research presented and discussed here that brown lemurs, unlike lemur species in which social behaviour had previously been studied, do not show the female dominance until recently thought to characterize all lemur species, but instead manifest age-based dominance in which older animals characteristically dominate younger ones regardless of sex. Smuts (1987) recently classified primate species into five major types on the basis of female-, male- or co-dominance in relation to varying patterns of sexual dimorphism or lack thereof. The fact that the nature of dominance in E. fulvus does not conform to any of these categories is further testimony to the argument that the study of primate social behaviour stands to gain much from the study of lemurs.

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APPENDICES

APPENDIX 1 DESCRIPTION AND DISCUSSION OF EULEMUR FULVUS AGONISTIC BEHAVIOUR

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1) AGGRESSIVE SIGNALS

a) THREATS:

Feint: The aggressor makes a sudden move towards the target animal suggesting intent to cuff or nip it (in the later case inferred because the mouth is open) but does not follow through.

Run at: This behaviour was usually observed when females were in estrus. It was typically performed by adult males and directed towards potential rivals. The "run at" is perhaps the closest thing to a formal or ritualized aggressive display in the brown lemur agonistic repertoire. In this behaviour, the aggressor stares at the target animal, stands up and takes a couple of bipedal steps towards him, and then runs (quadrupedally) slowly towards the target, stopping between less than one metre and 10m away; at this point, for several seconds, he stares with raised head at his rival, before turning and walking back to his original position, usually in a huddle with an estrous female. A similar occasionally observed threat, which I coded as a "run at", involves the aggressor, who has been in a huddle with a female, suddenly standing quadrupedally and staring at his rival, and then doing a quick run in a tight circle around or beside the female, before rehuddling with her. A "run at" can include a warble-like vocalization similar to but higher pitched than the "chuffle" (see below).

On 10 of 146 occasions the stop-and-stare part of the "run at" occurred only centimetres from the target animal, and the aggressor then reached out and touched him. Most, if not all, of these touches were light "tags" rather than cuffs.

Stare at: This threat behaviour was observed infrequently outside of the context of "run at". The aggressor stands stiffly with its head held high and gaze fixed on the target animal.

Chuffle: The chuffle is a vocalization given in the context of other aggressive signals or by itself. It consists of a series of unvoiced expulsions of air sounding like rapidly fluttering wingbeats.

Because of its usual aggressive context, I have decided to consider the "chuffle" an aggressive behaviour. However, it may also indicate alarm or at least annoyance. It seems plausible that such ambivalence of motivation could occur in certain circumstances. The chuffle may indicate nervousness rather than confidence. As mentioned above, it may occur in conjunction with a "run at". It is also given by females threatening others away from their infants, and, as a group vocalization, it is given sometimes in response to a potential terrestrial predator or general disturbance in the area.

Cough: A single cough vocalization, given as an aerial predator alarm, is also occasionally given in situations similar to those in which a chuffle is given by a mother with an infant: it may actually be given and then followed by a chuffle when such a female threatens another animal.

Grunt: Active brown lemurs frequently grunt almost continuously as a group cohesion vocalization. Occasionally, in a context that can otherwise be identified as threat or other aggressive behaviour, a single louder grunt will be given.

Lunge: In lunging, an aggressor quickly directs its upper body in the direction of the target animal, with its muzzle outstretched and mouth open. Essentially, the aggressor does not move the location of its entire body, or does so only minimally; i.e, this is an aggressive signal directed towards a target animal in close proximity but not within arm's length. A lunge may be combined with a cuff or nip/nosepoke.

b) PHYSICAL AGGRESSION and CHASES:

Cuff: A cuff of moderate intensity is by far the most common aggressive signal among brown lemurs : 552 out of a total of 1587 agonistic events at the DUPC, and 116 out of 251 at Berenty, were cuffs. The qualification "of moderate intensity" distinguishes such signals from hard and light cuffs: all three involve extension of the arm so as to strike or touch the other animal with the hand. Hard cuffs, which were smacks or genuine blows, were rare - a total of 14 at both study sites combined. Whether or not to consider light cuffs, or tags, as aggressive gestures was problematic. These signals were never responded to with submission, but the direction of tags was generally consistent with the usual direction of aggression in any dyad. I observed 48 such tags at the DUPC and 13 at Berenty.

Nip or nosepoke: This behaviour consists of the aggressor very lightly biting or else just poking with the end of its muzzle an individual with whom it is probably already in physical contact, in a huddle or grooming situation. It can function, as can a cuff in such a situation, as a communication about grooming, e.g., "don't groom so roughly"; or it can express annoyance at the target animal's presence, e.g., a fidgetting animal in a huddle might be nipped. Actual biting of another was observed only three times, and only at the DUPC: there was no apparent injury in any of these cases.

Chase: The aggressor runs after a fleeing animal. Usually I did not observe a preceding signal by the aggressor. It may be that in observing a chase alone I was not seeing the entire agonistic event. This is problematic in that the aggressive signal is essentially defined by the behaviour of the submissive or fleeing animal. For instance, if the subordinate's flight was precipitated by a subtle threat on the part of the aggressor, such as a stare, then this could really be classified as aggression leading to submission leading to further aggression. This would not change the analysis of the results in terms of which events can be used to define dominance (chapter 4), but this discussion is necessary in describing a chase, because obviously an aggressor cannot chase another animal which does not flee from it.

Charge: In this behaviour, the aggressor runs quickly towards the target animal. If the target were to flee, this might result in a chase. However, in a charge the target animal stands its "ground" and the aggressor then physically attacks it, which might institute a scuffle. Charges were rarely seen. Although, like a chase, this aggressive behaviour is defined partly on the basis of the target animal's reaction, a charge is distinct from a "run at" in that the aggressor is moving much faster, and does not stop before reaching the target. This distinction was not easy to make at Berenty, where, unlike at the DUPC, almost all agonism that I observed occurred in trees. At Berenty, there were aggressive rushes that were qualitatively like charges, but I never saw the aggressor in such a case make physical contact with a target animal. If the target animal ran off, I recorded this as chase; if it did not, I coded it as "run at", even though it was somewhat different from a terrestrial "run at" at the DUPC.

Scuffle: This is a description of an interaction rather than just of the behaviour of the original aggressor, the identity of which was not always clear to me. In a scuffle, a feint, cuff, lunge or nip/nosepoke by an original aggressor results in similar retaliation, which in turn stimulates more aggression, and so on. Scuffles rarely lasted longer than about 15 seconds, and aggression was mild, i.e., injury did not result. One or both parties in a scuffle might give squeak-vocalizations, which could result in agonistic aid to the squeaker(s).

Supplantations: Obvious supplantations, or displacement of one animal by another giving aggressive signals, were observed relatively infrequently - only 25 times out of 1587 agonistic events at the DUPC, and 6 out of 251 events at Berenty. The aggressive signal in this case consisted of an approach combined with a cuff or grunt, or both. It could therefore be considered at times to be a threat rather than an act of physical aggression.

Other aggressive signals: Other aggressive signals whose labels should be self-explanatory, and which were rarely observed, are "push", "pinch", and "grab". As for the latter, the grab often follows a cuff. Grabs were sometimes involved in grooming contexts, and done primarily, but not exclusively, by males on the back fur of females, sometimes in the context of intergroup encounters. It is perhaps not overly anthropomorphic to see such behaviour as possessive in motivation. A final aggressive behaviour which, like the above three, was observed only at the DUPC, is "bodycheck": in this behaviour, the aggressor shoulders another animal out of the way, sometimes while giving an open-mouth threat. This behaviour was included with "other combination" in Chapter 3, Table 3.1.

Combinations: A number of the above aggressive signals were commonly given together as well as separately, for example: cuff-lunge; or multiple lunge with aggressive vocalization. Aggressive vocalizations, though generally quiet or subtle, are commonly combined with a number of E. fulvus threats or physical aggression signals. Finally, some signals, such as cuff or nip/nosepoke, were sometimes given in multiples: a interval of three seconds was the criterion for determining whether to record such signals as one or more events.

c) AGONISTIC AID:

There are two ways in which a third party could be involved in an agonistic interaction between two others. It could help one of the parties right from the beginning, particularly if that party were a frequent affiliative partner. On the other hand, a third party could respond to the squeaks of another in an ongoing interaction, and intervene in one of two ways: it might threaten or attack the other individual, or it might simply interpose or place itself between the two scuffling animals. Such intervention, especially by interposition, seems to be most characteristic of the most dominant male in the group.

2) SUBMISSIVE SIGNALS:

Hurry away: This term covers running, jumping, or climbing suddenly away from the aggressor. This may or may not include squealing (below).

Flee: This refers to running away from an aggressor who is pursuit, i.e., it is the complement to "chase".

Squeal: A squeal is usually given in the context of "hurry away", but may also be given by the target animal while stationary. It is given mostly by juveniles. In some of my observations it appeared to stimulate aggressive behaviour on the part of the animal being squealed at, although it is possible that I did not detect the original aggressive signal.

Cringe or flinch: This behaviour, in response to an aggressive signal, was rarely observed, and only at the DUPC. It is similar if not identical to the turning away observed by Andrew (1964) discussed in chapter 3.

3) AVOIDANCE BEHAVIOUR:

Approach-retreat or approach-avoidance interactions (Rowell 1966) have often been discussed as part of agonistic behaviour. Some authors have suggested that inferring agonistic motives in such situations may sometimes be unjustified, as the individuals involved may, for example, be motivated to affiliate or avoid affiliation (e.g., Fedigan 1982; Hand 1986). Others, however, have used this behaviour as their primary or sole measure of dominance relationships (e.g., Cheney and Seyfarth 1990).

I did not collect approach-avoidance data per se at Berenty, partly with the above considerations in mind, and also because the usual arboreality of E. fulvus there made this virtually impossible. There were a few situations in which certain individuals avoided the approach of a commonly aggressive male, but these were equivocal as approach-avoidance behaviour, since the male was also threatening by grunting loudly and/or possibly staring at them.

At the DUPC, there were a number of situations which I coded as approach-avoidance because I could be fairly certain that aggressive signals were not being given, yet the avoider clearly seemed to be moving away from the approach of a potential aggressor (based on previous experience). Of course, one could always argue that the dominant animal in such cases knows it can supplant the other without any aggressive signals, and that this therefore constitutes aggressive behaviour. The issue remains open. I have considered avoidance behaviour to be submissive behaviour occurring otherwise than in response to immediate aggressive behaviour.

4) APPEASEMENT SIGNALS:

Creep-backwards-towards: An individual wanting to join a huddle in which there is at least one individual from whom it has recently been receiving aggression may hunch itself into a ball, with its tail thrown over its shoulder, and slowly back its way towards the huddle. It will likely stop at times, look towards the huddle, and give tongue-flicks (below). This was considered in this analysis to be a submissive signal.

Tongue-flicks: As just mentioned above, tongue-flicks may be given in the direction of a potential aggressor during a "creep-backwards-towards". This behaviour consists of extending the head in the above direction with the muzzle pointing above the horizontal, and rapidly flicking the tongue in and out of the mouth. This may have evolved in relation to grooming behaviour, which is carried out with the tongue and tooth-comb (procumbent lower incisors and canines, the first premolars being caniniform) in characteristic prosimian fashion. Tongue-flicks may thus have evolved as appeasement behaviour by their indicating a willingness to allogroom a potential aggressor. Tongue-flicking is not restricted to the "creep-backwards-towards" context. Individuals of similar rank, huddled in separate groups many metres apart, may tongue-flick to each other, particularly when there has been some social disturbance in the vicinity. Furthermore, individuals may tongue-flick or "kiss" with their muzzles in contact. A tongue-flick by itself was not considered to be a submissive signal.

5) IGNORING THE AGGRESSOR:

The majority of E. fulvus aggressive signals were not responded to with either submissive signals or retaliation. The possible implications of this, ranging from passive aggression - as if the target animal is signalling to the aggressor, 'You don't bother me" - to tacit submission as in "I'm not really afraid but I'd rather not tangle with you," have been mentioned in chapter 3.

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APPENDIX 2: ALLOGROOMING, MUTUAL GROOMING AND AGGRESSION IN ALL DYADS

		ALLOGROOMING				MUTUAL GROOMING	AGGRESSION	
group	sex combination	older recipient	younger recipient (same age if shaded)	minutes for dyad	% rec'd by primary recipient	minutes for dyad	aggression frequency for dyad	primary aggressor
Berenty 1a	females	af51	af52	0	n/a	0	0	n/a
		af51	af53	0	n/a	0	0	n/a
		af51	jf54	3.7	81%	1.4	3	af51 100%
		af52	af53	1	77%	0.2	0	n/a
		af52	af54	4.8	100%	0	1	af52
		af53	af54	0	n/a	0	1	af53
	males	am55	am56	0	n/a	0	1	am55
		am55	jm57	0	n/a	0	8	am55 100%
		am55	am58	0	n/a	0	5	am55 60%
		am55	am59	0	n/a	0	5	am55 80%
		am55	jm60	8.3	100%	0	2	am55 100%
		am56	jm57	2.8	89%	2.5	0	n/a
		am 56	am58	0	n/a	0	0	n/a
		am56	am59	4.2	90%	1.8	0	n/a
		am56	jm60	0	n/a	1.1	0	n/a
		am58	jm57	0.5	100%	0	0	n/a
		am59	jm57	0	n/a	0	0	n/a
		jm57	jm60	1.5	100%	0	1	jm60
		am58	am59	8.6	98%	0.4	1	am58
		am58	jm60	0	n/a	0	0	n/a
		am59	jm60	0.67	100%	0	0	n/a

APPENDIX 2: ALLOGROOMING, MUTUAL GROOMING AND AGGRESSION IN ALL DYADS (cont'd)

		ALLOGROOMING				MUTUAL GROOMING	AGGRESSION	
group	sex combination	older recipient (same age if shaded)	younger recipient	minutes for dyad	% rec'd by primary recipient	minutes for dyad	aggression frequency for dyad	primary aggressor
Berenty 1a (cont'd)	heterosexual	af51	am55	0	n/a	0	0	n/a
		af51	am56	1.5	54%	2.8	0	n/a
		af51	jm57	0	n/a	0	0	n/a
		af51	am58	0	n/a	0	0	n/a
		af51	am59	0	n/a	0	0	n/a
		af51	jm60	0	n/a	0	0	n/a
		am55	af52	0.2	100%	0	5	am55 100%
		af52	am56	0	n/a	0	1	af02
		af52	jm57	0.9	100%	0	0	n/a
		am58	af52	0	n/a	0	0	n/a
		af52	am59	0	n/a	0	0	n/a
		af52	jm60	0	n/a	0	0	n/a
		am55	af53	0	n/a	0	4	am55 100%
		af53	am56	0	n/a	0	0	n/a
		af53	jm57	0	n/a	0	0	n/a
		am58	af53	0	n/a	0	0	n/a
		am59	af53	15	100%	0	0	n/a
		af53	jm60	0	n/a	0	0	n/a
		am55	jf54	0	n/a	0	17	am55 100%
		am56	jf54	0	n/a	0	1	am56
		jf54	jm57	0	n/a	0	1	jm57
		am58	jf54	0	n/a	0	1	am58
		am59	jf54	0	n/a	0	0	n/a
		jf54	jm60	0	n/a	0	2	jm60 100%

APPENDIX 2: ALLOGROOMING, MUTUAL GROOMING AND AGGRESSION IN ALL DYADS (cont'd)

		ALLOGROOMING				MUTUAL GROOMING	AGGRESSION	
group	sex combination	older recipient (same age if shaded)	younger recipient	minutes for dyad	% rec'd by primary recipient	minutes for dyad	aggression frequency for dyad	primary aggressor
Berenty 1b	females	af51	af52	0	n/a	0	0	n/a
		af51	af53	0.5	100%	2	3	af51 100%
		af51	jf54	0	n/a	0	1	af51
		af52	af53	0	n/a	0	1	af52
		af52	af54	5.4	95%	5.2	1	af52
		af53	af54	2.1	100%	0	9	af53 100%
	males	am55	am56	3.3	100%	0	18	am55 100%
		am55	jm57	3.1	100%	3	22	am55 100%
		am56	jm57	5.6	67%	3.1	1	[illegible]
	heterosexual	af51	am55	1.1	63%	0	5	am55 80%
		af51	am56	8	95%	0.5	1	am55
		af51	am57	8.9	93%	6.4	8	af51 100%
		am55	af52	0.2	100%	3.8	1	am55
		af52	am56	0.5	83%	6.6	1	af52
		af52	jm57	0.8	100%	4.1	2	af52 100%
		am55	af53	7	90%	2	13	am55 100%
		af53	am56	1.1	100%	0	4	each 50%
		af53	jm57	5.2	100%	3.6	3	af53 100%
		am55	jf54	5.3	100%	5.3	29	am55 100%
		am56	jf54	6.8	98%	1.4	0	n/a
		jf54	jm57	1.5	100%	0.3	1	jf54

APPENDIX 2: ALLOGROOMING, MUTUAL GROOMING AND AGGRESSION IN ALL DYADS (cont'd)

		ALLOGROOMING				MUTUAL GROOMING	AGGRESSION	
group	sex combination	older recipient (same age if shaded)	younger recipient	minutes for dyad	% rec'd by primary recipient	minutes for dyad	aggression frequency for dyad	primary aggressor
Berenty 2	females	af71	af72	1.5	60%	8.9	0	n/a
		af71	jf73	2.3	100%	5.8	2	af71 100%
		af71	jf73	5.2	100%	1.1	1	af72
	males	am58	am59	4.9	92%	0	0	n/a
	heterosexual	af71	am58	0	n/a	0	2	am58
		af71	am59	1.7	100%	0	2	each 50%
		af72	am58	1.2	54%	0	2	each 50%
		af72	am59	3.2	100%	4.2	3	am59 100%
		am58	jf73	4.5	83%	1.7	12	am58 100%
		am59	jf73	1.5	100%	0	16	am59 88%

APPENDIX 2: ALLOGROOMING, MUTUAL GROOMING AND AGGRESSION IN ALL DYADS (cont'd)

		ALLOGROOMING				MUTUAL GROOMING	AGGRESSION	
group	sex combination	older recipient (same age if shaded)	younger recipient	minutes for dyad	% rec'd by primary recipient	minutes for dyad	aggression frequency for dyad	primary aggressor
DUPC-CI	females	af01	af02	4.4	76%	3.6	15	af02 67%
	males	am03	am04	0	n/a	0	25	am03 68%
		am03	am05	13.6	94%	9.5	14	am03 100%
		am03	am06	8.4	89%	9.6	10	am03 90%
		am03	jm07	13	59%	5.2	10	am03 100%
		am04	am05	2.3	90%	1.7	0	n/a
		am04	am06	1.9	82%	4.9	5	am04 80%
		am04	jm07	1.2	95%	2.1	8	am04 100%
		am05	am06	6.3	65%	7.9	3	am05 67%
		am05	jm07	2.7	94%	2.6	25	am05 96%
		am06	jm07	4.9	70%	3.5	5	am06 100%
	heterosexual	af01	am03	8.3	99%	3.9	3	am03 100%
		af01	am04	0.8	100%	0.2	0	n/a
		af01	am05	4.3	84%	0.9	4	af01 100%
		af01	am06	0.4	100%	1.5	5	af01 100%
		af01	jm07	3.5	100%	3	3	af01 100%
		am03	af02	8.4	64%	1.2	9	am03 78%
		am04	af02	1.1	100%	3	5	am04 100%
		am05	af02	9.7	66%	4.3	18	am05 56%
		am06	af02	6.1	98%	5.5	12	am06 58%
		af02	jm07	6.9	73%	5.5	54	af02 76%

APPENDIX 2: ALLOGROOMING, MUTUAL GROOMING AND AGGRESSION IN ALL DYADS (cont'd)

		ALLOGROOMING				MUTUAL GROOMING	AGGRESSION	
group	sex combination	older recipient (same age if shaded)	younger recipient	minutes for dyad	% rec'd by primary recipient	minutes for dyad	aggression frequency for dyad	primary aggressor
DUPC-HE	females	af20	af21	1.2	99%	0	43	af20 81%
		af20	af22	5.3	100%	5.3	1	af22
		af20	jf23	23	80%	17.6	7	af20 100%
		af20	jf24	3.4	83%	0.4	18	af20 100%
		af21	af22	0.8	64%	0	18	af22 56%
		af21	jf23	1.4	100%	3	44	af21 98%
		af21	jf24	0.8	100%	0	52	af21 98%
		af22	jf23	2	56%	16.8	10	af22 80%
		af22	jf24	20.5	73%	4.3	10	af22 100%
		jf23	jf24	0.75	56%	10.3	12	jf23 92%
	males	am25	am26	3.8	66%	1.2	6	am26 83%
		am25	am27	5.2	100%	17.5	66	am27 98%
		am25	am28	1.1	100%	1.6	40	am25 55%
		am25	am29	0.2	100%	5.6	7	am25 100%
		am26	am27	1.5	100%	0	10	am27 90%
		am26	am28	9.8	72%	7.2	17	am26 100%
		am26	am29	6.5	89%	0.3	6	am26 100%
		am27	am28	0.25	100%	1.8	36	am27 100%
		am27	am29	2.7	100%	1.6	2	am27 100%
		am28	am29	0	n/a	0	8	each 50%

APPENDIX 2: ALLOGROOMING, MUTUAL GROOMING AND AGGRESSION IN ALL DYADS (cont'd)

		ALLOGROOMING				MUTUAL GROOMING	AGGRESSION	
group	sex combination	older recipient (same age if shaded)	younger recipient	minutes for dyad	% rec'd by primary recipient	minutes for dyad	aggression frequency for dyad	primary aggressor
DUPC-HE (cont'd)	heterosexual	af20	am25	1.1	50% each	3.5	18	af20 83%
		af20	am26	3.6	100%	0	4	af20 75%
		af20	am27	4.2	83%	0.4	16	am27 75%
		af20	am28	1.2	100%	0	18	af20 89%
		af20	am29	0.3	100%	0	41	af20 85%
		am25	af21	22.7	98%	13.7	15	af21 80%
		am26	af21	0	n/a	0	6	each 50%
		am27	af21	4.8	58%	3.7	23	am27 74%
		af21	am28	17.5	100%	0	28	af21 75%
		af21	am29	3.3	58%	0.2	9	af21 89%
		am25	af22	0	n/a	0	10	am25 80%
		am26	af22	8.2	71%	4.8	4	am26 100%
		am27	af22	16.1	97%	7.2	27	am27 100%
		af22	am28	6.1	89%	4.1	11	am28 64%
		am29	af22	0	n/a	0.3	36	am29 78%
		am25	jf23	1.8	97%	0	8	am25 100%
		am26	jf23	0	n/a	0	10	am26 100%
		am27	jf23	19.3	85%	9.4	9	am27 100%
		am28	jf23	1.5	58%	2.9	9	am28 100%
		am29	jf23	0	n/a	0	24	am29 96%
		am25	jf24	0	n/a	0	12	am25 100%
		am26	jf24	6.1	60%	0	17	am26 100%
		am27	jf24	3.5	65%	1.6	26	am27 100%
		am28	jf24	2.9	85%	0.2	20	am28 95%
		am29	jf24	0	n/a	0	27	am29 81%

APPENDIX 2: ALLOGROOMING, MUTUAL GROOMING AND AGGRESSION IN ALL DYADS (cont'd)

		ALLOGROOMING				MUTUAL GROOMING	AGGRESSION	
group	sex combination	older recipient (same age if shaded)	younger recipient	minutes for dyad	% rec'd by primary recipient	minutes for dyad	aggression frequency for dyad	primary aggressor
DUPC-RO	females	af40	af41	18.6	81%	4.1	3	af40 67%
	males	am42	am43	11.1	91%	15.4	21	am42 100%
		am42	am44	4.2	100%	0	39	am42 72%
		am43	am44	5.1	50%	12.8	45	am43 51%
	heterosexual	af40	am42	12.1	66%	31.6	2	each 50%
		af40	am43	15.2	82%	17	19	af40 74%
		af40	am44	1.9	94%	1.6	50	af40 60%
		am42	af41	13.9	63%	7.6	3	am42 67%
		af41	am43	11.5	71%	7.8	15	af41 73%
		af41	am44	12.7	75%	6.6	35	af41 71%