The Development of Adult Sex-typed Social Behavior in *Lemur catta*

by

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ABSTRACT

Unanswered questions about the evolution of human gender abound and are salient across the anthropological disciplines and beyond. Did adult sex-typed behavioral tendencies actually evolve? If so, when? For what purpose? The best way to gain insight into the evolution of human gender is to understand the evolution and development of sex-typed behavior in comparative primate taxa. Captive research indicates that there are many proximate factors likely to shape the development of sex-typed behavior in non-human primates—prenatal and postnatal endocrinological experience, social experience, ecological factors, and their interactions. However, it is largely unknown how sex-typed behavior proceeds and is shaped by those factors in evolutionarily salient environments.

This study investigated one—whether extrinsic sexually differentiated social interactions are likely influential in the development of adult sex-typed behavior in wild-living *Lemur catta*. Little is known about sex-typed development in this species or in strepsirrhines in general. This research therefore addresses an important phylogenetic gap in our understanding of primate sex-typed development. Behavioral observations were carried out on mixed cross-sectional sample of adult females (n=10), adult males (n=8), yearling females (n=4), yearling males (n=4), and newborn females (n=16) and males (n=14) at Beza Mahafaly Special Reserve in southwest Madagascar from September 2008 to August 2009.

Twenty-three sex-typed behaviors were identified in adults using linear mixed effects models and models of group response profiles through time. Of those, only eight had a pre-pubertal developmental component. Infants did not exhibit any sex differences in behavior, but juveniles (prepubertal, weaned individuals) resembled

adults in their (relatively few) patterns of expression of sex-typed behavior. Most adult sex-typed behaviors in this species apparently develop at or after puberty and may be under gonadal hormone control. Those that develop before puberty do not likely depend on extrinsic sexually differentiation social interactions for their development, because there is no clear evidence that infants and juvenile male and females are not treated differently by others according to sex. If sexually differentiated social interactions are important for sex-typed behavioral development in subadult *Lemur catta*, they are likely intrinsically (rather than extrinsically) driven.

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CHAPTER 1: INTRODUCTION

Gender is a term that was introduced into the academic literature in the mid-1950s by the prominent sexologist John Money as a way to distinguish the behavioral standards marking membership in each biological sex from biological sex itself [Haig 2004]. Eventually, the term was embraced by second wave feminist academics of the 1970s [Haig 2004; Stockett and Geller 2006], who codified the binary opposition of biological sex versus culturally constructed gender, and who largely dismissed the importance of biological sex as a motivator of sexually differentiated behavior [Scott 1986; Stockett and Geller 2006]. Since then, third-wave feminist scholars have abandoned the binary opposition of sex and gender—shifting focus to the creation of identity and the ways in which sex, gender, and the entire male/female binary (among other things) are socially constructed through "discourse, representation, and repetitive performance" [p. 8, Fausto-Sterling 1993; Nicholson 1994; Stockett and Geller 2006]. Meanwhile, evolutionary psychologists have taken up the opposite position, treating sexually differentiated human behavior as an adaptive, fundamentally binary expression of our universal human nature [e.g., Cosmides et al. 1992; Tooby and Cosmides 1990a; Wilson 1994].

The literature is rife with vehement and sweeping claims about both the proximate and ultimate causes of human gender, often buttressed with untested assumptions. Some authors insist that socialization—learning processes in which species-typical behaviors are acquired through direct interaction [Fragaszy and Perry 2003]—is almost entirely responsible for the emergence of human sex differentiated behavior [e.g., Bleier 1984; Fausto-Sterling 1992]. Implicit in this stance is the assumption that socialization cannot produce adaptation, which is used as proofpositive that human sex-typed behavior is non-adaptive. Here, social behavior is extricated from biology and considered separate from it. Of course, this assumption is unfounded; it is quite plausible that socialization processes themselves have been targets of selection because they produce adaptive behaviors. On the other extreme, some researchers accept as a tenet that sexually differentiated behavior in humans is adaptive (even children's sex differences in object play [Gredlein and Bjorklund 2005]), and set about to conjure the selective scenarios and proximate mechanisms that might explain observed modern patterns of behavior [Bussey and Bandura 1999; Eals and Silverman 1994; Eswaran and Kotwal 2004]. But to date, the evolutionary history of most human and non-human primate sex-typed behaviors (and the processes that drive their development) is completely unknown.

Hypotheses of behavioral adaptation are challenging to test, but are best explored using the comparative method [Harvey and Pagel 1991]. The comparative method can reveal elements of adult sex-typed behavior that vary little across many species and that may have experienced stabilizing selection; and it can uncover patterns of sex-typed behavioral variation that co-vary in reliable ways with other factors, such as resource distribution, social system, or specific patterns of social interaction. Comparative study of sex-roles across the primate order, therefore, is the clearest way to gain insight into questions regarding the evolution of, and adaptation in, primate and human sex-typical behavior [Thierry et al. 2008].

There is good reason to consider human sex-typed social behavior in its broader evolutionary context because the rich historical tradition of research on these issues in non-humans may yield important insights for humans. Sociobiological and socioecological theories assert that in sexually reproducing species, selection may act to maximize the fitness of males and females via different behavioral strategies [Emlen and Oring 1977], and much of behavioral ecology and sociobiology focuses on understanding how reproductively mature individuals living in a particular environment, facing a particular set of constraints, are expected to allocate their time and energy to maximize their lifetime reproductive success. Indeed, adult sex-differentiated behaviors are plentiful and often complex in many taxa, cross-cutting a variety of important aspects of life such as: foraging [Agostini and Visalberghi 2005a], intra-group spacing and association [Borries 1993; Koenig 2000; Pepper et al. 1999; van Schaik 1989], and mating tactics [Hrdy et al. 1995; Koenig and Borries 2001; Utami et al. 2002; van Noordwijk and van Schaik 2001; van Schaik et al. 1999].

Infants of mammalian taxa, though, are not born into the world expertly doing all of the things that adults do. The number and complexity of sex-differentiated adult behaviors not present at birth among gregarious mammals begs the question: How do these behaviors develop? That is, what are the proximate causes underlying the sex-differential development of sex-typed adult behaviors? In primates in particular, neonate levels of physical activity and social interaction are very low compared to adults [Bentley-Condit 2003]. Therefore, many of the behaviors we expect to conform to a given set of theoretical principles must develop during the process of maturation from neonate to adult. And just as adult behaviors not present at birth must develop during maturation, the development of sex-differentiated adult behaviors not present at birth must proceed, during maturation, in sex-differentiated ways.

Research on these questions in non-human primates has been ongoing for decades, forming a vast "nature vs. nurture" literature, and overwhelming evidence indicates that sex-typed development (indeed, all development) results from the interactions thereof [Kelly et al. 1999; Wallen 1996]. Given that, a more refined question emerges: How do *particular* factors interact to shape the development of particular behaviors in particular taxa?

Understanding the proximate causal factors that drive and shape the ontogeny of adult behavioral patterns is not only interesting in its own right, but can also help to clarify how and why those adult behavioral patterns might have evolved by yielding insight into the factors that influence or constrain them [Beaupre et al. 1998; Duvall and Beaupre 1998]. If selection indeed acts to maximize the fitness of males and females via different behavioral strategies [Emlen and Oring 1977], then some elements of sex-typed behavior will be adaptive. But *which* elements of sex-typed behavior are adaptive and which are not? Understanding the proximate processes that shape the development of adult sex-typical behaviors from a comparative perspective can shed light on this question.

Non-human primates are the most useful model taxon for investigating the proximate and ultimate causes of human sex-typed behavioral development for a number of reasons—like humans, they are behaviorally complex as adults; like humans, they are behaviorally diverse as a taxon; they are relatively easy to observe compared to other behaviorally complex and diverse taxa; they have extraordinarily protracted developmental periods; and they are our closest relatives, most likely to share with us developmental processes due both to homology and convergence. The complexity of and wide range of variation in adult behavior across the primate order is probably underwritten by equally complex and varied interactive developmental processes. Therefore, broad investigation of developmental processes across primates maximizes our potential to identify meaningful regularity in the interactions of developmental processes and their outcomes. Identifying these patterns allows for the construction of logically supported inferences about their developmental causation. Compared to many other vertebrates, the environmental factors—such as resource availability and social interactions—likely to shape the development of behavioral diversity are relatively easy for humans to observe in primates, as none fly, and most do not hide their young away from sight in dens. Because of their protracted developmental periods, researchers may be more readily able to observe, measure, and tease apart the contributions of different proximate mechanisms to behavioral development in primates than in taxa that mature more quickly. And because they are our closest relatives, knowledge about developmental process derived from non-human primates is more likely to be directly applicable to humans than similar data from non-primate taxa.

Studying the proximate mechanisms of sex-typed behavioral development in primates will contribute importantly to understanding the evolution of sex-typed behavior in humans—a topic that is both highly contentious and analytically intractable when studied in isolation. It is logistically challenging (but not impossible) to amass data from numbers of carefully observed human groups sufficient to capture the range of variation humans exhibit in their adult sex-typed behavior. However, it is infeasible to carefully observe individuals from these groups during all of their waking hours over their entire developmental periods. For this reason, most work on the evolution of human gender roles either remains largely theoretical and unencumbered by data or consists of *post hoc* explanations of the *status quo*.

The objective of this study is to investigate whether and how socialization is involved in the production of adult sex-typed behavior in a non-human primate taxon, *Lemur catta*. In doing so, this study articulates with other developmental research and adds to our understanding of how one proximate cause (socialization) shapes the development of sex-typed behavior in primates. It also contributes to the comparative primate developmental knowledge base needed to eventually answer questions about adaptation in and evolution of human gendered behavior in general, and to begin to clarify whether the process of sex-typed socialization, itself, may have been a target of selection during primate evolutionary history.

CHAPTER 2: BACKGROUND

EVOLUTION OF HUMAN GENDER

The topic of human gender evolution is hotly debated within and across academic disciplines of anthropology, sociology, and psychology. The degree to which human gender differences represent evolutionary adaptation is a point of great contention [Wood and Eagly 2002; Worthman 1995]. Perspectives on this topic break down into three major scholarly camps—social constructivism, evolutionary psychology, and proponents of the biosocial model [reviewed in Wood and Eagly 2002].

Social constructionists assume that there are no universal laws underlying human behavior and begin inquiry into the mechanisms underlying human gender development with the assumption that cultural relativism is a necessary and sufficient explanation of human gendered behavior [Wood and Eagly 2002]. From this perspective, socialization is entirely responsible for the development of gendered behavior of the individual, and human gender differences do not represent long-term, evolutionary adaptations that characterize *Homo sapiens* as a species. Children's gendered behavior is either chosen for them or chosen by them, but is not an expression of innate, sexually differentiated qualities. Implicit in this position is the idea that the process of socialization, itself, cannot be a target of natural selection, and that behavior and biology are neatly separable.

On the other end of the spectrum, some evolutionary psychologists explicitly assume that all or very nearly all adult sexually differentiated human behavior is the product of natural or sexual selection during the Pleistocene in particular [Cosmides et al. 1992; Tooby and Cosmides 1990b], and that the underlying psychological and physiological profiles that motivate behavior result from sexual selection for those behaviors [Budaev 1999; Eals and Silverman 1994; Gangestad and Simpson 2000; Geary 1995; Joseph 2000; Luxen 2007; MacDonald 1995]. From this perspective, socialization is not responsible for the existence of sex differences, and is only important in determining their specific exhibition within an individual—perhaps only acting as a railroad switch operator sending individuals down a few, sex-typed psychological and behavioral paths [Tooby and Cosmides 1990a; Wilson 1994]. The phenomenon of human gender difference itself represents a long-term, evolutionary adaptation that characterizes (and has characterized) *Homo sapiens* as a species. This position views behavioral sex differences as the ineluctable products of a fundamentally sexually dimorphic human nature [Byrd-Craven and Geary 2007; Geary 1995; Tooby and Cosmides 1990a] and views children's gendered behavior as a necessary, adaptive, developmental precursor to "the" adult sex roles that have characterized *Homo sapiens* throughout its evolution [Byrd-Craven and Geary 2007; Gredlein and Bjorklund 2005; MacDonald 1995]. It has been used by some to explain the persistence of social phenomena such as inequality in the modern workplace [Browne 2006].

The biosocial model of human sex differences has been more recently proposed against the backdrop of the historical dichotomy between social constructivism and evolutionary psychology and seems to be an attempt to minimize the weaknesses and maximize the strengths of each of the other approaches. The biosocial model makes a somewhat more complicated, multi-step assumption about the evolution of human gender than either of its predecessors. It assumes that social structures placing males and females in different social roles within groups necessarily arise in order to best take advantage (at the group level) of evolved differences in male and female body size and reproductive biology, and that once those social roles are established, sex differences in endocrinology secondarily arise that create sex differences in psychology and canalize the sex roles [Wood and Eagly 2002]. Whether these secondary biological sex differences emerge from the practice of sexually differentiated behavior or are selected for in order to ensure the maintenance of sexually differentiated behavior (or both) is unclear. From this perspective, gendered behavioral development of the individual is socialized but may also be mediated by underlying, evolved psychological or hormonal mechanisms; human gender differences, on the whole, represent the results of an evolutionary feedback loop between individuals' biology and their social environments that was initiated with social responses only to biological differences in body size and strength and sexually differentiated reproductive behavior (but not to anything else) [Wood and Eagly 2002]. Children's gendered behavior, like that of adults, is driven by a complex amalgam of social and biological factors. Some elements of gendered behavior are evolutionary adaptations, and some are simply short-term, socialized responses to particular social environments.

All of these approaches share a common flaw—each makes a foundational assumption about the origination of gendered behavior that it never seeks to test. Social constructivism assumes that individual biology and social behavior are completely independent, that biology does not influence social behavior; and that social modulation of behavioral development cannot be a target of selection. It seeks to understand only the ways in which gendered behavior is socially mediated and to contextualize available data largely from this singular perspective. Evolutionary psychology assumes that most gendered behavior is substantially mediated by individual biology; it seeks to amass data that support this position and to contextualize available data on sexually differentiated development largely from this singular perspective. The biosocial model acknowledges the demonstrated importance of individual biology, socialization, and the interaction between them in the development of gendered behavior, but assumes that sexual dimorphism in body size and reproductive function controls the formation of social structure, and that biological sex differences that are not directly related to dimorphism or reproduction evolved secondarily, in direct response to social constraints.

Counter to the foundational assumption of social constructivism, a number of lines of evidence suggest that somatically motivated behavioral sex differences in humans do exist. First, non-human experimental models provide clear evidence of a few somatically based behavioral sex differences that might also exist in humans. In rodents in particular, the linkages between sexually differentiated endocrinology, neural structure and function, and mating behaviors have been explicated [Kelly et al. 1999]. While I do not assert that hormones control human behavior entirely, work on these mammalian models suggests that sex differences in physiology and anatomy may be important for shaping sexually differentiated human behavior. Second, clinical research suggests that some human behavioral sex differences may be motivated by somatic variation between the sexes. Girls with classical congenital adrenal hyperplasia, which results in elevated prenatal levels of testosterone, exhibit male-typical toy preferences and play styles compared to their unaffected sisters [Pasterski et al. 2005]. Third, some behavioral sex differences in adult humans are echoed in non-human species, suggesting that some behavioral sex differences may always have characterized the human lineage. Male superiority in spatial skills has been documented in both humans and rats [Kelly et al. 1999], and earlier development of vocal proficiency has been documented for both human [Bornstein et al. 2000; McGuiness 1981; Roulstone et al. 2002] and non-human primate females [Gouzoules and Gouzoules 1989]. And fourth, both experimental and correlational studies in humans suggest that naturally occurring endocrinological variation may underlie temperamental and behavioral variation. Naturally occurring individual morning testosterone levels were positively correlated with the daily profit margins of 17 British male stock traders [Coates and Herbert 2008]. Experimentally administered doses of testosterone decrease "trusting behaviors" in women who are inclined to be very trusting [Bos et al. 2010], and increase aggressive behavior in men [Kouri et al. 1995].

Counter to the foundational assumption of evolutionary psychology, a number of lines of evidence suggest that socialization is an important driver of behavioral sex differences in humans. First, the comparative research conclusively demonstrates that sexually differentiated social experiences are critical drivers of some elements of behavioral sex differentiation in non-human animals. In rodents, mothers anogenitally groom male pups more than female pups. This stimulation is important for the development of elimination in both sexes and for the eventual development of male sexual behavior. But maternal anogenital grooming also dampens hypothalamic-pituitary-adrenal reactions to stress in both sexes, and the sex difference in maternal anogenital grooming results in the sexually differentiated stress responses of male and female offspring [Kelly et al. 1999]. Second, some sex differences in treatment of children by others have been documented, but this varies across populations. In studies of American and Dutch pre-school teachers, American teachers positively reinforced "female-typical" play activities for both girls and boys, while Dutch teachers positively reinforced "sex-typical" play behaviors [Fagot 1977b]; in a study of American pre-school children, boys were criticized by peers for cross-gender play while girls were not [Fagot 1977a]; and a study of American parent-child interactions found that parents treat boys and girls differently even when they are not conscious of gender stereotyping [Fagot 1978]. Sex-differential treatment of children by others provides one opportunity for the social acquisition of gendered behavior. Third, children respond to at least some of their perceptions about gender expectations. Sex differences in children's toy preferences are greater for children who report a caretaker, sibling, or peer who thinks poorly of cross-gender play than for children who believe that their caretakers, siblings, and peers have a neutral position on cross-gender play [Raag 1999]. Fourth, some children adjust their gendered behavior in the presence of an observer. A study of Israeli kindergarteners found that children with less gender-stereotyped toy preferences made more strongly gender-stereotyped toy choices in the presence of an adult observer than when alone [Wilansky-Traynor and Lobel 2008].

The foundational assumption of the biosocial model of sex difference is less straightforward but problematic on several counts. First, there is no theoretically sound reason to assume that the selective pressures that produced or maintained body size dimorphism in humans did not simultaneously act on other elements of the human body, such as the brain or the hypothalamic-pituitary-adrenal axis, in ways that would produce sexually differentiated behavior. Why natural selection would be initially constrained to act on specific aspects of the soma but not others is neither explained by the biosocial model nor a necessary expectation of evolutionary theory. Indeed, there are multiple ways in which the heteromorphic sex chromosomes of sexually reproducing species produce sex differences in brain and other organ system tissues [Arnold 2004]. This argues against the idea that selection would have first acted *only* on body size and reproductive biology but not on other systems. Perhaps more importantly, it is unclear whether the assumptions of the biosocial model are even falsifiable. First, it is unclear whether its adherents suppose that the proposed relationships among body size dimorphism and mammalian sex differences in reproduction, the resultant emergence of particular social systems, and the secondary evolution of other behavioral sex differences hold across all taxa or whether they apply only to the origins of human behavioral sex differences. Hence, it is unclear where one should start to think about how to falsify the assumption. Second, it is not immediately apparent which particular sex dimorphic behaviors can be sorted into the category of "having to do with dimorphism and/or reproduction" and which belong in the "all else" bin, making it difficult to falsify the assumption. Third, even if the particular behaviors belonging in each category are clearly identified, if these proposed relationships are supposed to apply only to the origins of human behavioral sex differences, it may be impossible to falsify the assumption that behaviors related to dimorphism and reproduction evolved first, and that all others evolved later (depending on the amount of variation in trait covariation across modern human populations and the temporal resolution possible to achieve with intraspecific comparative methods).

A better approach to addressing whether human gendered behavior represents evolutionary adaptation, whether it emerges from short-term social pressures, or some combination of the two, is to think of these questions as hypotheses to be tested rather than as position statements to be buttressed—an approach supported by authors who have called for "the application of stricter scientific standards to arguments about the evolution of sex differentiated human behaviors" [p. 233, Fausto-Sterling 1997].

ADVANTAGES OF COMPARATIVE RESEARCH

Given that males and females across the animal kingdom are subject to different selective pressures [Emlen and Oring 1977; Nunn et al. 2009; Trivers 1972], there is no logical basis for many of the aforementioned assumptions. Some individual sex-typed behaviors may have emerged prior to others in evolutionary history, some may be physiologically mediated and/or socially mediated to varying degrees, and some may be adaptive, while others may not be physiologically motivated, socially motivated, or adaptive. To what degree particular human sex-typed behaviors are physiologically and/or socially mediated is an empirical question that can be appropriately investigated using the types of correlative and experimental studies of humans that are undertaken by both social constructivists and evolutionary psychologists and that can be further elucidated by comparative study in several ways. To what degree particular human sex-typed behaviors are adaptations is an empirical question that can be addressed by comparative study.

First, the extent to which experimental manipulation of humans is feasible is extremely limited; as such, experimental studies in a non-human model system may simply be required to answer some questions about the proximate drivers of sex-typed behavioral development. Fortunately, non-human primates have been shown to make good models for understanding some selectively important phenomena in humans already—such as the nature and workings of the infant attachment system [Bowlby 1969] and the influence of hormones on parental behavior [Maestripieri 1999]—and, due to their close phylogenetic relationships to humans, they are likely to share many other homologous and analogous behavioral and psychological traits (and trait functions) [Maestripieri 2005b].

Second, since non-human primates are good model systems for understanding human behavior, naturalistic comparative studies of non-human primate sex-typed behavior can also contribute substantially to a better understanding of the proximate drivers of human gendered behavior. An understanding of intraspecific variation in non-human primate sex-typed behavior and its covariates—e.g., ecology, social organization, social interaction—will pinpoint probable proximate drivers of sex-typed behavior that may be either overlooked by the narrow focus of experimental work or that may not be amenable to study in experimental settings. Comparisons of sex-typed behavior across captive and wild settings may also be very instructive for identifying its proximate causes. Sex-typed behaviors that are invariant across captive and wild settings, for example, are apparently not driven by ecological variation, which is at its extreme in such comparisons. Despite the ready availability of captive populations of many species of non-human primates, this type of comparison has only rarely been leveraged for understanding the proximate causes of naturally occurring intraspecific variation [but see Altmann and Alberts 1987; Altmann and Alberts 2005; Altmann and Altmann 1981; Borries et al. 2011; Johnson 2003; Panger 1998; Rangel-Negrín et al. 2009; Yamamoto et al. 2008].

Third and most importantly, questions regarding the evolution of sex-typed behavior require a comparative framework to answer [Nunn 2011]. Knowing the evolutionary timing of particular human sex-typed behaviors—an integral part of arguments from both evolutionary psychology and the biosocial model—requires pinpointing when in primate evolution they first appeared. Whether particular sex-typed behaviors are apomorphic or plesiomorphic for humans cannot be assumed *a priori*. Unfortunately, all three of the dominant perspectives on the evolution of human gender make *a priori* assumptions about the timing of the appearance of gendered behavior. The social constructivist perspective assumes that all gendered behavior is very recent in origin—as recent as the culture in which it is situated. The dominant narrative of evolutionary psychology about the Pleistocene as *the* human environment of evolutionary adaptedness (EEA) [Tooby and Cosmides], the selective pressures of a sexual division of labor on the human mind [Joseph 2000], and the behavioral dimorphism that results seems to assume that human sex-typed behaviors are apomorphic. But nonhuman data are used as support for particular evolutionary arguments (such as for the adaptive function of spatial superiority in human males and verbal superiority in females [Joseph 2000]), simultaneously implying that at least some sexually dimorphic behaviors are plesiomorphic for the hominin clade. The biosocial model, like the social constructivist perspective, seems to assume that human behavioral sex differences are apomorphic, although this assumption does not follow logically from the model itself, given that the presumed evolutionary basis of human behavioral sex differences are rooted in sexual dimorphism in body size and the sex-specific constraints of mammalian reproductive biology, which are not unique to humans [sexual dimorphism, e.g., Leigh 1992].

Being able to make data-based inferences about the evolutionary origins of particular human sex-typed behaviors would go a long way toward critically assessing the assumptions and suppositions of all three dominant perspectives on human gender evolution as well as toward understanding the adaptive nature (or not) of human gender. If some human sex-typed behaviors are shared with the other primates, cultural relativism alone is insufficient to explain their emergence and maintenance (although it would not preclude the potential importance of socialization as a driver). Plesiomorphic human sex-typed behaviors cannot be argued to derive from selective pressures associated with a Pleistocene division of labor. And only interspecific comparison can document the temporal relationships among the evolution of body size dimorphism, social structure, and behavioral sex differences.

Identifying the evolutionary origins of particular sex-typed behaviors through interspecific comparative work will tell us which elements of human gendered behavior we share with other taxa and which are uniquely human. This knowledge, while it does not identify adaptation *per se*, is critical to the formation of informed hypotheses of behavioral adaptation. For example, sex-typed behaviors with deep evolutionary histories that have been conserved across many lineages are likely to be adaptive, as they have apparently been maintained over long periods of time by stabilizing selection. In contrast, sex-typed behaviors unique to modern humans are much more likely to be the result of ephemeral, non-adaptive social pressures.

Identifying Adaptation

An adaptation can be defined as a derived trait that arose at a particular time in a lineage as a result of selection for a particular derived function [Coddington 1994]. Comparative knowledge of sex-typed primate behavior is prerequisite to the endeavor of inferring sex-typed behavioral adaptation, because testing hypotheses of adaptation requires knowledge of the historical origination or originations, respectively, of a hypothesized adaption and its purported function. This is because adaptational hypotheses must link observed patterns of trait variation to observed patterns of variation in specific purported causes [Coddington 1994]. Proposed causes of particular trait originations must precede or be temporally coincident with them [Coddington 1994; Kay and Cartmill 1977], regardless of whether one is using the homology or homoplasy approach to identifying adaptation [Coddington 1994].

Most evolutionary biologists prefer the homoplasy approach to inferring adaptation [e.g., Kay and Cartmill 1977; Pagel 1994], because it allows for a statistical assessment of the degree of covariance between or among traits that are hypothesized to be causally linked [Nunn 2011]. The ability to map trait originations onto a well-resolved phylogeny is crucial to the homoplasy approach to inferring adaptation, because it allows for the identification of independent and non-independent occurrences of trait/function covariation and thereby allows for inferences about the historical evolutionary processes that may or cannot have produced current patterns of trait diversity [Pagel 1997]. For the homoplasy approach, only independent instances of trait/hypothesized function correlation are of interest—instances of trait/function correlation due to shared ancestry are not considered. Selection will necessarily result in significant correlation between the adaptive trait and the function for which it is adapted, such that multiple, independent instances of trait/function covariation across a large sample are suggestive of a causal relationship between the two, but significantly correlated evolution should not inevitably be interpreted as adaptation [Coddington 1994]. The adaptive trait should also be shown to perform the function for which it is hypothesized to be an adapation [Kay and Cartmill 1977]. With respect to sex-typed behaviors, the hypothesized function is usually simply increased reproductive success [Buss et al. 1998], although intermediate functions which supposedly lead to increased reproductive success are sometimes proposed (e.g., sexually dimorphic spatial skills as a result of selection on men for better hunting capabilities and women for better foraging capabilities [Joseph 2000]). Whatever the adaptive hypothesis, effort should be made to demonstrate that the supposed adaptive trait has a performance advantage over either the primitive condition that preceded it or over less pronounced expressions of the supposed adaptive trait with respect to the function it is supposed to fulfill.

While the homoplasy approach to comparative analysis of trait covariation is often thought of as an interspecific comparative endeavor, it need not necessarily be. Detailed, cross-cultural comparative work within humans has successfully been applied to understanding the evolution of behavioral characteristics such as language [Pagel 2009], and may have great utility in clarifying the evolutionary relationships among ecology, social organization, and sex-typed behavior for *Homo sapiens*. However, cross-cultural comparative work faces special challenges. Like interspecific comparison, cross-cultural comparison is always challenged by the problem that not all instances of cultures with the same trait relationships can be regarded as independent of each other, because some cultures share those trait relationships due to common ancestry. Additionally, cross-cultural comparisons are plagued by the fact that not all social characters are transmitted vertically—undoubtedly, some transmission of social characters occurs horizontally, creating non-independence even among cultures without shared ancestry [Mace et al. 1994]. Researchers are making substantial progress in dealing with these difficulties [Mace et al. 1994; Nunn 2006], such that cross-cultural comparative work has increasing potential to reveal the recent history of human gendered behavior and the social and ecological factors that may drive them. Work on intraspecific variation in non-human primates, once population histories can be accurately assessed, may have similar potential to reveal the short-term selective pressures that shape sex-typed behavioral expression in primates generally.

Despite its potential, intraspecific comparative work has some limitations: it can only reveal the very recent history of sex-typed behavior and has no ability to illuminate the deeper evolutionary history of sex-typed behaviors—indeed, it cannot even assess whether particular behaviors are plesiomorphic or apomorphic for a species; it cannot address the selective factors that were involved in the production of plesiomorphic behaviors; and it cannot reveal any useful information about behaviors that are invariant within species. Interspecific comparative work on primate sex-typed behaviors can do all of these things, and is unlikely to be complicated by non-independence due to horizontal transmission of trait covariation; therefore, it has great potential to clarify the evolutionary history and adaptive nature of human gendered behavior.

But what if interspecific comparative studies identify some patterns of gendered behavior that really are found only in humans? The adaptive significance of ubiquitous, uniquely human sex-typed behaviors cannot be assessed using the homoplasy approach. While singular historical events are less analytically tractable than repeated ones, they can still be studied using the homology approach. The homology approach to identifying adaptation looks at all instances of evolutionary change as singular historical events with unique historical explanations. It considers a number of competing hypotheses—all of which must be falsifiable, and of which adaptation is only one of many—to explain the origin of the trait of interest [Coddington 1994]. Inferring adaptation using the homology approach requires that multiple, carefully considered, independent deductions have been tested against the observed data. As the narrative scenario surrounding the emergence of a unique adaptation is elaborated, it should be further tested against available data. In testing hypotheses of singular adaptation, it is especially important to recall that proposed adaptations should be shown to increase fitness in the derived context relative to the primitive condition [Coddington 1994], as this is one of the few ways to falsify a hypothesis of adaptation using the homology approach. It is also important that competing adaptive and non-adaptive hypotheses be simultaneously considered and weighed against the data, lest an adaptive hypothesis "persist by monopoly rather than competitive merit" [p. 66, Coddington 1994].

It should be acknowledged that not all traits originally evolved as adaptations will necessarily have retained their original, adaptive functions to the present day—a trait lacking current utility may still represent an adaptation, but will no longer have a performance advantage [Coddington 1994]. Furthermore, traits that confer a current fitness advantage but which were not actually derived to perform their current function are exaptations, not adaptations—just because a trait has current utility in performing a particular function does not mean it originally evolved to perform that function [Gould and Vrba 1982]. Lastly, some traits may be simply non-adaptive, having derived from some other process besides selection and offering no current utility [Gould and Lewontin 1979].

In cases where an adaptation has lost its original function due to subsequent environmental change, failure to find a performance advantage associated with the trait is not adequate cause to reject a hypothesis of adaptation [Coddington 1994]. Importantly for identifying adaptation in human gender, adaptations that have lost their original function are likely to be most common in cases where lineages have experienced dramatic environmental change since the origin of the adaptation [Maestripieri and Roney 2006]. *Homo sapiens* has undergone recent environmental change so dramatic that evolutionary psychologists assume we are no longer living in the selective environments that produced most of the underlying physiological and psychological mechanisms motivating our behavior, and, therefore, make no effort to demonstrate fitness effects for the traits they suppose are human adaptations [Maestripieri and Roney 2006].

In fact, they explicitly reject the demonstration of current utility as a necessary or informative endeavor in identifying adaptation [Cosmides et al. 1992; Tooby and Cosmides 1990a; Tooby and Cosmides 1990b] and assert, instead, that evidence of "special design" is sufficient evidence for claims of adaptation [Tooby and Cosmides 1990a]. Natural selection is given primacy as a shaper of variation; non-adaptive evolutionary processes, though formally acknowledged, are considered "weak" and only suitable as secondary explanations after a concerted attempt to find the adaptive features of a character has failed [Tooby and Cosmides 1990a]. If a feature or set of features is complex and is improbably closely coordinated with the adaptive problem presented by the environment of evolutionary adaptedness, this is taken as sufficient evidence of adaptation [Tooby and Cosmides 1990b].

Yet, there are no clear methods by which even to accomplish the limited goals of this adaptationist [Tooby and Cosmides 1990b] approach to identifying adaptation. There are no guidelines about how much correspondence between an evolutionary problem and its purported adaptive solution qualifies as "improbable," or even any explanation of how to measure "correspondence." Worse, evolutionary psychologists accept as tenets that the environment of evolutionary adaptedness for almost all human psychology (and the behaviors motivated by it) is limited to the Pleistocene (between approximately 2.5 million and 12 thousand years ago) and that modern humans' environments are dramatically different from "the" human environments of evolutionary adaptedness [Tooby and Cosmides 1990b]. If the human environment of evolutionary adaptedness bears no similarity with the present, how are researchers to divine the evolutionary problems that were faced by *Homo sapiens* over a period of more than 2 million years? That is, how is it possible to "meet the conceptual and evidentiary standards for invoking function"[p. 542, Buss et al. 1998] if one has no way of knowing if the proposed function actually existed? This problem is circumvented by yet another assumption—that the environment of human evolutionary adaptedness looks sufficiently like the environments of modern day hunting and gathering societies that we can use them as stand-ins for *Homo sapiens* during the period critical to the evolution of the human sexually dimorphic human nature [Cosmides et al. 1992].

Unfortunately, this Panglossian approach [Gould and Lewontin 1979] cannot distinguish adaptation from exaptation from evolutionary "spandrel" [Maestripieri and Roney 2006]. Just because a particular trait is well-suited to the solution of a particular problem does not mean that the problem preceded the trait and selected for it, and it does not even mean that problem existed in evolutionary history at all (e.g., a nosebridge is a complex structure well-suited to the problem of holding up eyeglasses, but the problem of where to place eyeglasses is not one with an evolutionary history [Kay and Cartmill 1977]). This is not a minor point. When adaptive hypotheses rely on untestable assumptions, they relinquish their status as hypotheses and become unfalsifiable conjectures, thereby ceasing to be scientific, [Sewell 2004], and ultimately boiling down to little more than "stories" [Gould and Lewontin 1979].

Plausible stories of adaptation can always be conjured, but "the key to historical research lies in devising criteria to identify proper explanations among the substantial set of plausible pathways to any modern result" [p. 588, Gould and Lewontin 1979]. Hypotheses regarding current utility (selective maintenance but not selective origin) are both interesting and biologically meaningful in the context of human gendered behavior, and are straightforwardly addressed using the homology approach because they must only be falsifiable with regard to the current trait-function relationship. They may also be falsified using the homoplasy approach. But because hypotheses of adaptation specifically address the cause of trait origination, they must be falsifiable either with regard to the temporal relationship between the trait of interest and the function that selected for it or with regard to the historical trait-function relationship. In the most straightforward adaptive hypotheses, where the historical trait-function relationship is supposed to be coincident with the current trait-function relationship, the validity of the proposed historical trait-function relationship can be tested simply by testing for current utility. But if the historical trait-function relationship is supposed to be obsolete, then tests should be devised both to rigorously assess whether the trait would have offered a performance advantage over the primitive trait and whether the origination of the trait and function have the appropriate temporal relationship for an adaptive scenario. It may be possible to devise tests of historical performance advantage from the homology approach using modeling. But a simpler way of testing the validity of a proposed historical trait-function relationship is through the homoplasy approach (by seeking out other, extant examples and counter-examples of the relationship), and tests of the temporal relationship between trait and function rely wholly on comparative analyses.

Given ideal datasets, the homoplasy approach to identifying adaptation has much greater utility than the homology approach (and can also uncover general evolutionary patterns); but the two methods are complementary, and the most convincing examples of adaptation will be those which have withstood testing by both approaches [Coddington 1994]. In reality, the homoplasy approach may not always be feasible. First, it is simply unsuited for truly unique historical events. Second, whether comparative analyses are inter- or intraspecific, sampling completeness is crucially important for the homoplasy approach, as incomplete sampling may lead to biased results [Coddington 1994]. As a result, the homoplasy approach may be infeasible in the early days of research on a particular topic, and until sampling resolution is sufficiently high, inferences about adaptation based on the homoplasy approach should be viewed cautiously. Unfortunately, amassing the necessary comparative data to achieve sampling resolution sufficient to utilize the major strengths of the homoplasy approach takes time. Realistically, progress toward understanding the adaptive and non-adaptive elements of human gender will require a combination of both the homoplasy and homology approaches. This is partly because interspecific comparative work is likely to reveal that some elements of human gender are unique to humans and are suited only to study via the homology approach, while others are shared with other species and are amenable to study via the homoplasy approach. It is also because work on the adaptive nature of human gender (using the homology approach) should not wait until primatologists and other field biologists have compiled sufficient comparative data on sufficient numbers of taxa to assess which aspects of human gendered behavior are shared with other taxa (either due to homology or homoplasy) and which are uniquely human.

WHY STUDY DEVELOPMENT?

All of the methods outlined above can be used to identify probable proximate causation and adaptation in adult sex-typed behavior; but focusing on the ontogeny of adult sex-roles will yield a more complete, mechanistic understanding of the causes underlying adult sex-typed behaviors, which can further elucidate their evolutionary history by revealing the factors that drive and/or constrain their development at the proximate level [Beaupre et al. 1998; Duvall and Beaupre 1998; Janson and van Schaik 1993]. Among primates, newborns exhibit very little physical activity and social interaction [Bentley-Condit 2003], such that development will be an important part of almost all of their adult behaviors (sex-typed or otherwise), and the advantages afforded by developmental study can likely be leveraged for most primate sex-typed behaviors. Furthermore, all of the advantages of comparative research outlined above for understanding the proximate and ultimate causes of adult sex-typed behaviors can also be leveraged for understanding the proximate causes underlying sex-typed *development*. Thus, comparative study of sex-typed development is the most incisive method by which to gain insight into the proximate and ultimate causation of human sex-typed behavior.

PREVIOUS RESEARCH ON SEX-TYPED DEVELOPMENT

The proximate causes mediating behavioral development have been a topic of concerted investigation in humans and non-human primates for decades, forming a vast "nature vs. nurture" literature. Especially since endocrinological research has become more logistically feasible, the development of sex-typed behavior, in particular, has received increasing attention, and the overwhelming evidence is that for all primates, normal, sex-typical behavioral development results from complex interactions between and among social, ecological, and somatic factors [Kelly et al. 1999; Wallen 1996; Wallen and Zehr 2004]. Important somatic factors that influence sex-differential development are internal physiological states, including hormones governed by the hypothalamic-pituitary-gonadal (HPG) axis [e.g., Beehner et al. 2005; MacLusky et al. 1997; Pereira 1993a; Wallen 2005] genetic [e.g., Agate et al. 2003; Arnold et al. 2003; Arnold 2004; Barske and Capel 2010] and neuronal factors [MacLusky et al. 1997; Sisk and Foster 2004]. Important social factors influencing sex-differential development and behavioral expression are individuals' social interactions with mother and others [Alberts and Altmann 1995a; Drea 1998].

Important ecological factors influencing sex-differential development are sexually differentiated nutritional needs [Agostini and Visalberghi 2005; Alberts and Altmann 1995a; Grassi 2002]. However, the relative importance of the social environment, ecological environment, and individual physiology in the development of specific sex-typed behaviors is almost entirely unknown for most primate species, and it is especially unclear how any of these factors function in natural environments to produce behavioral phenotypes [but see Alberts and Altmann 1995b].

Human Gender Development

Social causes of behavioral sex differentiation

Previous research suggests that both social and somatic factors are important in shaping the development of human sex-typed behavior. Because experimentation on humans is unethical, it is challenging to unequivocally establish the causal roles of either, but both enjoy considerable support. Research on the social factors that influence human gendered behavior involves both observational and experimental work. Research on the "biological" bases of human gendered behavior is primarily represented by clinical studies, correlational studies, and psychological experiments on infants.

That social factors are likely to be important in shaping the expression of human sex-typed behavior is well-evidenced. In western cultures, it is clearly documented that male and female children are regularly treated differently by others, and children respond to their perceptions of what is apparently expected of them in their performance of sex-typed behavior. Additionally, among different human cultures, there are different views on what constitutes appropriate sex-typed behavior, and in some cultures, these definitions have changed a great deal over short spans of time.

Children are treated in sex-differential ways by their parents, by non-parental adults, and by their peers. A number of studies of children from the 1960s to the 1980s (in western cultures) indicate that parents and teachers of children react to them in sex-differentiated ways prior to the age at which children exhibit sexually differentiated behavior of their own. Within 24 hours of birth, parents describe their infants in sex-stereotyped ways [Rubin et al. 1974]. Mothers exhibit more strongly affective vocal expression when talking to their infant sons [Roe et al. 1985] and engage in more physical contact with them than with infant daughters [Moss 1966], but look at and talk to their infant daughters more than their infant sons [Lewis 1972]. Higher rates of looking at and talking to infant daughters continues through the age of two, while the pattern of sex-differential contact time reverses at the age of 6 months, after which time mothers spend more time in contact with their daughters than their sons [Lewis 1972]. By five months of age, the physical environments of male and female infants are sexually differentiated by parent choices in clothing color, toy color, and toy type [Pomerleau et al. 1990]. Parents and teachers of toddlers 18 months or younger have been found to respond more positively to girls' attempts to communicate than boys', to pay more attention to boys' negative/assertive behaviors than girls', [Fagot and Hagan 1991; Fagot et al. 1985], and to respond more positively to children when they were engaged in sex-typed play behaviors and less positively to them when they were engaged in cross-sex play behaviors [Fagot 1977a; Fagot 1978; Fagot and Hagan 1991]. Parents more often respond negatively to girls' manipulations of objects than to boys', more often respond negatively to girls' gross motor activities (e.g., running, jumping, etc.) than to boys', and more often respond positively to girls' solicitations for help and negatively to boys' solicitations for help [Fagot 1978]. For two year old children, who have begun to exhibit sex differentiated activity preferences, teachers more often respond negatively to boys in general and especially more often negatively to boys engaged in female typical behavior (even though negative responses to children are rare at this age). Peers of two year old children begin to differentiate their responses to other children by sex: girls respond more positively to other girls than to boys, regardless of whether play is sex-typed or not, while boys respond more positively to other boys than to girls, but much more positively to boys engaged in male-typed behavior than to boys engaged in female-typed behavior [Fagot 1985]. At later ages, once sexually differentiated behavior is well-established, gender-typing and sex-differential treatment of children by others continues. Parents, teachers, and peers of three and to five year-old children reinforce sex-typed behavior by responding positively to gender-typed behavior and by ignoring or punishing cross-gendered behavior, with boys, but not girls, receiving harsh criticism for cross-gender behavior from peers, teachers [Fagot 1977a], and fathers [Langlois and Downs 1980]. Sex differential treatment by parents may be attenuated by the age of five [Fagot and Hagan 1991], but teachers are still more likely to attend to boys' attempts to communicate than girls' [Fagot et al. 1985]. Instances of sex-typed socialization across a these studies had small effect sizes and large variances, such that particular socialization effects were not statistically significant in all samples [Fagot and Hagan 1991]; but still, the socialization of sex-typed toy play in children up to four years old is particularly robust across studies and through time [Fagot

1977a; Fagot and Hagan 1991], as is the presence of the general phenomenon of sex-typed interaction with adults and peers. Interestingly, the ways in which adults respond to children in sexually differentiated ways does not always correspond to their ideas about gender-typed behaviors—for example, parents did not consider "asking for help" a sex-typed behavior, but did respond to this behavior differently based on the child's sex. This suggests that even when there is no intention to socialize children in gender dichotomous ways, it occurs anyway [Fagot 1978].

While it could be argued that sex-differential treatment of children by others is actually a response to innate sex differences in the children themselves (and while some of it may actually be, particularly mother-infant interaction), a series of "Baby X" experiments has shown that, at least with some characteristics of adult-infant interaction, adult perception of a child's sex strongly influences the ways in which they interact with children from three to fourteen months of age and swamps any effect that might be due to the actual sex of the child [Seavey et al. 1975; Sidorowicz and Lunney 1980]. The original "Baby X" experiment [Seavey et al. 1975] introduced a three month old female dressed in yellow to unfamiliar graduate students (with no children of their own) as a either a boy, a girl, or without giving a gender identification, and observed which toys adults used to play with the infant. If the baby had been introduced as a girl, both men and women chose a sex-stereotyped toy for the infant. If the baby had been introduced as a boy, this effect was not found, but the authors posit that this was probably because the male-stereotypical toy provided—a football—was not age appropriate [Seavey et al. 1975]. For the gender unknown condition, adults guessed the infant's gender and justified their guesses using sex stereotyped behavioral and physical characteristics—i.e., softness for "girl" and strength for "boy" [Seavey et al. 1975]. A repetition of this study using infants of both sexes aged three to eleven months found a similar (but stronger) pattern of sex-typed toy choices according to the infants' perceived sex by undergraduate men and women. A third experiment on law students and their spouses (who were, themselves, parents) using toddlers of both sexes aged 13 to 14 months also found that adults play with unfamiliar children in gender-stereotyped ways according to their perception of the child's sex, but not according to its actual sex [Frisch 1977]. A fourth experiment on parents of young children found that they direct more verbal attention, more interaction without eye contact, and use more neutral facial expressions with a perceived girl and more often look directly at a perceived boy. This sex differential treatment of the infant was despite the fact that most of the parents did not believe that children are sexually differentiated at six months, or that it was important for them to be so [Culp et al. 1983], and suggests that even when not intended, gender dichotomous social signals are continuously sent to children.

Given how early and repeatedly children receive cues from others about their own gender, it is reasonable to think, as social constructionists do, that they would tend to respond to those gendered behavioral expectations. Given that children are almost certainly active agents of their own gender construction [McIntyre and Edwards 2009], it is difficult to say how much of their gender construction or performance is in response to external social pressures rather than expressions of their own innate tendencies. But some research clearly demonstrates that children's perceptions of gender expectations can constrain their behavioral expression. In an experimental setting in which more and less stereotypically gendered five year old children were observed playing with a choice of gender typical and atypical toys, the presence of an adult observer significantly changed the toy choices of less stereotypically gendered boys (but not those of less stereotypical girls)—less masculine boys chose more masculine toys when they knew they were being observed than when they thought they were not being observed [Wilansky-Traynor and Lobel 2008]. Four year old children have also been found to play less with opposite-sex toys when peers are present than when alone [Serbin et al. 1979]. These data suggest that external social factors do influence children's behavioral expression with respect to gender.

Another line of evidence that suggests external social factors are an important cause of sex-typed behavioral expression in humans is the existence of variation in the particulars of that expression across modern human cultures. While behavioral differences that are associated with each biological sex may be ubiquitous across societies [Whiting and Edwards 1973] many of the particular expressions of those behavioral differences are not. In some cultures, it is considered inappropriate for women to operate motor vehicles, but this certainly does not represent expectations of women everywhere. In present-day Mahafaly culture in rural Madagascar, it is acceptable for a man to wear a hot pink, floppy gardening hat but not for a woman to have short hair (personal observation); in present-day American culture it is acceptable for a woman to have short hair, but a boy with pink nail polish causes a media flap [Netburn 2011]. Furthermore, the particular behaviors considered appropriate for each gender can change rapidly within a culture through time [Tallichet and Willits 1986]. A thorough treatment of cross-cultural and temporal variation in sex-typed human behavioral expression is beyond the scope of this study, but its existence suggests that external social factors are strongly at play in the development and maintenance of human gender roles.

"Biological" causes of behavioral sex differentiation

There are well-documented differences in western men and women in spatial skills and attention; since this is an area less obviously subject to socialization than many other adult human sex differences, they have often been assumed to represent innate, biological human sex differences. Without any instruction or specific training, men tend to focus on the "geometrical positions of objects in space" while women concentrate on "the position of objects relative to one another" [Ecuyer-Dab and Robert 2004]**.** This sex difference in attention to object location is manifest in the ways men and women spontaneously attend to maps and directions—men use Euclidean, geometrical features and women use more landmarks [Ecuyer-Dab and Robert 2004]. Similarly, several studies have demonstrated female superiority in object and object location memory [Duff and Hampson 2001; Eals and Silverman 1994; Silverman and Eals 1992], but female advantage disappears when specific instructions are given to note object locations [Silverman and Eals 1994], suggesting a sex difference in attention to particular object features. However, some sex differences in visual skill are not due to simply to sex differences in attention. When test subjects are asked specifically to recall object location, females still outperform men, but only for objects are located on the right side of the field of vision [Alexander et al. 2002]. That these sex differences in visual processing habits are spontaneous and are not actively constrained by social factors in any obvious way has been taken to suggest that they result, at least partly, from innate differences between males and females as opposed to entirely from experiential factors. But still, they may result from sex differential experience with certain kinds of activities (possibly socialized ones) that demand particular kinds of visual processing and attention, much like feline visual capability depends on the nature of post-natal visual input [Blakemore 1976].

A more convincing set of data for the importance of biological motivators of behavioral sex differences comes from clinical research on medical conditions that disrupt sex-typical hormone function. Congenital adrenal hyperplasia (CAH) is caused by mutations in the CYP21A2 gene that causes a defect in the 21-hydroxylase enzyme, which is needed for the synthesis of cortisol. The resultant cortisol deficiency ultimately results in downstream overproduction of adrenal testosterone during gestation [Minutolo et al. 2011]. Girls with CAH are usually characterized by masculinized genitalia and male-typical play behaviors [Pasterski et al. 2005] and toy preferences [Berenbaum and Hines 1992]. Boys with CAH seem to be exposed to slightly lower than normal levels of gestational testosterone, as they exhibit sex-typical toy preferences but less than typical rough play [Hines and Kaufman 1994]. (It has been proposed that the increased adrenal testosterone production somehow "clamps" the normal production of gonadal testosterone in the fetus, resulting in lower than average gestational testosterone exposure [Wallen 2005].)

Correlative studies have attempted to follow up on the role of non-pathogenic variation in prenatal testosterone exposure on childhood behavioral tendencies. A study of the circulating testosterone of nearly 14,000 pregnant British women and their children's behavioral tendencies at three and a half years of age found that girls of mothers with high levels of circulating gestational testosterone exhibited more male-typical play while girls of mothers with low levels of circulating gestational testosterone exhibited more female-typical play; there was no relationship between boys' play styles and maternal gestational testosterone, possibly due to the swamping effects of the amount of testosterone produced by male fetuses [Hines and Golombok 2002]. These studies suggest that fetal physiology and the fetal hormone environment organize innate behavioral tendencies of children, and given that the particular fetal physiological peculiarities of CAH also effect genital masculinization in girls to varying degrees, it is not unreasonable to attribute the behavioral tendencies of this group of children to fetal physiology, even if there is not a one-to-one causal relationship between the two. Still, these types of studies of older children cannot control for the possibilities that behavioral tendencies of their subjects are instead produced through unconscious socialization or genetic similarity between parents and daughters, mothers in particular [Cohen-Bendahan et al. 2005].

In an effort to minimize the influence of socialization and to pinpoint more definitively innate sex differences in human children, some studies have attempted to focus on the youngest infants possible. Numerous studies have sought to establish whether or not infant boys are more physically active than infant girls [Campbell and Eaton 1999; Cossette et al. 1991], but results are inconclusive. Researchers have attempted to determine whether the well-established sex difference in children's toy preference is rooted in innate sex differences in object preference [Alexander et al. 2009; Connellan et al. 2000]. This research has found a neonatal sex difference with small effect size in visual preference when given a choice between a human face and a complex picture comprising mixed up fragments of a human face (girls tend to look preferentially at the face while boys tend to look preferentially at the complex picture), and that a sex-typed preference for red versus blue does not exist for toddlers', as has often been proposed (in fact, both sexes prefer pink and red over blues) [Alexander et al. 2009]. Alexander [2003] suggests that the slight, innate sexual bias in visual preference apparently demonstrated by Connellan et al. [2000] leads male infants to selectively attend to male-typed objects, and through their increased exposure to them, to develop their visual processing skills for male-typed objects and *vice versa*—a feedback loop between preference for and experience with certain types of visual cues, an idea supported by a previous finding that boys' visual-spatial ability is correlated with sex-typed activity preferences [Connor and Serbin 1977]. But critics reject the interpretation of the sex differences in these studies as innate because the Connellan et al. [2000] study did not control for whether the infant was being held or was in a bassinette during experimentation, and it is well-documented that western adults handle and interact with children in sex-differential ways based on their belief about the child's sex, and even with day-old infants, the opportunity for sex-differential handling by adults has arisen (K. Clancy, personal communication).

Distinguishing the roles of "nature" and "nurture" in sex-typed development

Sorting out how much of human sex-typed behavior derives from innate motivations, how much is experientially motivated or constrained, and how much of an interaction there is between the two is quite a challenge. The methodological constraints of research on humans are greater than for any other species. A number of tools that might yield more insight into this puzzle are unethical (i.e., experimental manipulation of prenatal hormone concentrations) [McIntyre and Edwards 2009] while others are simply infeasible (i.e., observing all of a subject's social interactions or establishing the reproductive success of individuals who adopt different behavioral strategies). Furthermore, because this is such an emotionally charged topic, interpretations of even the same data tend to be polemical. For example, a number of elements of adult treatment of infants have been found to vary according to sex, but many have not, and the effect size of sex-differential treatment by others is usually small (the effect size of sex differences in infant behavior are fewer and smaller). Although all researchers today admit the importance of complex biocultural interactions in human sex-typed development [McIntyre and Edwards 2009], discerning the weight of the importance of each type of causal factor is open to interpretation. Researchers with a social constructionist bent tend to highlight the presence of adult sex-differential treatment of infants, downplay the behavioral sex differences of infants, and point out small differences in treatment by adults are potentially more important than is belied by their initial size due to the ways in which they can be elaborated through cumulative experience and response by children [Sidorowicz and Lunney 1980]. In contrast, researchers with a biological bent will highlight the small effect size of adult treatment of infants, emphasize the potential importance of the role of infant sex differences in temperament in an interaction feedback loop between infants and adults, thereby downplaying the importance of external pressures in the process of sex-typed development [McIntyre and Edwards 2009]. Social constructionists will interpret the dramatic and very consistent results of the Baby X experiments as evidence that adults rely heavily on children's gender in order to structure interactions with them [Sidorowicz and Lunney 1980], while researchers with a biological perspective on human gender will point out that in the experimental paradigm, with no previous familiarity with the individual preferences of the child, adults have nothing other than stereotypes to rely on to structure their interactions with the child [McIntyre and Edwards 2009]. Thus, even when contextualizing the same data, social constructionists tend to give the impression that sex-typed treatment of children by others is likely the most important driving force in sex role development and researchers with a biological focus tend to give the impression that children's expression of innate sex differences is probably the most important driving force in sex role development. One way around this problem may be to study these questions in non-human model taxa for which most researchers probably have less investment in a particular result versus another.

Captive non-human primate sex-typed development

With regard to the causes of behavioral sex differentiation, the common rat, mouse, and rabbit models are not likely to be entirely applicable to more precocial taxa such as primates [Wallen 2005]; non-human primate models are much more likely to be of use in attempting to explain human sexual differentiation and other complex, human biobehavioral phenomena [Carroll and Maestripieri 1998; Maestripieri 1999; Maestripieri 2005b; Maestripieri and Carroll 1998; Plant 2001]. Like humans, non-human primates have an extended period of infancy and juvenility during which their behavioral phenotypes fully develop [Altmann and Pereira 1985]. But most non-human primate species develop much faster than humans, are more experimentally tractable than humans, and are therefore valuable as a model for inquiry into the causes of human sexual differentiation [Altmann and Pereira 1985; Curry 2001; Maestripieri 2005b; Wallen 2005]. Like humans, there is convincing evidence that behavioral development in non-human primates is driven both by social and somatic factors. Social influences on the normal development of sex-typed behaviors, in particular, have not been subject to such intense scrutiny as in humans, but a great deal of experimental work on the behavioral effects of early social experience suggests that social factors are likely to be important in normative sex-typed development. Somatic influences on sex-typed behavioral development, on the other hand, have been and continue to be much more thoroughly investigated than is possible in research on humans.

Social causes of behavioral sex differentiation

Decades of captive research on the proximate mechanisms of primate social development have unequivocally demonstrated that the social environment is fundamentally important to the development of later behavior. A number of studies involving manipulation of the early social environment have demonstrated that complex social environments result in more normative infant and juvenile behavior, while socially deprived environments generally lead to poor behavioral outcomes [Harlow and Harlow 1962a; Harlow and Harlow 1962b; Ruppenthal et al. 1976; Wallen 2005]. Macaques reared in more socially complex or less stressful environments exhibit less fear and fewer fear-related behaviors [Capitanio 1984; Champoux et al. 1991], less agonism [Capitanio 1984; Champoux et al. 1991], more dominant social behavior [Capitanio 1984], more social play [Champoux et al. 1991], less self-directed behavior [Champoux et al. 1991], and develop the ability to discriminate between strangers and their mothers earlier in life [Rosenblum 1987]. Chimpanzee infants reared alone exhibit suppressed levels of distress vocalizations when exposed to stressors [Randolph and Mason 1969]. Even when subjected to rearing differences during only the first 30 days of life, chimpanzee infants reared in an enriched environment are happier, more alert, more able to quiet themselves, are less fussy, less fearful, more cooperative, have greater attention spans, are more persistent, exhibit less object attachment, and are less tense during testing for the first year of life [Bard and Gardner 1996]. This suggests that behavior may be sensitive to early, brief periods of social stress. While much of this research has not focused on the development of sex-typed behaviors, *per se*, the importance of the social environment for normal behavioral development in general suggests that it is almost certainly influential for normal sex-typed behavioral development in particular. Where investigation has focused on rearing effects of sex-typed behavioral development, results echo those on species-typical behavioral development: more socially complex environments promote the development of more proficient sexual behavior [Capitanio 1984; Champoux et al. 1991; Goldfoot 1977; Goy and Wallen 1979; Harlow 1965; Mason 1978; Wallen 1996; Wallen et al. 1977; Wallen et al. 1981] more sex-typical play behaviors [Spijkerman et al. 1995; Wallen 1996; Wallen 2005], and more species-typical behavioral sex differentiation [Meredith and Fritz 2005; Spijkerman et al. 1996; Spijkerman et al. 1997]

Despite the paucity of data on social development in strepsirrhines [Gould 1990], some data indicate that species-typical socialization is also important for their normative development. Though the Duke University Primate Center has had much success in breeding aye-ayes using wild-caught males, captive bred males have failed to breed successfully on their own. The first successful breeding by a captive-born male was only achieved after two years of behavioral coaching by Primate Center staff. Due to husbandry constraints, upon the birth of a younger sibling, older offspring were historically removed from their mothers and housed with an opposite-sex peer. The Primate Center now introduces younger males to animals of all ages and reproductive states, because they suspect that social learning plays an important role in the development of mating behavior (Gibson D., pers. comm.). Together, these data indicate that relationships with conspecifics may be important to the development of sex- and species-typical social behavior in all primates, not just in anthropoids [Nash 1993; Nash 2004], a point which deserves much increased attention and research.

Most of the aforementioned manipulations of early social and/or hormonal environments are far outside the normal range of variation a primate experiences under natural conditions and are therefore of questionable utility in determining whether normal social interactions with group members influence behavioral development under normal circumstances. But a few captive studies have shown that even "normal" variation in early social environment can produce short and long-term effects on behavioral development.

Non-manipulative studies suggest that normally occurring variation in particular elements of the social environment influence developmental outcomes. For example, in many cercopithecoid taxa, infant play patterns are correlated with maternal rank—offspring of higher ranked mothers play more, use more dominant behaviors in their play, and are more independent [Fedigan 1972; Gard and Meier 1977; Norikoshi 1974; Tartabini and Dienske 1979]. Dominant mothers are usually more relaxed in their mothering style, so that infants are in contact with them less, which allows them to play more [Altmann 1978; French 1981; White and Hinde 1975]. But even in cases where maternal rank is uncorrelated with maternal style, maternal style is still correlated with infant play patterns and later adult behavior—early maternal rejection within normal limits seems to promote less anxiety and more independence, and this effect is long-lasting [Hemelrijk and Dekogel 1989;

Schino et al. 2001]. In free-ranging rhesus macaques, infants exhibit patterns of social interaction that mimic their relatives'. Infants in high-ranking lineages spend more time with their relatives than infants in low-ranking lineages, irrespective of differences in mother-infant relationships [Berman 1983].

Although these studies lend strong circumstantial evidence that the nature of the mother-infant relationship or social environment influences the behavior of offspring, they cannot control for the possibility that the correspondence of maternal style and infant behavior are due to the genetic relatedness of mothers and infants.

Rosenblum and colleagues [Andrews and Rosenblum 1991; Rosenblum and Paully 1984] convincingly demonstrated that the social milieu during rearing, specifically, can strongly affect infants' later behavior. They changed the foraging demands placed on social groups of bonnet macaque mothers and infants without changing the amount of food actually available to the animals [Andrews and Rosenblum 1991; Rosenblum and Paully 1984]. Groups were subjected to low foraging demand, high foraging demand (food was hidden and animals had to forage longer to find food), and variable foraging demand (foraging demand protocol oscillated randomly between high and low demand). These changed foraging demands affected both female-female relationships and mother-infant relationships. Females subjected to low foraging demand (LFD) were least aggressive and most affiliative; variable foraging demand (VFD) females were most aggressive; high foraging demand (HFD) females were intermediate. Mother-infant dyads that experienced VFD were more often in contact, spent less time out of visual contact, and made and broke contact more often than dyads in the other groups. Infants reared in the VFD environment exhibited reduced social behavior, less object exploration, less play, and eventually showed signs of depression—long bouts of sitting hunched over with closed eyes, often self-clinging. Previous to this study, depression had only been recorded when infants were separated from their mothers [Rosenblum 1987]. VFD infants were also more subordinate to LFD infants [Andrews and Rosenblum 1991; Rosenblum and Paully 1984]. Because these individuals were reared identically other than the foraging demands placed on their mothers, these long-term effects must have arisen from changes in the social environment borne of changes in foraging demand.

Maestripieri [2005a] demonstrated that a month's exposure to an abusive foster mother resulted in dramatically increased odds of a female becoming an abusive mother herself. This pattern was uncorrelated with genetic relatedness—none of the biological daughters of abusive mothers fostered by non-abusive mothers grew up to be abusive mothers—and suggests that the transmission of patterns of maternal behavior from generation to generation can be mediated experientially. Other cross-fostering studies have also shown that the mother-infant relationship affects infant behavior. Infants cared for by punitive females spend less time in ventral contact with them and exhibit more self-directed disturbance behaviors than infants cared for by nurturant females, and these effects are independent of genetic relatedness or individual physiology (which could be inherited, or a result of prenatal experience) [Suomi 1987].

These experimental data demonstrate unequivocally that some aspects of the early social environment can affect later social behavior. The particular elements of the social environment that mediate normal behavioral development are still unclear, as is how the early social environment shapes sex-typed behavioral development in particular. But another important line of evidence supporting the importance of the social environment in normative primate sex-typed behavioral development is that not all manipulations of rearing environment affect males and females in the same way. Sackett [1972] tested the exploratory behavior of rhesus monkeys from 5 variously complex rearing environments. Complexity of rearing situation was positively correlated with motor activity, exploration, and responsiveness to complex visual stimuli, but females were more robust to the effects of deprivation rearing than males. Males and females also respond differently to different combinations of rearing and post-rearing environments. In highly aggressive environments, female rhesus present to others more than males do, irrespective of rearing experience. In low-aggression environments, there is no sex difference in presenting, except if infants were reared in isosexual groups, in which case males present more than females [Wallen 1996]. On Cayo Santiago, free-ranging rhesus macaque infants apparently do not differ by sex in grooming and play behavior until their mothers resume sexual behavior. But at this point, male infants increase the amount of time they spend playing [Berman et al. 1994] while females decrease the amount of time they spend playing, and increase the amount of time they spend grooming non-maternal group members [Berman et al. 1994]. After a sibling birth, males spend more time farther from their mothers [Devinney et al. 2001]; females spend more time in close proximity to their mothers, approach their mothers more, and groom their mothers more than males do [Devinney et al. 2001]. This represents a sex difference in social response to a normal but probably stressful life event, and implies that the birth of a sibling (or not), and the sex of the yearling partly determine the resultant yearling behavioral phenotype. These cases illustrate that the two sexes may be affected differently by their early social environment, and that their pattern of responses to later social environments may also differ by sex. Such sex differences in response to environment could serve as one mechanism of sexual differentiation in behavioral development.

Biological causes of behavioral sex differentiation

Identification of somatic causes of behavioral sex differentiation has been one of the greatest contributions of captive, experimental research in this area. A large body of work beginning with the search for the underlying causes of human hormonal disorders [Wallen 2005] and based on testing and further exploring the mammalian model of sexual differentiation [Jost et al. 1970] has revealed much about the biological motivators of sexually differentiated behavior in non-human primates.

A number of studies suggest that some non-human primate behavioral sex differentiation may be innate, but does not identify the proximate drivers involved. For example, sex-typed toy preferences common in humans are also found in vervet and rhesus monkeys presented with novel toys [Alexander and Hines 2002; Hassett et al. 2008]. Both studies suggest that there is some degree of innate sex difference in object preference, because neither species of monkeys had previous familiarity with these toys, so they did not have sex differential experience with them. Male superiority in spatial memory in captive rhesus macaques is another sex difference with no obvious environmental cause, social or otherwise, suggesting the presence of innate sex differences for this trait in this species [Lacreuse et al. 1999].

Many experimental studies have been able to isolate the effects of particular hormonal factors on specific sex-typed behaviors. Experimental manipulation of the prenatal androgenic environment in macaques has clearly demonstrated that prenatal hormones affect later sexual differentiation in play behavior and sexual behavior in both males and females, but that not all behaviors respond similarly to a given androgenic manipulation regime [Goy et al. 1988]. For example, levels of prenatal androgen sufficient to produce masculinized mounting behavior in female Japanese macaques do not masculinize rough and tumble play [Eaton et al. 1990] and levels sufficient to induce male-typical mounting and play behaviors in female rhesus are insufficient to suppress female-typical infant interest [Herman et al. 2003]. Additionally, the timing of androgen exposure during gestation is important in determining its effects on later behavior. The behavioral effects of androgen manipulation during late gestation are usually more pronounced than those in early gestation [Wallen 2005]. For example, rhesus juvenile mounting behavior seems to be particularly sensitive to androgen manipulation in late gestation even though it can also be affected by early gestational hormone manipulation [Goy et al. 1988]. This phenomenon may result from the importance of androgen influence on sexual differentiation of the mammalian brain, which occurs perinatally, and which depends on the presence of gonadal testosterone for the development of a number of male brain traits related to adult sexual behavior [Hines 2003; McCarthy et al. 2003]. Within this overall pattern of increasing androgen sensitivity as gestation progresses, though, different behaviors still have their own unique timing of peak sensitivity to androgens [Hines 2003]. Female rhesus macaques who experience elevated levels of prenatal testosterone early in gestation exhibit masculinized mounting behavior, but no increased frequencies of rough play; females who experience elevated levels of prenatal testosterone late in gestation exhibit both more mounting and rough play than unmanipulated females [Goy et al. 1988]. This indicates that different behaviors have different schedules of sensitivity to androgens, which makes sense in light of the fact that neurological development is protracted in primates [Wallen 2005].

Some gestational androgenic effects on behavior have been less clear. The administration of flutamide (an androgen blocker) and androgens to rhesus macaque fetuses at different times in gestation produced a suite of results that did not coincide with expectations derived from previous studies [Wallen 2005]. In particular, flutamide did not produce de-masculinization effects consistent with androgen suppression, which it should have. However, one clear and important result from this study was that the effects of variation in the prenatal hormonal environment on behavior may sometimes be latent, rather than immediate. Increased androgenic exposure did not increase females' rates of rough play during the first year of life as expected, but did so in the second year of life [Wallen 2005].

Available data indicate that some aspects of juvenile social behavior might be sensitive to neonatal hormones, but that, in general, the developmental component of primate behavioral sex differentiation is not strongly driven by neonatal hormones, because sex-typical behavior does not appear to be strongly affected by neonatal castration or pharmaceutical suppression of the neonatal testosterone surge. In rhesus macaques, infant and juvenile sexually dimorphic play and mounting behaviors are unaffected by experimental manipulation of neonatal hormones [Brown and Dixson 1999; Wallen et al. 1995] and by gonadectomization at birth [Goy and Phoenix 1971; Wallen 2005]. However, suppression of neonatal testosterone does affect adult male sexual behavior; adult males who experienced neonatal testosterone suppression masturbate and copulate less with receptive females than control males [Eisler et al. 1993]. These data suggest that sexual differentiation of social behavior through juvenility is relatively independent of postnatal circulating hormones [Goy and Phoenix 1971], but that ". . . hormonal influences during the neonatal period elaborate predispositions that are organized prenatally" [Wallen 2005, p.11].

There is evidence that puberty involves increased structural changes in the brain [Sisk and Foster 2004], but it is unknown whether this is due to increased sensitivity to the organizing effects of androgens during this developmental time. It is also unknown whether puberty affects post-pubertal androgen sensitivity or how pubertal androgens influence the development of fully adult mating behavior [Wallen 2005]. Regardless of the precise mechanisms of influence, pubertal hormones are important drivers of sexual differentiation. Male and female rhesus monkeys exhibit differences in the ages at which they can perform visual discrimination tasks, which can be altered by manipulation of peripubertal hormone concentrations [Bachevalier and Hagger 1991; Hagger and Bachevalier 1991]. And it is clear that some sex-typical juvenile behaviors that are independent of post-natal hormonal influence during juvenility come under hormonal control (or at least influence) in adulthood. For example, in rhesus macaques, adult male mounting behavior is dramatically decreased when testosterone is artificially suppressed [Wallen 2001; Wallen et al. 1991], and in pig-tail macaques, adult female interest in infants is increased by estrogen treatment [Maestripieri and Zehr 1998]. By adulthood, then, some sex-differential behaviors are at least partially controlled by the presence of sex-differential gonadal hormones.

Though non-human primates are probably the best models of human sexual differentiation, two caveats bear consideration. First, the traditional mammalian model of androgenic sex differentiation [Jost et al. 1970] has been found to be an oversimplification; sexual differentiation also relies on hormonal feminization processes [Fitch and Denenberg 1998] and other, non-hormonal processes, such as Y chromosome presence and X-gene dosage effects on the brain [Arnold et al. 2003]. Second, not all primates are alike in how hormones affect their behavior. In rhesus macaques, male sex-typical mounting and play behavior is mostly determined by prenatal hormones [Brown and Dixson 1999; Brown et al. 1999], but neonatally castrated marmosets and tamarins display no later mounting behavior even when testosterone is artificially administered, indicating that neonatal hormones are more important for sexual differentiation of behavior in these taxa [Dixson 1993; Epple et al. 1990]. Developmental endocrinology studies on primates have all been done in captivity, and have therefore largely been limited to macaques, mangabeys, and callitrichids [Brown and Dixson 1999]. Little is known about the normative developmental endocrinology of other primate taxa or its effects on sexual differentiation of behavior, and it should not be assumed that other taxa conform to known patterns.

Social/somatic interaction

Another strength of captive research has been its ability to document the interaction between social and hormonal causes of behavioral development in general, if not sexual differentiation in particular. Captive research has clearly shown that the early social environment can create variation in individuals' brains and physiology. In a study of 29 male rhesus monkeys, nursery reared monkeys had smaller midsagittal corpus callosum areas associated with a decrease in white matter volume and performed poorly in cognitive testing compared to monkeys reared with their mothers in a naturalistic setting [Sanchez et al. 1998]. Insufficient tactile stimulation experienced by isolate-reared rhesus monkeys alters later hormone secretion patterns [Champoux et al. 1989]. Pigtail macaques separated from their mothers and subsequently provided with a juvenile allomother experience significant immunosuppressive effects from the separation, but not if they have an already established attachment to their allomother [Boccia et al. 1994]. And animals reared in variable foraging demand environments have highly reactive stress hormone profiles compared to those reared in low foraging demand environments at 3 and 4 years of age [Suomi 1997]. Because an individual's brain and physiology influence its later behavior, the effects of early social environment on the brain and physiology could serve as a mechanism by which early social environment influences behavioral development. The importance of this phenomenon should not be underestimated; for example, in the wild, highly reactive female macaques often exhibit inadequate maternal care, and highly reactive males often emigrate late and enter new groups with low rank [Suomi 1997].

Individuals' brains and physiologies may also prime them to react in different ways to the same environmental stimuli [Ellis et al. 2011]. For example, highly reactive macaques, which in most circumstances suffer deficits compared to their less reactive peers, do very well if reared by the "right" kind of mother. Suomi [1997] selected highly-reactive and normally reactive infant rhesus and cross-fostered them with either normal or especially nurturant mothers. Extra nurturing had no effect on normal monkeys, but had drastically ameliorative effects for highly reactive monkeys. Instead of suffering all of their typical behavioral deficits, highly reactive monkeys reared by especially nurturant mothers became behaviorally precocious. Later in life, they became adept at recruiting and maintaining allies in response to agonistic encounters, rose to high rank, and stayed there. Furthermore, when these females had their own offspring, they exhibited the highly nurturant maternal style of their foster mothers, not the inadequate care of their biological mothers that contributed to their reactive stress physiology in the first place [Suomi 1997].

Given that males and females do differ in some aspects of their physiology and anatomy, these differences may prime the sexes to have different outcomes from their interactions with the same environmental stimuli. In some cases, males and females do indeed have different phenotypic responses to the same environmental stimulus. Female peer-reared rhesus macaques have higher stress hormone levels in response to alcohol infusion than mother-reared animals of either sex. Male stress hormone response to alcohol, though, is unaffected by rearing condition, suggesting that the function of the neuroendocrine stress axis responds differently to early stressors in each sex [Barr et al. 2004]. Sex-differential responses to similar environmental stimuli could serve as one mechanism by which social environment could shape sexual differentiation in behavior.

The idea that individual phenotypes result from complex interactions between an individual's innate characteristics and its experience with characteristics of its social and physical environment is not a new one [Capitanio 1984; Capitanio 1985; Deputte and Quris 1996; Galef and Wright 1995; Lewis and Cherry 1977; Pasterski et al. 2005; Pereira 1995]. Primates, especially, are born into complex social environments and maturity takes years to achieve. In that time, an individual must navigate its changing social environment so as to survive and eventually reproduce. The adult behavioral phenotype is the result of a long period of maturation, and it would be unreasonable to think that such a protracted process would not be affected by the environment in which it occurs.

Wild non-human primate sex-typed development

Non-manipulative research in the wild cannot establish with as much certainty either the environmental or somatic causes of sex-typed development as manipulative research in captivity. As a result, naturalistic research in this area lags substantially behind manipulative and non-manipulative captive work, and it is difficult to neatly separate research on external factors that motivate behavioral sex differentiation from research on innate factors. Despite its challenges, naturalistic research on the causes of behavioral sex differentiation has a number of strengths. Naturalistic studies are valuable because an important potential environmental motivator of sexual differentiation—realistic ecological variation and/or sexually differentiated responses to the natural environment—can only be investigated in the wild. Additionally, animals are not artificially constrained in their association patterns and may therefore exhibit sex differential behavior in the wild that is made impossible for them in captive settings—e.g., dispersal behavior. As a result, the findings of research conducted on naturally occurring populations may be more valid than captive research for understanding development as it occurs in natural populations [Borries et al. 2011].

Social and ecological causes of behavioral sex differentiation

Wherever adult sex differences in diet and foraging behavior are present, those sex differences must develop during the postnatal period, as primates are not strongly sexually differentiated in either social [Barthold et al. 2009; Förster and Cords 2005; Nash 1978] or dietary behavior at birth. Sex differences in adult social behavior are numerous and varied—adults differ by sex in levels of aggressive behavior [Cords et al. 2010], dominance, in how overtly sociable they are [Clarke 1990; Cords et al. 2010; Strier 2002], in how diversified their social networks are [Clarke 1990], and in their three-dimensional spacing relative to other individuals [Ekernas and Cords 2007; Robinson 1981]. Given that social factors have been shown to influence the course of behavioral development in captivity, it is reasonable to suppose that any sex-differential treatment by others during the developmental period may contribute to behavioral sex differentiation.

In general, few sex differences in treatment by other group members have been found at early ages in wild primates. No sex differences have been found in treatment of infants by others in blue monkeys [Förster and Cords 2005] until the age of six months, when mothers begin grooming female infants much more than male infants, and when male infants dramatically increase their rates of approaching and leaving their mothers [Förster and Cords 2002]. No sex differences have found in treatment of infants by others in red-fronted brown lemurs [Barthold et al. 2009], ring-tailed lemurs [Gould 1990], or olive baboons [Nash 1978]. But some sex differences have been observed in some species. Female-female pairs of common marmoset twins are carried more by fathers than male-male or male-female pairs [Yamamoto et al. 2008]. And in yellow baboons, infant maternal rank influences the suckling time of female but not male infants, and experienced mothers initiate contact more with male infants than with female infants [Nguyen et al. 2010]. While sex differences in treatment by others are few and subtle compared to those documented at later ages (below), Nguyen et al. [2010] suggest that adult behavioral sex differentiation might be rooted in very early sex differences in social interactions.

By juvenility, behavioral sex differences are typically more numerous and more pronounced. Females typically show more interest in infants than their male peers [Cheney 1978; Clarke et al. 1998; Cords et al. 2010; Crockett and Pope 2002; Förster and Cords 2005], when sex differences in play are found, males typically play more frequently and more intensely than females, and juveniles often preferentially associate and interact with like-sex partners in both foraging and non-foraging contexts [Cheney 1978; Crockett and Pope 2002; Milton 2002; Pereira 1988; van Noordwijk et al. 1993], although the intensity of those social associations varies by species [Clarke et al. 2007] and this pattern is not ubiquitous [Cords 2000; Nikolei and Borries 1997; Strier 2002]. By juvenility, though, it is very challenging to sort out which parts of sex differential social interaction are internally motivated versus externally motivated or constrained, at least until detailed studies with fine temporal resolution of behavioral sampling and large sample sizes are available.

Studies focusing on the development of sex-typed foraging behavior in the wild are few, but have generated intriguing results regarding the proximate mechanisms that might be involved. Agostini and Visalberghi [2005a] found a number of sex differences in the foraging behavior of both adult and juvenile tufted capuchins. They also found that juvenile males (but not juvenile females) preferentially associated with and directed their food interest toward same-sex adults, and that the amount of time juvenile males spent in association with adult males was positively correlated with their targeting of animal prey, but not with other male-typical foraging characteristics (such as microhabitat foraging preference). The authors suggest that especially complex sex-differential foraging behaviors may require some type of social learning, while simpler ones arise independently. In the same vein, Lonsdorf [2005] convincingly demonstrated that juvenile female chimpanzees imitate their mothers' termite-fishing techniques—a very complex foraging behavior that takes years of practice to perfect. Juvenile males, in contrast, learn termite-fishing only through goal emulation (and are less proficient than females, in the end), but both sexes rely on some degree of social learning for the development of this foraging behavior. Studies of wedge-capped capuchins [Robinson 1981] and long-tailed macaques [van Noordwijk et al. 1993], have demonstrated that juveniles of these species exhibit some elements of adult, sex-typed foraging behaviors, and that they also associate preferentially with like-sexed individuals over opposite-sexed individuals. While particular types of social learning in these species have yet to be identified, social learning of any type [Lonsdorf 2005], if present, would be facilitated by sex-segregated spacing during foraging.

While these studies suggest that the development of some sex differences in foraging behavior might rely on factors such as interaction with same-sex social models, this may not be the case for all species or for all behaviors. In some species, such as white-faced capuchins and common marmosets, juveniles are proficient foragers at young ages [MacKinnon 2006; Schiel et al. 2010]. Additionally, the development of species-typical sex-typed dietary behavior can sometimes develop without role models, as occurred in the population of black-handed spider monkeys who survived initial release onto Barro Colorado Island as subadults and went on to develop species-typical diets and sex-typical association patterns and behaviors on their own [Milton 2002]. Additionally, in some species, such as vervet monkeys, the sex differences in adult diet and foraging schedules are not found in juveniles at all [Harrison 1983]. The variation in developmental schedules of particular sexually differentiated elements of foraging behavior suggests that they are canalized by different proximate mechanisms in different species, and that some may rely on social or environmental factors for their development, while some may result from internally motivated differences in interaction with the same environmental cues.

Biological causes of behavioral sex differentiation

Although primate infants are not strongly sexually differentiated in their behavior at young ages, some infant sex differences have been noted. The earlier a behavioral sex difference appears, the more likely it is to be innate rather than environmentally motivated. As in captivity, sex differences in play behavior have been noted for wild infant blue monkeys and olive baboons, in which males play longer and rougher than females [Förster and Cords 2005; Owens 1975]. And mantled howling monkey infant females react more positively to social interactions initiated by non-maternal group members and engage in social interactions with more group members than male infants [Clarke 1990].

Very little is known about endocrinological development among wild primates [Gesquiere et al. 2005], making it difficult to assess how endocrinological factors might motivate behavioral sex differentiation in natural settings. In yellow baboons, Gesquiere et al. [2005] found that infant males were characterized by high and rapidly declining levels of fecal testosterone, which remained low through juvenility and increased again during the months just before testicular enlargement; female infants were characterized by a similar rapid decline of fecal estrogen, which then increased again as females approached menarche. Testosterone levels also increase in male chimpanzees [Seraphin et al. 2008] and vervet monkeys [Whitten and Turner 2009] as they approach sexual maturity. Notably, the increase in testosterone and estrogen in male and female yellow baboons, respectively, as they approached sexual maturation occurred prior to the unequivocal development of secondary sexual characteristics. Therefore, the use of somatic indicators of sexual maturation may overestimate the age at which hormonal maturation begins and should be used as proxies for sexual maturation with due caution.

Social/biological interaction

Overall, data from the wild are still insufficient to draw conclusions about environmental or biological motivators of sexual differentiation or their interactions across primates as a whole. Even at their best, as previously acknowledged, non-experimental studies in the wild cannot conclusively identify causal factors that motivate sexual differentiation in social behavior. But these studies can reject specific hypotheses of causation, and, where multiple lines of developmental data are available, particular factors likely to be influential in the development of particular sex-typed behaviors can be identified by revealing their correlational relationships [Fragaszy and Perry 2003].

One example of the potential of this approach to understanding the complex causes of behavioral sex differentiation comes from the large body of work on the population of yellow baboons at Amboseli, Kenya. The development of sex differences has been at least a partial focus of many studies on the Amboseli baboons, from a number of perspectives, and from before birth to the end of the reproductive lifespan.

A number of maternal effects on aspects of life history that are closely tied to reproductive success have been noted in this population. For offspring of both sexes, maternal dominance rank is positively correlated with the pace of offspring maturation—the offspring of high ranking females reach maturational milestones earlier. For daughters, maternal dominance rank influences both the age at first menarche and the age at first birth [Altmann et al. 1988]. For sons, maternal dominance rank influences the age at testicular enlargement (a signal of pubertal onset) and the age at which adult rank is achieved [Alberts and Altmann 1995b]. This is partly due to the fact that offspring of high-ranking mothers grow faster, but maternal rank has an independent positive effect on the attainment of reproductive maturational milestones, even after controlling for growth rates [Altmann and Alberts 2005]. For daughters, these benefits of a high-ranking mother translate directly into increased reproductive success. For sons, the age of first consortship is dependent on a number of additional factors, not least of which is the number of reproductively available females, but age at adult rank achievement and age at first consortship are positively correlated [Alberts and Altmann 1995a]. The proximate mechanisms that underlie these maternal effects on maturational schedule are not yet clear, but the Amboseli data provide a number of interesting possibilities, discussed below.

First, maternal dominance rank during pregnancy and shortly after birth may influence the development of offspring endocrine profiles. In wild snowshoe hares, predation pressure has been shown to increase maternal stress hormone levels, and offspring conceived in high-predation environments also have increased stress hormone levels as adults. It has been suggested that this phenomenon may be responsible for the enigmatic persistence of suppressed population-level reproductive rates even after population-level predation pressure has decreased [Sheriff et al. 2010]. The evidence for similar mechanisms operating in baboon development is not entirely clear. Early maturing baboon males consistently have higher fecal glucocorticoid and testosterone levels than late maturing males, but in a study of a large sample of males, this effect was not statistically significant across the lifespan [Gesquiere et al. 2005]. Given, though, that a number of other factors influence circulating glucocorticoid and testosterone levels in both males and their mothers—such as rainfall, temperature [Beehner et al. 2005; Gesquiere et al. 2005; Gesquiere et al. 2008; Gesquiere et al. 2010], variation in the social environment, and individual variation in hormone response [Sapolsky 1991; Sapolsky 1985]—the lack of statistical significance here may not indicate a lack of biological significance. Regardless, maternal rank at the time of a male's conception was found to be unrelated to hormone levels for either sex across the subadult period [Gesquiere et al. 2005], suggesting that this is not the pathway by which maternal dominance rank regulates sons' maturational schedules. On the other hand, another study on the same population found that maternal dominance rank at the time of a male's conception accounted for 42% of the variance in adolescent male fecal glucocorticoid concentrations in the 20 months prior to their natal dispersal—sons of high-ranking mothers had lower fecal glucocorticoid levels than sons of low-ranking mothers [Onyango et al. 2008]. Onyango et al. [2008] suggest that this could be of selective importance because chronically elevated levels of glucocorticoids are associated with stress-related disease pathology. Perhaps the maternal effects on sons' stress physiology are only detectable during the developmental stage when sons are gearing up for what will likely be their most costly life event—natal dispersal [Alberts and Altmann 1995a]; perhaps, over the subadult period in general, underlying maternal effects on sons' stress physiology are attenuated by the effects of other factors. While these results have not yet clarified exactly how maternal rank is related to offspring endocrine development, they do suggest that *something* about maternal rank is an important proximate factor.

Second, maternal physiology may modulate mothers' behavioral responses toward their offspring. Late gestational fecal glucocorticoids are positively correlated with maternal responsiveness to infants [Nguyen et al. 2008], suggesting that hormonal modulation of some characteristics of the mother-infant relationship does occur in baboons. Late gestational fecal estrogen and testosterone concentrations in multiparous females are significantly higher when the fetus is male versus when the fetus is female [Altmann et al. 2004], suggesting that fetal sex may influence maternal hormone profiles in different ways, which may in turn influence maternal behavior toward infants in ways that vary according to infant sex. Prenatal fecal estrogen concentrations are negatively correlated with suckling time in infant daughters, but even though prenatal estrogen levels are higher when carrying sons, they do not influence suckling time in sons [Nguyen et al. 2010], suggesting (unsurprisingly) that the relationships among fetal sex, maternal gestational physiology, and maternal-infant interaction are complex.

Even though the physiological (or other) causes of variation in maternal behavior toward infants are not yet well-understood, it is clear that the mother-infant relationship sometimes varies according to offspring sex in potentially important ways. Experienced mothers initiate changes in infant contact more than less experienced mothers, but this effect is more pronounced with male infants [Nguyen et al. 2010]. High ranking mothers carry their infants the least, and this effect is stronger with male infants than with female infants [Samuels and Altmann 1992].

And high maternal dominance rank is negatively correlated with suckling time in infant daughters, but not in infant sons [Nguyen et al. 2008]. Decreased rates of infant carrying and more changes in infant contact may both promote infant independence, which may in turn promote the earlier acquisition of social and ecological competence. This would be an important effect, as foraging efficacy in yearling females (with respect to protein and energy intake) has been shown to reliably predict the probability of surviving to adulthood, female fertility, and female reproductive lifespan [Altmann 1991]. The apparent maternal bias toward encouraging the independence of sons more than daughters and the apparent maintenance of suckling rates for sons despite the action of maternal hormone physiology that reduces them in daughters could reflect the much greater potential impact that increased caloric intake has on subadult male growth rates and maturation as compared to those of subadult females [Altmann and Alberts 2005].

Mothers, of course, are not the only individuals who can influence subadult developmental trajectories; indeed, in baboons, fathers also influence the maturational schedules of their offspring. Fathers selectively support their juvenile offspring in agonistic encounters [Buchan et al. 2003], and paternal presence in the group is associated with reduced time to maturation for daughters. Paternal presence is also associated with reduced time to maturation for sons, but only for fathers of high rank at the time of their sons' births [Charpentier et al. 2008].

Certainly, subadults, themselves, are expected to be active participants in shaping their developmental trajectories, as they, above all others, have the most to gain from their own development. Nguyen et al. [Nguyen et al. 2010] suggest that this effort may begin in the womb, with fetuses producing glucocorticoids that induce maternal responsiveness. Postnatally, yellow baboons, like those of many other species, exhibit sexually differentiated choices of social partners and social interactions. Juvenile males put more effort into maintaining proximity to adult males than do juvenile females, while juvenile females put more effort into maintaining proximity to unrelated adult females than do juvenile males [Pereira 1988]. Among unrelated adult female social partners, juvenile females preferred lactating females and those from high-ranking matrilines, while juvenile males preferred cycling females and showed no preference for female rank [Pereira 1988]. These types of juvenile social preferences seem to correspond well with the expectation that juveniles will tailor their social associations in ways that will facilitate the acquisition of current and/or future benefit [Pereira 1988]. Male coalitionary support is an important factor in the acquisition of and maintenance of male dominance and/or access to females [van Schaik et al. 2004], which is closely tied to male reproductive success [Schülke et al. 2010]. Since yellow baboons are female philopatric, resident females (but not males) will be the lifelong social partners for juvenile females. Relationships with lactating females provide the possibility of access to interaction with their infants, which are attractive to females of most species, possibly because female primates have long been under selection to be responsive to infants, as it makes them better mothers (thereby increasing their reproductive fitness) [Silk 1999]. Relationships with higher ranking females are likely to be of more current and future benefit than relationships with lower ranking ones. Males, though, rise above all females in dominance rank as they surpass them in physical size [Pereira 1995], so the rank of their female social partners is likely to be much less important than the reproductive status of those partners. Lastly, juveniles may structure their social relationships so as to help them modulate the negative effects of stressors, as seen in adult female chacma baboons [Wittig et al. 2008].

The available data on sexually differentiated development from Amboseli is beginning to shed light on the workings of the complex and interactive system of social, ecological, and endocrinological factors that together underpin the differentiated life histories and social relationships of male and female baboons. It illustrates the promise of work that seeks to understand linkages between maternal physiology and offspring physiology, maternal physiology and behavior, and offspring physiology and behavior in naturally living primates.

SHORTCOMINGS OF PREVIOUS RESEARCH

The false dichotomy of social versus biological, and environmental versus innate

All available data indicate that the social environment shapes individual biology in selectively important ways (e.g., human life history schedule [Ellis et al. 1999; Kuzawa et al. 2010] or modulation of hormonal effects on primate aggression [Zumpe and Michael 1996]), which then shapes how individuals interact further with their social environments. Sometimes, even, historical environments that individuals themselves did not experience affect their biology via environmental effects on the biology of their forbears [Sheriff et al. 2010], and this could be true of social environments as well. All researchers of sex-typed development in humans and non-humans probably now acknowledge that the social environment and individual biology are so interactive that they really do not stand alone: “We should not be tempted to think that even the bodies of infants are, so to speak, all biology and no culture” [p. 90, McIntyre and Edwards 2009]. But still, the tendency to dichotomize and oppose social and biological causes of behavioral development persists, especially in the arena of human sex-typed development. Granted, it is possible to use a dichotomy as a heuristic while still recognizing and seeking to understand the variation within/around it [Worthman 1995]. But often it seems as if some researchers consider biologically motivated behavioral sex differences to be immutable, natural, adaptive, and therefore desirable, while socially motivated sex differences are considered easily changed, separate from the natural world, non-adaptive, and therefore of questionable value.

How, though, in studies of mammals, can the social be considered non-biological? If the social interactions of infant rats effect sexually differentiated physiological change that results in sexually differentiated behavior, is this a biological or a non-biological process? Insofar as all mammalian biology has in common a single, defining feature that is simultaneously somatic and social—infant nourishment by mother's milk—nurture is an integral part of successful mammalian nature, and there was never really any good reason to conceive of the two as separable. It is for this reason that I distinguish between motivators of behavior that are intrinsic versus extrinsic to the individual. Intrinsic motivators of sexual differentiation stem from within an individual; extrinsic motivators of sexual differentiation are external to the individual. Intrinsic factors can be social, psychological, somatic, hormonal, genetic, etc., depending on the research question. Extrinsic factors are ecological and social. Both intrinsic and extrinsic behavioral motivators may have been previously shaped by each other. There is no claim that intrinsic factors are "innate" and, by implication, independent of previous influence by extrinsic factors.

The implications of a continued reliance on a false social/biological dichotomy in research on sex-typed behavior are not insignificant. Often built on this shoddy foundation is the implicit (and sometimes explicit), incorrect assertion that elements of human gendered behavior that are shared with non-human animals must be somatically rather than socially mediated [Joseph 2000]. But this assumption is unfounded. Instead, the fact that some elements of behavioral sex differentiation in non-human animals are socially mediated suggests that some human socially motivated behavioral sex differences may have been selected for throughout human evolutionary history. Some socially mediated behavioral characteristics may be adaptive. Additionally, some sex-typed social/physiological/psychological feedback loops may be self-perpetuating and stable over long periods of time, but that does not necessarily mean that they are immutable, intrinsic properties of the biological sexes [contra Browne 2006; Byrd-Craven and Geary 2007; Joseph 2000]. This point is most clearly illustrated by Sapolsky's "pacific" baboons, a troop that developed atypically affiliative patterns of social interaction among males and between males and females after the most aggressive and dominant males in the group died of tuberculosis. Not only did the original low-ranking surviving males have unusually friendly interactions for baboons, but so did later immigrant males [Sapolsky and Share 2004].

Although the assumption of many that sex differences that are found across mammals can be assumed to be "biological" or "ecological" in nature and not "socialized" is unfounded, it is an empirical question that can be tested. Additionally, the best way to tease apart which socialized human sex differences can reasonably be considered adaptive, and which cannot, is through comparative analysis of socialized sex differences in non-human primates.

Shortcomings of non-human primate data for understanding adaptation in sex-typed development

Unfortunately, this type of comparative analysis is not yet possible, [Förster and Cords 2005], because studies that have investigated the development of sex differences in behavior in unprovisioned, wild primate populations remain too few [Agostini and Visalberghi 2005; Altmann 1980; Altmann and Pereira 1985; Clarke et al. 2007; Förster and Cords 2002a; Förster and Cords 2005; Gould 1990; Hashimoto and Furuichi 1994; Hiarawa-Hasegawa 1989; Pereira 1988; Zucker and Clarke 1992]. Most of our knowledge of primate sex-typed biobehavioral development derives from captive research on catarrhines—specifically, common chimpanzees [Anestis 2005; Anestis 2006; Bard 1994; Bard and Gardner 1996; Davenport et al. 1973; Fritz et al. 1992; Howell et al. 2006; Maki et al. 1993; Randolph and Mason 1969; Spijkerman et al. 1995; Spijkerman et al. 1996; Spijkerman et al. 1997; Turner et al. 1969] and cercopithecine monkeys [Andrews and Rosenblum 1991; Andrews and Rosenblum 1994; Bachevalier and Hagger 1991; Boccia et al. 1991; Boccia et al. 1994; Brown and Dixon 2000; Chamove et al. 1967; Champoux et al. 1989; Chism 1986; Clarke and Snipes 1998; de Waal and Johanowicz 1993; Deputte and Quris 1996; Deputte and Goy 1991; Drago and Thierry 2000; Eaton et al. 1986; Fairbanks and McGuire 1988; Goy et al. 1988; Gust 1995; Harlow 1962; Maestripieri 1994; Maestripieri 2001; Maestripieri 2004; Maestripieri 2005a; Maestripieri and Megna 2000; Maestripieri and Ross 2004; Parker et al. 2006; Preston et al. 1970; Richards et al. 2009; Rosenblum 1987; Rosenblum and Paully 1984; Rowell and Chism 1986;

Ruppenthal et al. 1976; Ruppenthal et al. 1974; Ruppenthal et al. 1991; Sackett 1972; Sackett et al. 2002; Sanchez et al. 2010; Schino et al. 2001; Seay et al. 1972; Setchell and Dixson 2002; Setchell et al. 2001; Suomi 1997; Suomi et al. 1983; Suomi 1987; Tartabini and Dienske 1979; Thornton and Goy 1986; Tomaszycki et al. 2001; Tomaszycki et al. 2005; Toscano et al. 2009; Wallen 1996; Wallen 2005; Wallen et al. 1977; Wallen et al. 1981; Wallen et al. 1995; Wallen and Zehr 2004; Worlein and Sackett 1997]. Important contributions on other taxa can be found in the literature on captive primates [Birnie et al. 2011; Byrne and Suomi 1998; Dixson 1993; Epple et al. 1990; Mayeaux et al. 2002; Mayeaux 2008; Nash 1991; Nash 2003; Palagi et al. 2002; Paukner and Suomi 2008; Pereira 2002; Pereira 1995], and some of this work is on free-ranging captive animals living in species-typical social settings that may mirror developmental environments in the wild [Berman 1980; Berman 1992; Berman 1997; Devinney et al. 2001; Fedigan and Zohar 1997; Pereira 1995]. But nutritional constraints are usually relaxed in captivity, often accelerating some aspects of development [e.g., Altmann and Alberts 1987], and altering the social milieu in ways that can impact social development [Rosenblum and Paully 1984] and intrinsic physiology [Rangel-Negrín et al. 2009]. As a result, studies of wild populations are needed to validate extrapolation from captive studies to wild populations, to discover evolutionarily significant processes of behavioral sex differentiation that do not occur in captivity, and to identify developmental processes that are appropriate for further investigation in captivity.

Overall, captive work has demonstrated that the social environment drives social development, but has shed less light on *which* particular elements of the social environment are causally linked to the development of later behaviors, especially in natural environments. This body of research details the behavioral components necessary for the socialization of sex-typed behavior in non-human primates, but has yet to clarify whether, which, or how particular patterns of social interaction shape particular elements of primate sex-typical social development in complex socioecological settings. Comparative study performed on developmental systems in the wild will generate data that are unquestionably applicable to understanding the functioning of those systems in natural environments as well as to the evolution of developmental system components.

RESEARCH GOALS

The overall goal of this study is to increase scientific understanding of the intrinsic and extrinsic social factors likely to be involved in the development of adult sex-typical primate behavior in order to help clarify the evolutionary history of the intrinsic and extrinsic social factors thought to be important in human sex-typed gender socialization. Because causation of developmental sex differentiation is complex and the social factors involved in normative sex-typed development remain poorly understood, further investigation is best focused on simple, fast-developing primate models. Knowledge gained from these models can be applied to and will help focus future investigations of more complex, slower-developing taxa. Captive research has shown that gonadal hormones in most species are quiescent after infancy and prior to adolescence, and that in general, primate prepubescent behavior is largely unaffected by gonadal hormones [Wallen 2005]. In order to isolate social causes and limit, as much as possible, the confounding influences of sexual differentiation due to gonadal hormone production and ecological niche differentiation and, study will focus on the prepubescent developmental stages of a gregarious, monomorphic species.

This study will compare male and female social development from birth to just prior to sexual maturity in wild ring-tailed lemurs in order to identify social factors likely to be important for sex-typed development in this species. Ring-tailed lemurs were chosen as a study taxon for a number of reasons.

First, ring-tailed lemurs are among the most primitive of the gregarious primates. Because strepsirrhines have not received much attention in studies of sexual differentiation compared to the haplorhines, this study will help to fill out our understanding of primate sex-typed development and ameliorate one of the major shortcomings of previous developmental research. Second, infant *Lemur catta* have substantial opportunity for social interaction at early ages. Infants first break contact with their mothers in the second week of life and engage in dyadic social play as early as the third [Gould 1990]. Additionally, mother-infant pairs are the objects of intense affiliative contact initiated by other group members during infants' first weeks of life, providing opportunity for interaction between infants and non-maternal group members while infants cling to their mothers [Nakamichi and Koyama 2000]. Third, ring-tailed lemurs develop relatively quickly and have a relatively simple demographic structure (annual age cohorts) resulting from their strict seasonality. They have a one-year inter-birth interval, and reach sexual maturity in two years in captivity (and sometimes in free-ranging food-supplemented populations) [Gould et al. 2003; Overdorff et al. 1999]. As a result, and in contrast to species with slower life histories, all group members occupy discrete, easily identifiable age/sex classes, and it is feasible to examine the entire (or nearly so) prepubescent period over the course of one year using mixed longitudinal sampling of infants and juveniles. Fourth, they live in relatively large multi-male, multi-female social groups (*L. catta*, 5-30 individuals [Gould et al. 2003] but have relatively small home ranges [Sussman 1974; Sussman 1991], such that 6-8 large social groups typically provide sufficient numbers of infants and juveniles for study by a single researcher (in contrast to most other lemur species that live in smaller groups). Lastly, they are not strongly size-dimorphic [Kappeler 1990], minimizing, as much as possible for species with multi-male multi-female social organization, the contribution of sex differences in ecology and life history schedule to the development of sex-typed behavior.

Study of sex-typed development in ring-tailed lemurs will also maximize opportunities for more immediate comparative study in several ways. Because of their phylogenetic distance from the better-studied cercopithecoids and their particular combination of social similarities to and differences from the baboons in particular—multi-male, multi-female social structure, promiscuous mating, stable dominance relationships, and matrilocality in common [Pereira 1993b] but body size monomorphism and female dominance in contrast [Pereira and Kappeler 1997]—ring-tailed lemurs make a good comparative taxon to those that have already been well-studied. Furthermore, study focusing on the social causes of behavioral sex differentiation in ring-tailed lemurs dovetails with previous and ongoing work by the Lemur Biology Project at Beza Mahafaly Special Reserve and its associates on ring-tailed lemur ecology [Sauther et al. 1999], health [Sauther et al. 2002], life history [Gould et al. 2003], social behavior [Gould 1997], endocrinology [Gould and Ziegler 2007; O'Mara 2008], and ecological and endocrinological development.

Theoretical Model and Hypotheses

Whenever adult social roles differ between the sexes, as long as infants are less sexually differentiated than adults, infants' developmental trajectories (and the processes that drive them) will also differ between the sexes [Hemelrijk and Dekogel 1989] (Figure 2-1). In such cases, if socialization plays a driving role in the development of sex-typical behavior, sex differences in extrinsic and/or intrinsic subadult social behavior must be present.

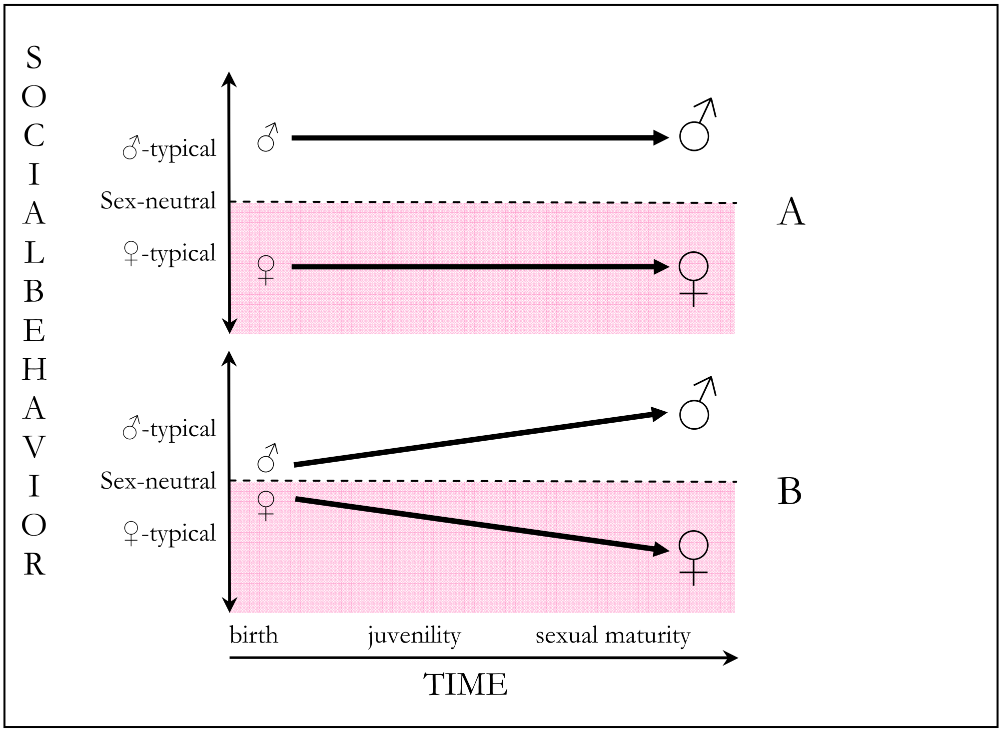


Fig. 2-1. Schematic of hypothetical behavioral developmental trajectories when infants are born differentiated by sex versus undifferentiated.

This study aims to test, specifically, whether extrinsic sexually differentiated social interactions are important for the development of intrinsic behavioral sex difference. This approach should definitively identify extrinsic social factors that are not important in sex-differential socialization, preventing them from obfuscating relationships among those that are, both in this and future work. Furthermore, it will identify extrinsic social factors likely to be influential in the development of particular sex-differential intrinsic social behaviors by revealing their correlational relationships [Fragaszy and Perry 2003]. Socialization can be intrinsically driven just as it can be extrinsically driven—recall that individuals may have sex-typed responses to the same stimulus. However, because this study does not address variation in prenatal, neonatal, and postnatal physiological experience, it is impossible to assess whether the intrinsic subadult behavioral sex differences identified in this study represent sex-differential responses to the same social stimulus or intrinsically motivated sex-differential behavior unrelated to extrinsic social factors. Therefore, this study will be limited to investigating the importance of extrinsic processes of socialization involved in sex-typed behavioral development in this species.

Identifying which adult sex-differential behaviors are candidates for socialization is pre-requisite to identifying potential extrinsic socialization processes. In order for sex-typical behaviors to be shaped by patterns of subadult social interaction, they must have an ontogenetic component. They cannot be strongly present at birth, and cannot arise suddenly upon sexual maturity, when gonadal hormones become active and start to play a significant role in driving sex-differential behavior [Wallen 2005] (Figure 2-2). If infants are adult-like in their degree of behavioral sexual differentiation, then no developmental explanation is needed to account for adult sex-typical behavior (Figure 2-1).

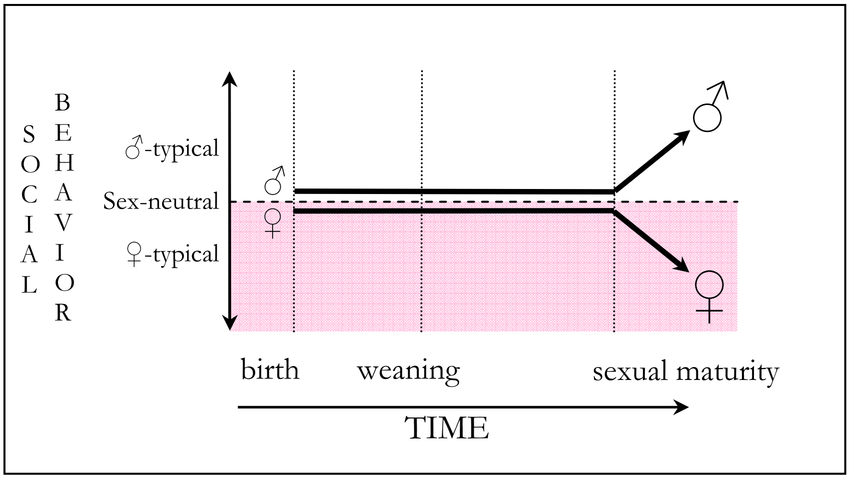


Fig. 2-2. Schematic of hypothetical behavioral sex differentiation caused only by sexual maturation.

Intrinsic adult sex-typed social behaviors that were candidates for socialization during the subadult period were identified by testing for:

1) Quantifiable sex difference in intrinsic social behavior in adulthood and

2) demonstrable ontogenetic components of those sex-typed behaviors prior to sexual maturation (adult levels of sex difference cannot be present at infancy and sex difference must be apparent before sexual maturity).

Tests for quantifiable adult behavioral sex differences in patterns of aggression, dominance, submission, affiliation, proximity, infant interest, responsibility for proximity maintenance, and scent marking are explicated in chapter 4. Tests for the ontogenetic components of documented intrinsic adult sex-typed social behaviors are explicated in chapter 5.

After adult sex-typed social behaviors with a subadult developmental component were identified, patterns of extrinsic social interaction with group members that might play a causal role in shaping the development of species-typical sex differences in intrinsic adult behavior were isolated by identifying:

3) sex differential treatment of subadults by other group members—specifically, sex differences in receipt of agonism and affiliation from, and proximity patterns to and responsibility for proximity maintenance to mother and others.

Once sex differences in subadult treatment by others were identified, I qualitatively assessed:

4) whether the appearance of those sex differences in extrinsic social interactions preceded or coincided with the development of particular intrinsic sex differential behaviors (e.g., increased receipt of aggression by infant males compared to infant females might precede the development of spatial segregation by sex).

Extrinsic social interactions that do not differ by sex, and that do not precede or coincide with sexual divergence in a given intrinsic social behavior cannot be responsible for sexual differentiation of that social behavior.

Although the present study focuses on discovering social factors responsible for shaping the development of sex-differential behavior, it is probable that the development of sex differences in ecology also causes sex differences behavior. In that case, sexual differentiation in behavior is expected to coincide with sexual differentiation in ecology (Figure 2-3). Behavioral sex differentiation that occurs prior to the onset of sex differences in ecology, though, cannot be explained by these factors. Tests for extrinsic sexually differentiated social and ecological factors and qualitative assessments of their importance in the development of intrinsic sex-typed social behavior are presented in chapter 6.

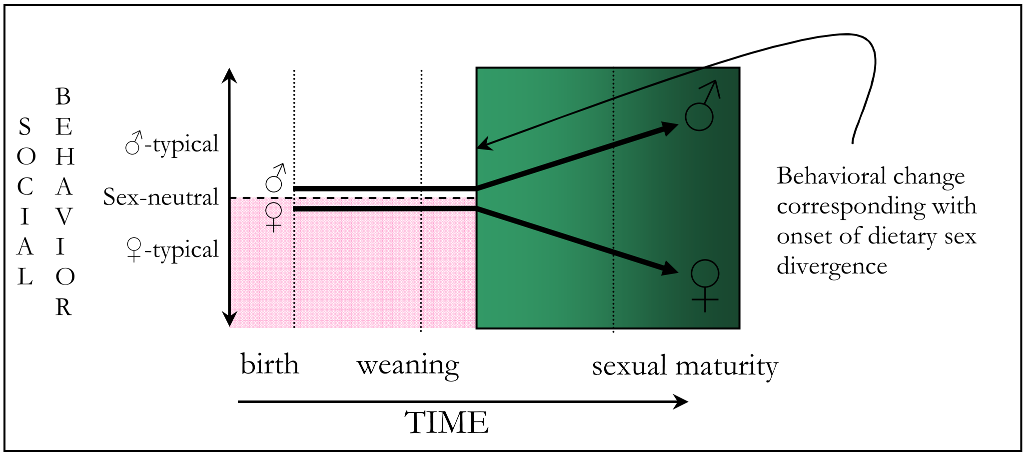


Fig. 2-3. Schematic of hypothetical behavioral sex differentiation caused only by ecological sex differentiation.

CHAPTER 3: METHODS

FIELD SITE

Beza Mahafaly Special Reserve (BMSR) is situated in a dry forest in southwestern Madagascar [Sauther et al. 2002] at 23° 30' S latitude and 44° 40' E longitude [Loudon 2006] (Figure 3-1). The reserve comprises two parcels of land situated within a larger tract of continuous forest. Parcel 1 contains 80 ha of riverine gallery forest [Sauther et al. 1999]. Due to a recent park expansion, Parcel 2 now contains approximately 4,000ha of didierea spiny forest. This study was carried out in and around Parcel 1. Forest to the west and south of Parcel 1 is relatively degraded as a result of firewood collection and grazing by local livestock. Parcel 1 is bordered in the east by the Sakamena River, which forms a water barrier in the rainy season but not the dry season, when the riverbed is completely dry. East of the river and at the river's western edge south of Parcel 1, land has been cleared for cultivation of crops (Figure 3-1). As of this writing, the reserve operates under the auspices of Madagascar National Parks. There is no hunting of lemurs in this area, and Parcel 1 is fenced to prevent incursion by cows and goats from surrounding villages. The fence does not entirely prevent forest use for grazing purposes, but Parcel 1 is substantially more vegetated than the surrounding forest [Sauther and Cuozzo 2009].

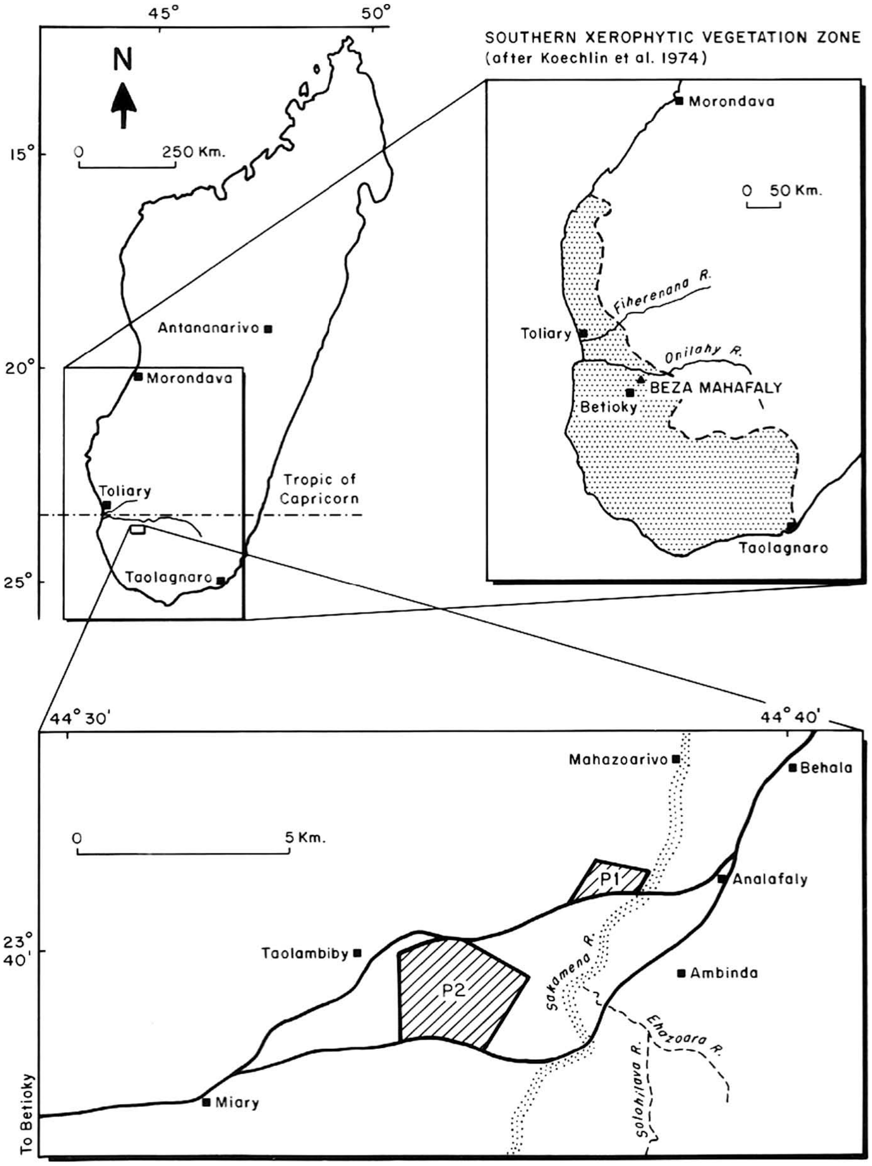


Fig. 3-1. Map of Beza Mahafaly Special Reserve [Sussman and Ratsirarson 2006].

INDIVIDUAL IDENTIFICATION

The ring-tailed lemurs in Parcel 1of BMSR have been studied for decades [Sauther et al. 1999] and are well-habituated to the presence of human observers. Most individuals of ≥ 2 years of age from nine social groups were individually marked with collars and tags prior to the beginning of behavioral data collection in September, 2008. A few adults and all juveniles and infants were not marked with collars and tags at the onset of data collection. To facilitate quick, reliable individual identification, some of these individuals were dye-marked. Six adults, six juveniles, and eight infants were marked with Nyanzol-D, a long-lasting, non-toxic dye [Honess and MacDonald 2003]. Using a solution of Nyanzol-D, isopropyl alcohol, and hydrogen peroxide according to Honess & MacDonald [Honess and MacDonald 2003], I squirted target individuals from a distance of 1.5m-3m using a hypodermic syringe with a needle, making sure that the individuals were not looking at me when they were squirted. This was so that dye did not accidentally reach their eyes, noses, and/or mouths, and to ensure that they did not learn to associate human observers with being squirted with liquid. After the successful application of dye, I followed the individuals to ensure that they did not groom the dye before it was dry. If they tried to groom the dye, I distracted them by making noises or following them closely enough that they kept moving until they lost interest in grooming the dye. Usually, I marked individuals while they were foraging, and most of them returned to foraging within a minute of dye application. I marked young infants when they were clinging to their mothers to avoid getting dye on their faces. I did not dye infants less than 2 months old, as their regular association with their mothers prior to that time made them easy to identify. Dye re-application was necessary for some individuals after a period of 3-4 months. After my initial stock of isopropyl alcohol was exhausted, I used locally distilled rum in its place, which was equally effective, much less costly, and reliably available. It should be noted that before I was able to acquire hypodermic needles in Tulear, I attempted dye-marking with only an open syringe, but this made aim rather poor, and when I did succeed in "hitting" animals, too much dye was applied by this method, such that the dye did not dry quickly, and it was a challenge to prevent animals from ingesting it. I therefore strongly discourage the use of any application method that results in a relatively large stream of Nyanzol-D hitting an animal (water gun, syringe without a needle-like applicator, etc.).

BEHAVIORAL SAMPLING

Behavioral data were collected from a mixed longitudinal, cross-sectional sample of infant (0-1 years old), juvenile (1-2 years old), and adult (>2 years old) *Lemur catta* from September 2008 to August 2009 using focal individual sampling [Altmann 1974]. Behavioral data collection began during the September 2008 birth season. Thus, the 2008 infant cohort was newborn at the onset of data collection and approximately 1 year old at the termination of data collection, while the 2007 cohort (juvenile, in this study) was approximately 1 year old at the onset of data collection and 2 years old at the termination of data collection. All adult females in the sample were non-maternal during data collection—they did not have infant offspring. All adult males and most adult females in the adult dataset were ≥3 years old during data collection, but in order to maintain a sufficient sample size of adult females without infants, a few 2-3 year old females were sampled. Each age class was evenly divided by sex to the extent possible given availability of individuals across the nine individually marked, habituated study groups.

Adult females without dependent offspring were chosen to represent the adult behavioral trajectories to which infants and juveniles would be compared because the sex-typed behavior of adult females with dependent infants would be overlain by the constraints and motivations of motherhood. Adult females without infants should provide a better estimate of baseline adult sex-typed behavior and because infants, juveniles, and adult males cannot have dependent infants, adult females without infants are a better comparator against which to assess the development of baseline sex-typed social behavior in subadults. Adult females with dependent infants were still considered “adult females” when they were the social partners of subjects.

Sampling of groups rotated through a set group order. Data collection for a given group continued until each study subject in the group had been sampled for one to two hours. Completion of a sampling cycle for one group could take anywhere from one to four days, depending on the number of individuals sampled in the group and observation success. Completion of the entire group rotation took an average of 10 days, such that each group, and thus each subject, was usually sampled twice per calendar month. The target was 2-4 hours of focal data per subject per month.

Data were collected 6 days per week from just after dawn until just before dusk with a daily lunch break that commenced upon the onset of the individuals’ mid-day rest period. The observation day was divided evenly into 4 temporal segments: early morning, late morning, early afternoon, and late afternoon. Within groups, individual sampling order was random, except that it was balanced across the day during a single group observation cycle as much as possible. Focal individual follows were 30 minutes in duration to ensure that each subject could be sampled at multiple times of day within each group sampling cycle. Focal individual follows included a combination of continuous data collection of social interactions with the focal individual and instantaneous data collection for other behavioral measures at three-minute intervals (detailed below). If an individual was out of sight on the interval, the behavior exhibited closest to the interval within ± 15 seconds of the interval was recorded. If the focal individual was not seen within ± 15 seconds of the interval, it was designated "out of sight." Focal observations with more than two "out of sight" scans were discarded. If a focal observation was discarded, I attempted to relocate the focal individual. If the individual could be located within 10 minutes, I re-started focal observation of the same individual. If the individual could not be found (or seen due to visibility constraints) within 10 minutes, I moved on to observation of the next visible individual in the sampling order.

Behaviors were recorded using a detailed ethogram that was designed to be as comparable as possible to those used in other studies of lemur social behavior (Table 3-1) [e.g., Pereira and Kappeler 1997]. Focal individual activity (Table 3-1), distance from the nearest neighbor within 5m, identities of all neighbors in contact, within reach ($0m > x \geq 0.3m$) and within 3m ($0.3m > x \geq 3m$), position within group (Figure 3-2), canopy position (Figure 3-3), and group activity state were recorded at three-minute intervals [Altmann 1974]. Not all behaviors in the ethogram were used in instantaneous sampling; those that were are marked as "scan" or "both" in Table 3-1.

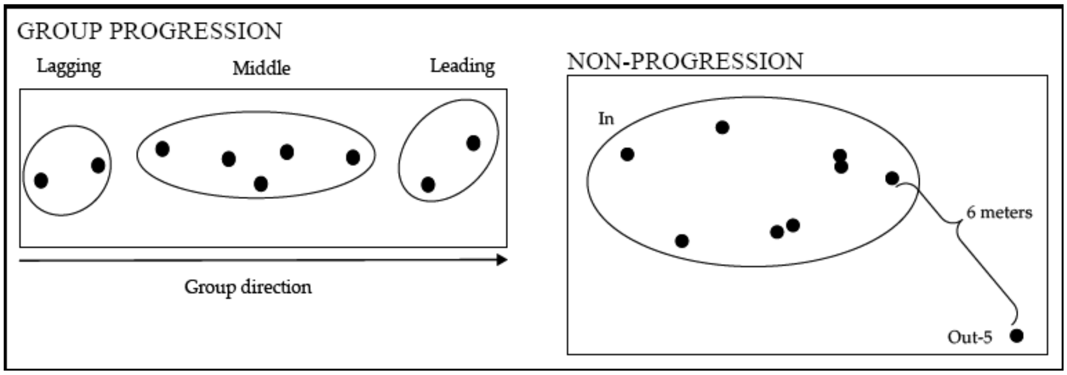


Fig. 3-2. Position within group. During linear group progressions, focal individuals were designated as leading, middle, or lagging. All other times, focal individuals were

designated as "in" or "out." When designated "out," distance from the nearest group member was recorded in 5m increments.

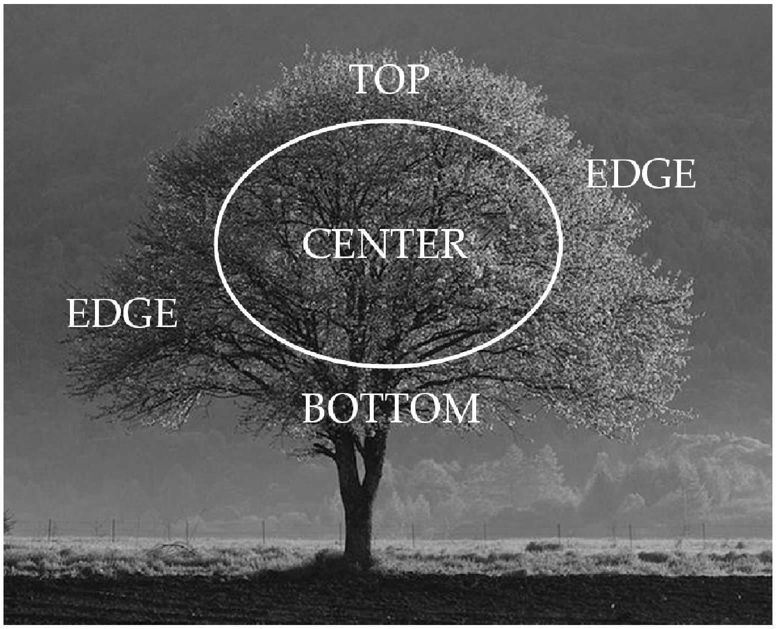


Fig. 3-3. Canopy position.

All social interactions with the focal individuals and the direction of those behaviors (*i.e.*, groom other versus groomed by other) were recorded continuously on a handheld Raon micro-PC using JWatcher V1.0 [Blumstein et al. 2000]. Behaviors recorded are marked as "continuous" or "both" in Table 3-1. Time spent passively in contact with and within reach of a nearest neighbor were recorded during continuous data collection, but all overt social interactions that occurred while in contact with or within reach of another were recorded preferentially over passive contact and passive time within reach. Similarly, though the occurrences of all social interactions were recorded, the JWatcher software can only record the elapsed time of a single behavior. Multiple behaviors cannot be simultaneously timed. Therefore, for cases in which simultaneous social interactions occurred, I recorded the occurrence of all behaviors in order to preserve the sequence of events associated with approaches to and leaves from the focal, but then preferentially recorded the time of the behavior that was more active on the part of the focal individual (e.g., the time the focal groomed another over the time the focal was groomed by a third). As a result, I do not have accurate bout counts for behaviors like grooming—they are inflated.

Scent marking events were recorded during continuous data collection as social interactions because they are social communications. Vocalizations, although they are rightly considered social interactions, were not recorded during continuous data collection for two reasons. First, the number of social interactions that could be recorded during continuous data collection was limited by the JWatcher software, and the number of distinct *Lemur catta* vocalizations catalogued by Pereira & Kappeler [1997] were too numerous to include. Second, the recording equipment and analytical software necessary for a rigorous bioacoustical analysis of vocalizations was not available to me, and such an analysis was beyond the scope of this study.

During instantaneous sampling, only one behavior was assigned for each time interval [Martin and Bateson 1986]. However, the behaviors in the ethogram used during instantaneous sampling are not all mutually exclusive. Therefore, if two behaviors occurred simultaneously on an interval (e.g., avoidance of another individual during travel), priority was given to social behaviors over non-social behaviors. Similarly, more than one social behavior can occur simultaneously (e.g., cling to mother and groom). In such cases, priority was given to the more overt social interaction of the two, or the social interaction that is more active on the part of the focal individual (groom supercedes cling, and cuff supercedes receipt of grooming). If an individual was engaged in overt social interaction with more than one individual (e.g., the focal could be grooming one individual and groomed by another), the behavior directed by the focal individual toward another was given preference.

Nearest neighbor designation can be similarly ambiguous. Here, nearest neighbor designation was always preferentially assigned to individuals with whom the focal was engaged in overt social interaction. Rarely, an individual was engaged in overt social interaction with an individual that was not its physically closest conspecific (e.g., an individual can engage in the agonistic "look away" with another, physically distant individual for long periods of time while other individuals are in closer proximity to the focal). More often, an individual was equidistant to more than one individual without being engaged in social interaction with any of them. For non-contact proximity decisions of these types, if the focal individual was equidistant to more than one individual on an interval, the individual that the focal individual was facing was designated the nearest neighbor. If the focal individual was in contact with more than one individual on an interval, the individual with whom the focal had the most body contact was designated as the nearest neighbor. If the focal individual had the same amount of body contact with more than one individual, the neighbor that the focal individual was facing was designated as the nearest neighbor. In the very few cases where a nearest neighbor could not be assigned using the above decision rules, I chose the nearest neighbor based on my subjective assessment of which of the individuals in question was more often the focal individual's nearest neighbor. On the rare occasions in which this last decision rule was employed, it biased nearest neighbor assignments in the direction of offspring and mothers associating preferentially—a bias which should be rendered insignificant by the strong real preferential associations of those individuals.

SAMPLES

The aforementioned sampling regime resulted in just over 1000 hours of behavioral data: 375 hours of focal data on infants, 148 hours on juvenile females, 157 hours on juvenile males, 168 hours on adult females, and 170 hours on adult males. These samples averaged 14 hours of observation/month for each age/sex class. Age/sex class membership changed throughout the year when individuals disappeared from the study population, but infants who were observed from birth to study termination were observed for an average of 39.6 hours each, juveniles observed for the entire 12-month study period were observed for an average of 39 hours each, and adults observed for the entire study period were observed for an average of 34 hours each. These samples are comparable to published developmental studies both in captivity [e.g., 1 hour/week per mother-infant dyad, Maestripieri 2003] and in the wild [e.g., 38.5 hours/subject, total, Förster and Cords 2005]. See Table 3-2 for timing and observation time of all individuals sampled.

During data collection, individuals who left the dataset due to disappearance were replaced by other individuals in the same age/sex category, if available, in order to maintain a sample size of as close to five individuals per age/sex category as possible. Sample sizes could not be maintained throughout the study at n=5 for all age/sex classes (Figure 3-4) due to lack of availability of individuals in those age/sex classes throughout the entire collared BMSR population. This was especially true for male infants as a result of high mortality rates in the 2008 cohort.

SEASONS

During data collection in 2008-2009, the rainy season began in mid-October and ended in late March. Infants of the 2008 cohort were fully weaned by their 7th month of age, in March or April. All infants in the sample were still nursing at low rates in March, but only half of the, nursed in April. No nursing was observed in May. Mating pulses were late April to mid-May and mid-June to mid-July, 2009.

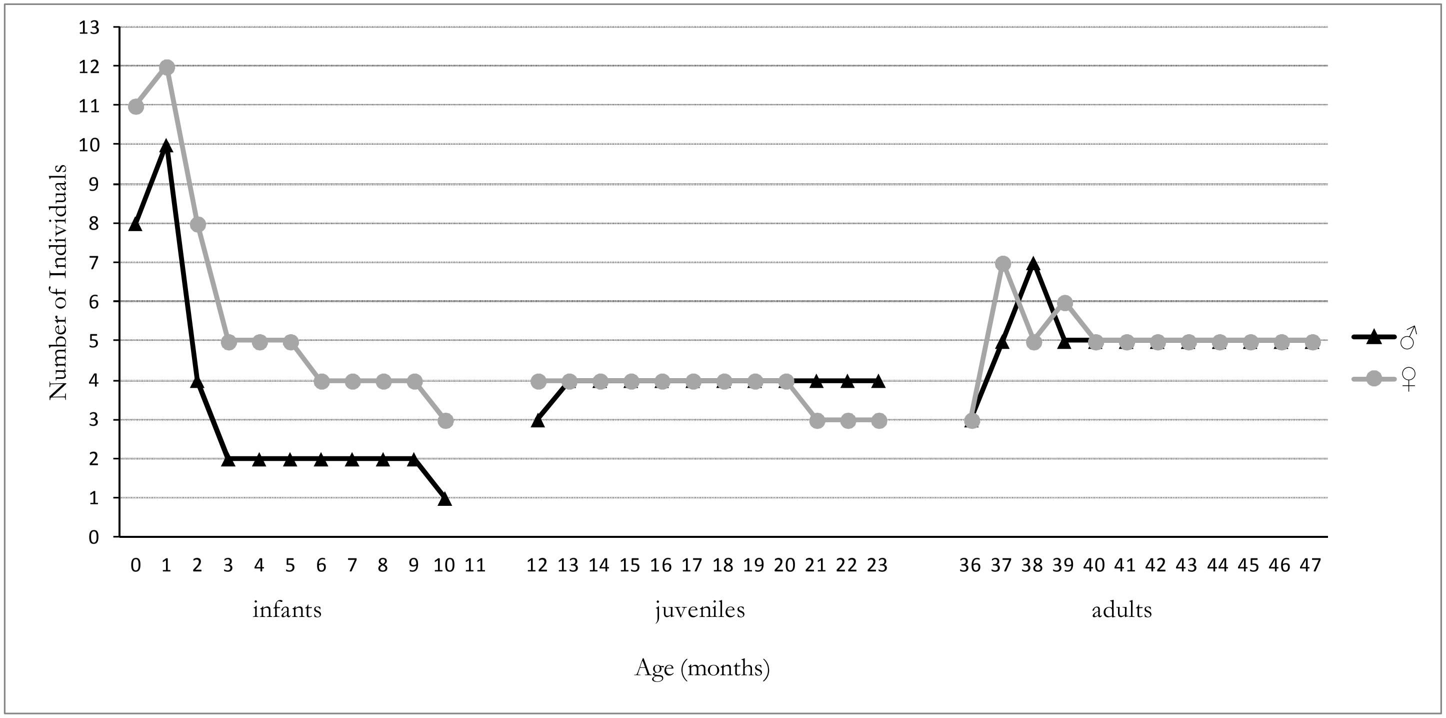


Fig. 3-4 Individuals sampled per month for each age/sex class.

ANALYTICAL METHODS

Counts of behavioral events and summations of time spent in behavioral states were extracted from JWatcher .txt files using a custom-written program in SAS 9.2. Individual monthly mean rates (# event occurrences per hour) were calculated for behavioral events that were included in analyses performed and individual monthly mean times were calculated for behavioral states that were included in analyses. These were derived from continuous data. Individual monthly mean distances from and proportions of time spent in proximity to nearest neighbors were calculated from scan data. Group size varied across study subjects and through time, providing subjects with different numbers of individuals at which to direct behaviors or from which to receive them. When appropriate, rates of and time spent engaged in behaviors were therefore corrected for partner availability before analysis. For analyses involving overall rates of or time engaged in interaction with others, this was accomplished by dividing by the number of group members available to the focal individual and multiplying by a constant (in this case, the overall average group size) to bring values back to their original scale. This correction allows for testing of the null hypothesis that individuals direct their social behavior toward others at uniform rates based on probability of encounter, and assumes a Brownian motion model of higher probability of inter-individual encounter in larger groups than in smaller ones. For analyses involving rates of or time engaged in interaction with particular age/sex classes, correcting for partner availability was accomplished by calculating deviations from rates/times of interaction with each age/sex class expected if the focal individual distributed those interactions randomly across all available group members. This controls for inter-individual differences in overall rates/times of interaction (tested in the analyses described above), allows for testing of the null hypothesis that individuals distribute their behavior randomly toward group members of each age/sex class based on probability of encounter, and assumes a Brownian motion model of higher probability of encounter of age/sex classes that have more members.

Even though the actual dates of behavioral collection each month were not the same for every individual, generating monthly mean behavioral measurements for all individuals created a balanced longitudinal dataset—one in which all individual share the same measurement occasions. This is advantageous because the methods available for analysis of unbalanced longitudinal data due to mistimed measurement occasions are comparatively limited [Fitzmaurice et al. 2004]. Individual monthly mean measurements were used as units of analysis in two types of regression models for correlated responses. These classes of regression models appropriately account for the dependence and correlation in the data due to repeated measurements on the same individuals [Fitzmaurice et al. 2004].

Linear mixed effects models (LMEMs), which model the mean response as a combination of fixed effects—those assumed to be shared by all individuals—and random effects—those unique to particular individuals [Fitzmaurice et al. 2004; Singer and Willett 2003] were used whenever possible. These analyses model group response profiles through time while accounting for individual differences that underlie natural heterogeneity within the groups [Fitzmaurice et al. 2004]. These very flexible models impose minimum restrictions on individual and group responses through time [Fitzmaurice et al. 2004]. In these analyses, when addressing questions about sex differences, individual ID was assigned as a random effect with sex and time (in months) as predictor variables. When addressing questions about age differences, individual ID was assigned as a random effect with cohort and/or time (in months) as predictor variables.

After the model-fitting protocol outlined in Singer and Willett [2003], individual response profiles were first qualitatively examined in order to determine whether they should be modeled as linear or quadratic responses, but sample sizes were rarely sufficient to model quadratic individual response profiles and linear individual response profiles were usually used. In most circumstances, the most complex LMEMs that could be fit were linear individual response profiles and linear group responses profiles. In some cases, it was not even possible to estimate individual slopes, and the LMEM was simplified to address only individual and group intercepts, effectively reducing analysis to a test of sex differences, but one which appropriately handles repeated measurements and uneven sampling due to missing data for some individuals.

Because LMEMs could not always be fit, response profiles of group means were also fit. These are conceptually straightforward analyses that characterize patterns of temporal change in the mean response in each group and determine whether they differ from each other [Fitzmaurice et al. 2004]. These analyses are well-suited to questions about a single covariate (e.g., sex) when the pattern of differences between groups is not known *a priori* [Fitzmaurice et al. 2004] (as in these data, in which the yearly temporal patterning of specific behaviors is unknown). Response profiles analyses impose minimal structural restrictions on the mean response through time and the covariance among repeated measurements, allowing arbitrary patterns of variation in both. As a result, they are relatively robust to bias resulting from model misspecification of the mean and covariance [Fitzmaurice et al. 2004]. Because these analyses summarize the data by the estimated group mean response at each measurement occasion, they require that the data are balanced with respect to timing of repeated measurements [Fitzmaurice et al. 2004], a requirement satisfied by using monthly mean individual values. In some cases in which sample size was very low, the model was reduced to test only for yearly mean sex differences. All models were fit using restricted maximum likelihood estimation, which is usually less biased in small samples of correlated data than traditional maximum likelihood methods of estimation [Fitzmaurice et al. 2004].

Both types of models can appropriately cope with unbalanced samples due to missing data on specific individuals (a problem common in longitudinal studies) without simply discarding those individuals from the analysis, as long as the data are "missing completely at random" or "missing at random" [Fitzmaurice et al. 2004; Singer and Willett 2003]. If the missing data mechanism—the reason underlying the missingness—is non-random with respect to the variable of interest, missing data may introduce bias [Fitzmaurice et al. 2004].

When data are "missing completely at random," the reason they are missing is unrelated both to the specific responses that, in principle, would have been observed but for the missingness of the individual, as well as to the responses that were observed. In such cases, the missing data do not complicate analysis [Fitzmaurice et al. 2004]. Here, the observed data represent a random sample of the complete data, which, themselves, should be a random sample of the population data.

Data are considered "missing at random" when they are unrelated to the specific responses that, in principle, would have been observed but for the missingness of the individual, but *are* related to the set of observed responses [Fitzmaurice et al. 2004]. For example, if individuals who are most aggressive leave the sample more often as a result of death due to higher incidence of fatal fights, the data are "missing at random." An analysis of rates of aggression that does not correct for this will be biased (in this case, underestimating mean population rates of aggression). Incidentally, in such cases, analyses such a rmANOVA that are restricted to individuals with data at all measurement occasions will also be biased in exactly this way [Fitzmaurice et al. 2004]—eliminating these individuals from the analysis does not solve the problem. To deal with this, the sample can be stratified by so-called "completers" and "non-completers," and non-completers' values are modeled based on their own observed values [Fitzmaurice et al. 2004]. When data are "missing at random," the likelihood-based methods used by LMEM and response profile analysis are still capable of providing unbiased estimates of the mean response though time as long as the model for the mean response and the within-subject correlation (random effects structure and covariance, respectively) are correctly specified [Fitzmaurice et al. 2004].

Regardless of the missing data mechanism, missing data will result in a reduction in the precision of estimation of the mean response, and the more missing data, the less precise the estimation [Fitzmaurice et al. 2004], which may be important to consider when comparing groups with different degrees of missingness. In this sample, missingness was a problem of varying severity for each cohort.

Model fitting was performed using PROC MIXED in SAS 9.2 according to the methods outlined in Singer and Willett for LMEMs [Singer and Willett 2003] and according to the methods in Fitzmaurice et al. [Fitzmaurice et al. 2004] for analysis of response profiles. For all models, the best model and the best fit variance structure were chosen using Akaike Information Criterion for small samples (AICc) [Fitzmaurice et al. 2004; Singer and Willett 2003]. The Akaike Information Criterion (AIC) measures the amount of information in the data that is lost by fitting a given model, providing a relative measure of how well a given model fits the data compared to other models. The AIC is only a relative measure of fit and does not provide information about whether a model is a good or poor fit to the data. The AICc provides a correction for small sample sizes and was, therefore, used here. The advantage of the AICc over likelihood-ratio tests of model fit is that it can be used to compare models that are not nested—i.e., that are not subsets of one another [Singer and Willett 2003].

In order to assess the assumptions of fit LMEMs, the functional form assumptions, normality, and homoscedasticity were qualitatively examined after the protocol of Singer and Willett [2003]. The functional form assumptions for individual-level change were examined using ordinary least squares (OLS) estimated individual trajectories of change plotted against the individual data. The functional form assumptions for group-level change were examined using ordinary least squares estimates of individual growth parameters plotted against the predictors. Normal probability plots of the raw residuals were examined for substantial departures from normality, which is rather difficult to assess at such small sample sizes. The assumption of homoscedasticity was assessed by plotting raw residual values against the predictors.

In order to assess the assumptions of the fit response profile models, residual analysis and diagnostics were performed using Cholesky transformed residuals after the protocol outlined in Fitzmaurice et al. [2004]. The Cholesky decomposition transforms the residuals such that they have constant variance and zero correlation [Fitzmaurice et al. 2004]. The fit of the model for the mean response and the assumption of constant variance were tested by examining a scatterplot of transformed residuals versus the transformed predicted vales. If time was modeled, the model for the mean response was tested by examining a scatterplot of transformed residuals versus transformed time. The normality assumption was tested using normal probability plots of the transformed residuals. The fit of the model for variance was tested by examining a scatterplot of the absolute values of the transformed residuals versus the transformed predicted values and versus transformed time. The Cholesky transformed residuals were output using the VCIRY option in PROC MIXED.

It should be noted that for most tests, the model assumptions were not well-met, and the models were not particularly well-fitting. The residuals were rarely normally distributed and were usually skewed due to the high number of real zeros recorded for many behaviors (*e.g.*, rates of adult male aggression directed at adult females), as well being characterized by a "floor effect" of zero for behaviors that occur at low rates. Several transformations of the data for a number of variables were attempted, but had little ameliorative effect; due to the poor outcomes of attempted transformations and the large number of behavioral variables, the data were left untransformed. Due to small sample sizes, it was not possible to fit more complex models that might have better described the temporal patterns of some variables. Therefore, the results of individual analyses should be considered cautiously. The specific models used to generate each result (and my confidence in them) are explicated with each result in the sections that follow.

Because LMEMs account for inter-individual variation, they should yield more precise estimates of group mean responses than RP models. Therefore, whenever an LMEM could be fit, its results are discussed. When the LMEM is not the best-fitting model according to the AICc, its results are discussed in conjunction with the results of the best fitting mean response profile model.

In some cases, the most complex LMEM that could be fit was one that allowed random individual intercepts (yearly means) but did not incorporate individual or group slopes. In other words, a test of sex differences in response across the year while accounting for inter-individual variation only in the starting value, but not accounting for individual variation in slope. I will refer to this type of model as the random intercepts LMEM. I will refer to LMEMs that incorporate both random individual intercepts and random individual slopes as linear LMEMs. Similarly, in some cases, the best fit response profile model was a simple model of group sex differences in mean response across the year, assuming no systematic change through time. This is equivalent to a single summary measure analysis in which the summary measures are the yearly group means (with a slope of zero), but appropriately accounts for correlation between repeated measurements on the same individuals, which summary measure analysis cannot do when the data are unbalanced due to missingness, as they are here [Fitzmaurice et al. 2004]. I will refer response profile models that assume no systematic change through time as mean RP models and those that characterize systematic change through time as linear (or quadratic) RP models.

In some cases, LMEMs could not be fit. This might occur for a number of reasons. LMEMs are more complex models than RP models because they are multi-level models (modeling both individual and group change through time) and because they are fit using a more complex variance structure (unstructured). In some cases, there may not have been enough observations to fit such a complex model. In other cases, there may have been too little interindividual or temporal variation to specify a non-zero variance or covariance model. In other cases, there may have too much intraindividual variation to fit a variance or covariance model. In these cases, I used the less complex RP models to interpret the data.

In these analyses, no particular outlying observations were thought to be due to an observation or recording error. The types of outliers usually seen were instances of high rates of behavior or high numbers of social partners compared to other individuals in a given month. Because these variables were calculated by summing individual events and records of specific individuals in proximity to a focal individual, these types of outlying observations could not derive from a single, random observational or data entry error. In investigating outliers, special attention was paid to the data from "non-completers." If an outlying individual was also a non-completer, careful consideration was given to whether the individual's values might be related to the reason it left the sample. Two adult males left the sample early in the observation year because they emigrated from their groups. Two adult females left the sample because they gave birth to infants. Many infants and one juvenile left the sample due to death. If the two adult males were outliers, consideration was given to whether their values for the behavior under consideration may have been related to the process of emigration. If the two adult females were outliers, consideration was given to whether their values for the behavior under consideration may have been related to their nearing parturition. In the case of infants, so many of them were "non-completers" that the unusual individuals in the sample were really the "completers." In no case were there sufficient data to stratify the model by completers and non-completers. As previously discussed, removing individuals from analysis who are only "missing at random" does not solve the problem of bias in the analysis. Therefore, when "non-completers" were outlying in ways that were likely to bias analysis, this issue was explicitly discussed.

TABLE 3-1. Ethogram of behaviors used in continuous and scan sampling. Bi-directional behaviors can be directed by or toward the focal individual. Uni-directional behaviors are only exhibited by the focal individual.

Behavior	Sampling type	Directionality	Behavior type	Definition
Alarm	scan	uni-	state	a state of extreme arousal and tense attention in response to perceived danger, immediately after alarm calling
Alarm call	scan	uni-	state	yaps, barks, and/or shrieks [Pereira and Kappeler 1997] given to arboreal and terrestrial predators
Contact call	scan	uni-	event	tonal, mew-like monosyllable used in attempts to locate other individuals, or to respond to contact calls of others (includes "moan," "inflected moan," and "peep" of Pereira and Kappeler [1997]
Cry	scan	uni-	state	insistent, repeated contact calls used by infants when unaware of their mothers' locations
Defecate	scan	uni-	event	eliminate feces
Drink	scan	uni-	state	consume water
Feed/forage	scan	uni-	state	search for food, manipulate food, consumption of food, locomote within one tree crown while intermittently feeding or manipulating food objects, does not apply to nursing
Howl (bugle)	scan	uni-	event	loud long call issued by males that usually begins with a 'hiccup'

TABLE 3-1. Continued.

Locomotor practice	scan	uni-	state	walking, jumping, standing, reaching, etc. without changing location by more than 1m
Mouth	scan	bi-	state	chew object within ingesting it, chew body parts (other than the nipple) of another individual
Move	scan	uni-	state	movement within a tree crown in a non-foraging context
Object play	scan	uni-	state	solitary play using an object, such as a leaf
Positional behavior	scan	uni-	state	non-resting, static positional behaviors such as stand, cling, bipedal stand, hang, etc .
Rest	scan	uni-	state	sitting or lying down with eyes open or closed
Scratch	scan	uni-	event	raking the nails or grooming claws repeatedly over the fur
Self-groom	scan	uni-	state	use tooth comb to repeatedly stroke fur of self
Solitary play	scan	uni-	state	play alone, involves jumping, climbing, hanging, rolling, etc.
Stare	scan	bi-	state	agonistic, steady, focused gaze at partner
Sun	scan	uni-	state	sit with ventral surface exposed to direction of sun
Thermoregulate	scan	uni-	state	repeatedly lick and salivate over hands
Travel	scan	uni-	state	movement between tree crowns or a longer distance than the diameter of an average tree crown; can involve multiple positional behaviors such as climbing, running, jumping, walking, etc.
Urinate	scan	uni-	event	excrete urine

TABLE 3-1. Continued.

Allogroom	both	bi-	state	use tooth comb to repeatedly stroke fur of another, often involves holding onto partner with hands
Ano-genital mark	both	uni-	event	rub an object with the ano-genital region
Anoint tail	both	uni-	event	drag tail repeatedly between forearms, even if ante-brachial glands are not yet mature, 1 bout ≤ 5s
Attend to	both	uni-	state	direct visual attention to for > 3 seconds; may be directed toward an individual, an object, or something unidentifiable by observer in distance
Avoid	both	bi-	event	move around an individual, usually while attending to it, when passing it would be a more direct path; may also involve changing original direction upon seeing another individual
Bite	both	bi-	event	sudden motion involving oral contact, can be soft or hard
Charge	both	bi-	event	sudden, aggressive burst of running toward an individual that ends abruptly as soon as the recipient runs away
Chase	both	bi-	event	running toward an individual that is simultaneously running away, aggressive
Cling	both	bi-	state	to be carried ventrally or remain in ventral carrying position without nipple contact
Cower	both	bi-	event	lower the body in response to proximity of or threat by another individual, submissive submissive

TABLE 3-1. Continued.

Cuff	both	bi-	event	use hand to aggressively swat or grab another individual (includes cuff-push of Pereira and Kappeler [1997])
Feint to cuff	both	bi-	event	raise hand aggressively toward another individual without making contact
Flee	both	bi-	event	run away from another individual, usually as a result of being charged or chased
Follow	both	bi-	state	walk behind an individual that has just walked away, maintaining proximity of <1m
Greet	both	bi-	event	groom partner for < 5s immediately after an approach to within reach
Huddle	both	bi-	state	postural behavior involving sitting in contact with another (or multiple) individual(s) who is (are) also sitting, involves a large amount of body contact, often ventral-dorsal contact; in young infants, distinguished from cling and ride in that the infant’s body weight is largely supported by the substrate.
Jump fight	both	uni-	event	aggressive encounter involving simultaneous vertical jumping
Jump play	both	uni-	event	simultaneous, stereotyped vertical jumping in the context of a play bout
Lick	both	bi-	state	repeatedly touch with tongue, may be directed toward another, self, or inanimate object

TABLE 3-1. Continued.

Look away/glance	both	bi-	state	look repeatedly toward and away from social partner; often accompanied by a chewing motion, agonistic
Lunge	both	bi-	event	sudden aggressive movement toward another individual with the front of the body while the hindlimbs maintain their position on the substrate
Mount	both	bi-	event	cling with hands and touch ventral surface of pelvis against another individual
Mount-thrust	both	bi-	event	mount another individual, followed by pelvic thrusting
Mutual groom	both	uni-	state	simultaneous allogrooming between two individuals
Nurse/nipple	both	bi-	state	resting with mouth on another's nipple; suckling motion may or may not be visible
Play chase	both	bi-	state	running after another individual that is running away during play for ≥ 3s
Ride	both	bi-	state	to be carried dorsally by another individual as it moves, or to remain in a jockey position on another individual while it rests
Sniff	both	bi-	event	place nose ≤ 3cm of an individual or object with apparent attention for ≥ 1 s and without subsequent foraging; can be directed toward objects, others' scent marks, other individuals, other's ano-genital regions

TABLE 3-1. Continued.

Social play	both	uni-	state	play with another individual, involves rapid sequence changes of grappling, jumping, short play charges, etc. that are too short in duration to qualify as a more specific play type
Stink fight	both	uni-	event	simultaneous tail-marking and tail waving between two males, 1 bout $\leq$ 5s
Supplant	both	bi-	event	approach another individual and immediately take its resting or feeding position, dominance
Tail play	both	uni-	event	anoint tail or tail wave in the context of a play bout, 1 bout $\leq$ 5s
Tail wave	both	bi-	event	quiver tail over head toward another individual, 1 bout $\leq$ 5s
Take food	both	bi-	event	remove food from another individual's hand or mouth
Threat	both	bi-	event	sharp, short aggressive vocalization toward another individual which results in submissive behavior by the target
Wrestle	both	uni-	state	grappling during play for $\geq$ 5s
Wrist mark	both	uni-	event	grasping a branch with a sterotyped, hyperflexed wrist posture, followed by a forceful rotation of wrist around the branch; results in scarring of branch is carpal spur is present
Wrist to pit	both	uni-	event	rub wrist against axillary region
Approach	continuous	bi-	event	move toward another individual to a distance $\leq$ 1 meter

TABLE 3-1. Continued.

Break contact	continuous	bi-	event	move out of contact with an individual while remaining within 1 meter
Leave	continuous	bi-	event	move > 1m from an individual who was previously < 1m away
Make contact	continuous	bi-	event	move from within proximity to physical contact with another individual, apparently unintentional tail contact excluded
Pass	continuous	bi-	event	move toward another individual to within proximity (or closer) and immediately move out of proximity without any overt social interaction
Passive contact	continuous	NA	state	describes two individuals whose bodies or limbs are in physical contact but are not engaged in overt social interaction, used when it is unclear which individual initiated contact, unintentional tail contact is not included
Passive within reach	continuous	NA	state	describes two individuals whose heads or bodies (but not tails or extended limbs) are ≤ 0.3m from each other, without other overt social interaction
Reject	continuous	bi-	event	push another away from a nursing or riding attempt, may involve a soft bite, vocalization, or a move away from infant without leaving the infant

TABLE 3-2. Individual samples by observation month for adults and juveniles and by real age for infants.

Observation month (adults and juveniles) / Age (infants)	ID	Age/Sex	time observed (hours)
0	ADF185	AD♀	1.5
0	ADF23	AD♀	0.5
0	ADF276	AD♀	2
0	ADM175	AD♂	3
0	ADM192	AD♂	1.5
0	ADM263	AD♂	1
0	08F(154)	INF♀	5.5
0	08F(171)	INF♀	5.5
0	08F(176)	INF♀	3
0	08F(185)	INF♀	3.5
0	08F(214)	INF♀	5
0	08F(23)	INF♀	2
0	08F(268)	INF♀	1.5
0	08F(300)	INF♀	2.5
0	08F(328)	INF♀	6
0	08F(334)	INF♀	5.5
0	08F(364)	INF♀	4.5
0	08M(167)	INF♂	3.5
0	08M(172)	INF♂	2.5
0	08M(181)	INF♂	3.5
0	08M(183)	INF♂	6
0	08M(184)	INF♂	4
0	08M(321)	INF♂	5.5
0	08M(338)	INF♂	5.5
0	08M(368)	INF♂	4
0	08M(9)	INF♂	4.5
0	07F(9)	JUV♀	2.5
0	07F326	JUV♀	1.5
0	07F329	JUV♀	1.5
0	07F336	JUV♀	3
0	07M(44)	JUV♂	2
0	07M331	JUV♂	1.5

TABLE 3-2. Continued.

0	07M335	JUV♂	1.5
1	06F325	AD♀	2
1	ADF167	AD♀	1
1	ADF207	AD♀	2
1	ADF23	AD♀	2
1	ADF235	AD♀	2.5
1	ADF276	AD♀	3
1	ADF334	AD♀	2
1	ADM175	AD♂	2
1	ADM245	AD♂	3.5
1	ADM263	AD♂	4
1	ADM3/0P	AD♂	4
1	ADM4/0P	AD♂	4
1	08F(137)	INF♀	3.5
1	08F(154)	INF♀	4
1	08F(171)	INF♀	3.5
1	08F(176)	INF♀	3.5
1	08F(185)	INF♀	3
1	08F(214)	INF♀	4
1	08F(217)	INF♀	0.5
1	08F(297)	INF♀	3
1	08F(297o)	INF♀	2
1	08F(300)	INF♀	4.5
1	08F(328)	INF♀	4
1	08F(364)	INF♀	3
1	08F(44)	INF♀	1.5
1	08M(167)	INF♂	4.5
1	08M(172)	INF♂	1.5
1	08M(181)	INF♂	3
1	08M(183)	INF♂	2
1	08M(184)	INF♂	2
1	08M(227)	INF♂	2
1	08M(234)	INF♂	1.5
1	08M(246)	INF♂	2.5
1	08M(319)	INF♂	3
1	08M(321)	INF♂	1.5
1	08M(9)	INF♂	5.5
1	07F(9)	JUV♀	3

TABLE 3-2. Continued.

1	07F326	JUV♀	5.5
1	07F329	JUV♀	5
1	07F336	JUV♀	3.5
1	07M331	JUV♂	6
1	07M335	JUV♂	3.5
1	07M337	JUV♂	6.5
1	07M340	JUV♂	6.5
2	06F325	AD♀	4
2	ADF207	AD♀	3
2	ADF23	AD♀	3.5
2	ADF235	AD♀	4
2	ADF276	AD♀	3.5
2	ADM175	AD♂	4
2	ADM245	AD♂	4
2	ADM263	AD♂	3.5
2	ADM3/0P	AD♂	1
2	ADM4/0P	AD♂	0.5
2	ADM5/2P	AD♂	2.5
2	ADM7/1P	AD♂	1.5
2	08F(154)	INF♀	4
2	08F(171)	INF♀	4
2	08F(176)	INF♀	2
2	08F(185)	INF♀	2
2	08F(214)	INF♀	3
2	08F(300)	INF♀	5
2	08F(328)	INF♀	3
2	08F(44)	INF♀	3.5
2	08M(155)	INF♂	5
2	08M(234)	INF♂	3.5
2	08M(319)	INF♂	0.5
2	08M(9)	INF♂	3.5
2	07F(9)	JUV♀	4
2	07F326	JUV♀	3
2	07F329	JUV♀	4
2	07F336	JUV♀	4
2	07M331	JUV♂	3.5
2	07M335	JUV♂	4
2	07M337	JUV♂	4

TABLE 3-2. Continued.

2	07M340	JUV♂	4
3	06F305	AD♀	3
3	06F325	AD♀	2
3	ADF207	AD♀	2
3	ADF231	AD♀	0.5
3	ADF235	AD♀	3
3	ADF276	AD♀	3
3	ADM175	AD♂	3.5
3	ADM245	AD♂	1.5
3	ADM263	AD♂	3
3	ADM5/2P	AD♂	2.5
3	ADM7/1P	AD♂	2
3	08F(154)	INF♀	1.5
3	08F(214)	INF♀	2.5
3	08F(300)	INF♀	1
3	08F(328)	INF♀	2
3	08F(44)	INF♀	3
3	08M(234)	INF♂	2
3	08M(9)	INF♂	3.5
3	07F(9)	JUV♀	3
3	07F326	JUV♀	4.5
3	07F329	JUV♀	4
3	07F336	JUV♀	3
3	07M331	JUV♂	4.5
3	07M335	JUV♂	3
3	07M337	JUV♂	2
3	07M340	JUV♂	3
4	06F305	AD♀	3
4	06F325	AD♀	3
4	ADF207	AD♀	3.5
4	ADF235	AD♀	2.5
4	ADF276	AD♀	1.5
4	ADM175	AD♂	2.5
4	ADM245	AD♂	2.5
4	ADM263	AD♂	1.5
4	ADM5/2P	AD♂	3
4	ADM7/1P	AD♂	3
4	08F(154)	INF♀	3.5

TABLE 3-2. Continued.

4	08F(214)	INF♀	3
4	08F(300)	INF♀	3
4	08F(328)	INF♀	4.5
4	08F(44)	INF♀	5
4	08M(155)	INF♂	4
4	08M(234)	INF♂	5
4	08M(9)	INF♂	4
4	07F(9)	JUV♀	3.5
4	07F326	JUV♀	1.5
4	07F329	JUV♀	1.5
4	07F336	JUV♀	3.5
4	07M331	JUV♂	1.5
4	07M335	JUV♂	3.5
4	07M337	JUV♂	3.5
4	07M340	JUV♂	3
5	06F305	AD♀	4
5	06F325	AD♀	3.5
5	ADF207	AD♀	3
5	ADF235	AD♀	3.5
5	ADF276	AD♀	4.5
5	ADM175	AD♂	4
5	ADM245	AD♂	4.5
5	ADM263	AD♂	4.5
5	ADM5/2P	AD♂	3
5	ADM7/1P	AD♂	3
5	08F(154)	INF♀	3.5
5	08F(214)	INF♀	4.5
5	08F(300)	INF♀	5
5	08F(328)	INF♀	3
5	08F(44)	INF♀	1.5
5	08M(155)	INF♂	5
5	08M(234)	INF♂	1.5
5	08M(9)	INF♂	3
5	07F(9)	JUV♀	5.5
5	07F326	JUV♀	5
5	07F329	JUV♀	5
5	07F336	JUV♀	5.5

TABLE 3-2. Continued.

5	07M331	JUV♂	5
5	07M335	JUV♂	5
5	07M337	JUV♂	3.5
5	07M340	JUV♂	3
6	06F305	AD♀	1.5
6	06F325	AD♀	3
6	ADF207	AD♀	3
6	ADF235	AD♀	1
6	ADF276	AD♀	2
6	ADM175	AD♂	1.5
6	ADM245	AD♂	1.5
6	ADM263	AD♂	2
6	ADM5/2P	AD♂	3
6	ADM7/1P	AD♂	3
6	08F(154)	INF♀	3.5
6	08F(300)	INF♀	4.5
6	08F(328)	INF♀	3.5
6	08F(44)	INF♀	4.5
6	08M(155)	INF♂	2
6	08M(234)	INF♂	4.5
6	08M(9)	INF♂	3
6	07F(9)	JUV♀	1.5
6	07F326	JUV♀	2
6	07F329	JUV♀	2
6	07F336	JUV♀	1.5
6	07M331	JUV♂	2
6	07M335	JUV♂	1.5
6	07M337	JUV♂	3
6	07M340	JUV♂	3
7	06F305	AD♀	2.5
7	06F325	AD♀	3
7	ADF207	AD♀	2.5
7	ADF235	AD♀	3
7	ADF276	AD♀	4.5
7	ADM175	AD♂	2.5
7	ADM245	AD♂	3
7	ADM263	AD♂	4.5

TABLE 3-2. Continued.

7	ADM5/2P	AD♂	3
7	ADM7/1P	AD♂	3
7	08F(154)	INF♀	3
7	08F(300)	INF♀	3
7	08F(328)	INF♀	3.5
7	08F(44)	INF♀	4
7	08M(155)	INF♂	4
7	08M(234)	INF♂	4
7	08M(9)	INF♂	4.5
7	07F(9)	JUV♀	3
7	07F326	JUV♀	4
7	07F329	JUV♀	4.5
7	07F336	JUV♀	3
7	07M331	JUV♂	4
7	07M335	JUV♂	3
7	07M337	JUV♂	3
7	07M340	JUV♂	3.5
8	06F305	AD♀	4.5
8	06F325	AD♀	2.5
8	ADF207	AD♀	3
8	ADF235	AD♀	4
8	ADF276	AD♀	3.5
8	ADM175	AD♂	4
8	ADM245	AD♂	4
8	ADM263	AD♂	3
8	ADM5/2P	AD♂	3
8	ADM7/1P	AD♂	3.5
8	08F(154)	INF♀	3.5
8	08F(300)	INF♀	3.5
8	08F(328)	INF♀	3.5
8	08F(44)	INF♀	5.5
8	08M(155)	INF♂	4
8	08M(9)	INF♂	2
8	07F(9)	JUV♀	1.5
8	07F326	JUV♀	3
8	07F329	JUV♀	3
8	07F336	JUV♀	4.5

TABLE 3-2. Continued.

8	07M331	JUV♂	3
8	07M335	JUV♂	4.5
8	07M337	JUV♂	4.5
8	07M340	JUV♂	3.5
9	06F305	AD♀	3
9	ADF207	AD♀	2.5
9	ADF235	AD♀	4
9	ADF276	AD♀	3
9	ADF334	AD♀	3.5
9	ADM175	AD♂	3.5
9	ADM245	AD♂	3
9	ADM263	AD♂	3
9	ADM5/2P	AD♂	2.5
9	ADM7/1P	AD♂	3
9	08F(154)	INF♀	4
9	08F(300)	INF♀	3
9	08F(328)	INF♀	5.5
9	08F(44)	INF♀	4
9	08M(155)	INF♂	5.5
9	08M(9)	INF♂	2
9	07F326	JUV♀	3.5
9	07F329	JUV♀	3.5
9	07F336	JUV♀	4
9	07M331	JUV♂	3.5
9	07M335	JUV♂	4
9	07M337	JUV♂	2
9	07M340	JUV♂	2.5
10	06F305	AD♀	3
10	ADF207	AD♀	5
10	ADF235	AD♀	3
10	ADF276	AD♀	3.5
10	ADF334	AD♀	4.5
10	ADM175	AD♂	3.5
10	ADM245	AD♂	3
10	ADM263	AD♂	3.5
10	ADM5/2P	AD♂	4
10	ADM7/1P	AD♂	4.5

TABLE 3-2. Continued.

10	08F(154)	INF♀	3.5
10	08F(300)	INF♀	4.5
10	08F(328)	INF♀	1.5
10	08M(155)	INF♂	2
10	07F326	JUV♀	4
10	07F329	JUV♀	4.5
10	07F336	JUV♀	3.5
10	07M331	JUV♂	3.5
10	07M335	JUV♂	3.5
10	07M337	JUV♂	5
10	07M340	JUV♂	4.5
11	06F305	AD♀	1.5
11	ADF207	AD♀	1.5
11	ADF235	AD♀	1.5
11	ADF276	AD♀	1.5
11	ADF334	AD♀	1.5
11	ADM175	AD♂	1.5
11	ADM245	AD♂	1.5
11	ADM263	AD♂	1.5
11	ADM5/2P	AD♂	1.5
11	ADM7/1P	AD♂	1.5
11	07F326	JUV♀	1.5
11	07F329	JUV♀	1.5
11	07F336	JUV♀	2
11	07M331	JUV♂	1.5
11	07M335	JUV♂	2
11	07M337	JUV♂	1.5
11	07M340	JUV♂	1.5

CHAPTER 4: ADULT SEX DIFFERENCES

In this study, the behavior of individuals toward others is considered intrinsic to the individual and the behavior of others toward individuals is considered extrinsic to the individual. The purpose of this study is to pinpoint differences in extrinsic social factors that may be responsible for shaping the development of intrinsic adult behavioral sex differences. Achieving this goal requires several foundational steps. First, intrinsic adult behavioral sex differences must be identified. Second, in order to identify social factors that may drive the development of those adult sex-typed behaviors, the presence of sexual differentiation in those behaviors must be identified in subadults. This is because once gonadal maturation has occurred, it is presently impossible to determine, in a non-experimental setting, whether hormones or social interactions are more likely the cause of sexual differentiation, but before sexual maturation, gonadal hormone activation can be excluded as a confound. Third, extrinsic sex differences must be identified for subadults. Fourth, the temporal relationships between extrinsic and intrinsic sex differences in subadults must be qualitatively examined, and any extrinsic sex differences that postdate the development of intrinsic sex differences can be excluded as causal to intrinsic sex differences. This chapter presents results on tests of sex differences in adult patterns of agonism and affiliation toward others, patterns of proximity to others, expressions of interest in infants, and scent marking behavior.

Adult ring-tailed lemurs are female-dominant; females enjoy priority of access to food and resting places and are able to supplant adult males at will. They are more aggressive than males and are, on average, more spatially cohesive than males [Pereira 2002]. While adult behavioral sex differences in *Lemur catta* are generally well-understood, quantifying them in this population allowed me to control for differences in detectable effect size that might be due to temporal variation, intra-specific variation, or statistical power and creates an appropriate benchmark against which to compare juvenile behavioral development in the present sample.

As mentioned in Chapter 3, when LMEMs were the best fitting models, only those results are presented. When they were not, the results of the best fitting RP model is also presented. In many cases, the results of the best fitting LMEM and RP models agree. When they did not, the data were explored qualitatively to make a decision about which results seemed most reasonable; my decision-making process is explained in those instances. Scatterplots of the data are provided to allow for visualization of the temporal trends and amount of variation present. Results of fit models are presented in tabular format for each variable including: model type, effect parameter estimates (intercept, time, sex, sex*time, etc.), standard errors, degrees of freedom, t-statistics, and p-values. P-values of <0.05 are considered significant and those between 0.10 and 0.05 are discussed as "tendencies." Throughout, positive parameter estimates for the effect of sex indicate that female values exceed male values, and negative parameter estimates for the effect of sex indicate that male values exceed female values.

AGONISM

Agonism subsumes aggressive, fearful, dominant, and submissive interactions. The agonistic behavioral events recorded in this study were: avoid, bite, charge, chase, cuff, feint to cuff, flee, jump fight, look away/glance, lunge, reject, stink fight, supplant, take food, and threat. Because "take food" was sometimes an expression of dominance and was at other times a behavior that mothers tolerated from their infants, this behavior was excluded from all analyses. “Reject” is an agonistic behavior that is mostly directed by mothers, who were not study subjects, toward infants, and is therefore not considered in the following analyses of adults. The following analyses investigate adult sex differences in the four types of intrinsic adult expressions of agonism in order to identify those that are quantifiably sexually differentiated: 1) aggression directed toward others, 2) fear of others, 3) non-aggressive dominance of others, and 4) submission to others. The individual behaviors that each type of agonism comprises are summarized in Table 4-1 and are listed at the beginning of each of the following subsections.

TABLE 4-1. Individual component behaviors of the four types of agonism.

AGONISM			
Aggression	Dominance	Submission	Fear
bite	supplant	avoid	flee
charge			
chase			
cuff			
feint to cuff			
jump fight			
look away/glance			
lunge			
stink fight			
threat			

Aggression

Aggressive behaviors are the subset of agonistic behaviors that are active and overtly interactive. They are more energetically costly than less overtly aggressive forms of agonism, and they have more potential for aggressive escalation than less overtly aggressive forms of agonism. In this study, aggressive behaviors are: bite, charge, chase, cuff, feint to cuff, jump fight, look away/glance, lunge, stink fight, and threat. Analyses of aggression toward others were performed on monthly mean hourly rates of aggressive events.

Rates of Aggression toward others

An LMEM could not be fit. The best mean RP model indicates that females have significantly higher rates of aggression than males (Table 4-2). Qualitatively, it appears that adult female rates of aggression increase during the later part of the observation year, but given that the best fit model is a mean model and not a linear one, this temporal trend was not statistically significant.

TABLE 4-2. RP model parameter estimates for rates of aggression in adult males and females.

Variable	Model	Effect	est	SE	DF	t	p
Aggression	mean RP	INT	0.22	0.09	16	2.39	0.03*
		SEX	0.30	0.13	16	2.34	0.03*

INT = α, the regression intercept.; when the parameter estimate for SEX is positive, ♀>♂, and vice versa; * $p \leq 0.05$. All tables follow these conventions.

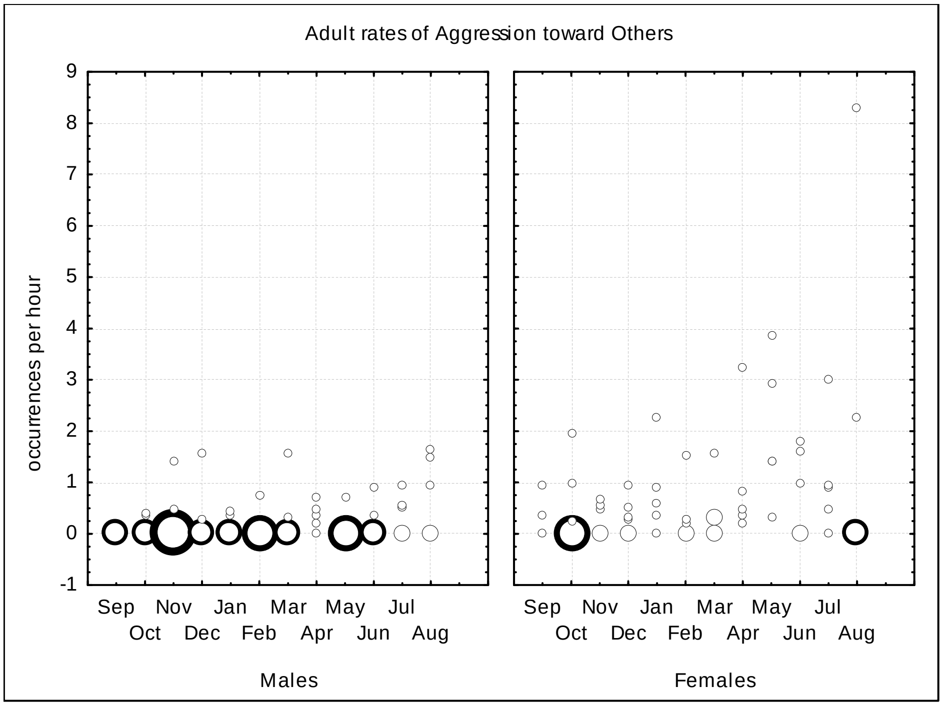


Fig. 4-1. Adult rates of aggression toward others. Circle size and line thickness are weighted by number of repeated values. All figures of this type follow these conventions.

Considering aggression toward all others may obscure patterns of aggressive behavior toward specific age/sex classes. It is possible that adult males and females target different age/sex classes with their aggressive behavior. Therefore, adult sex differences in rates of aggression directed toward particular age/sex classes was also examined.

Aggression toward Adult Females

Because adult females exhibit higher rates of aggression overall than adult males, if both sexes exhibit their aggression toward others at random, adult females will exhibit higher rates of aggression toward particular age/sex classes as an artifact of their higher rates of aggression overall. Therefore, expected rates of aggression toward each age/sex class were calculated based on individual rates of aggression and the availability of members of each age/sex class. Deviations (abbreviated Dev in Tables) from those expectations were then calculated and used in analyses of aggression toward each age/sex class. Focal animals were all non-maternal adult females, but they could express aggression toward any adult female. The identities of the mothers of adults were unknown in this sample. Therefore, adult females to whom adult female subjects exhibited aggression could have been their mothers, sisters, aunts, etc., and may or may not have been carrying dependent offspring.

In these models, an intercept of zero indicates no bias either toward or away from exhibiting aggression to particular age/sex classes at the beginning of the observation year. A positive intercept indicates more aggression toward a particular age/sex class than expected at random, and a negative intercept indicates less than expected at random. In models that do not include a time effect, the intercept represents yearly mean values.

The best fit mean random intercept LMEM and mean RP models for the deviations from rates of aggression toward adult females expected if individuals randomly distributed their aggressive behavior across all group members reveals that the sexes do not differ from each other in their bias of aggression toward adult females. Rather, both sexes tend to exhibit slightly less aggression toward adult females than expected if their distribution of aggression were random (Table 4-3, Figure 4-2).

TABLE 4-3. Model parameter estimates for deviations of rates of aggression toward adult females.

Variable	Model	Effect	est	SE	DF	t	p
Dev Aggression to AF	random int. LMEM	INT	-0.09	0.05	16	-1.67	0.11
		SEX	-0.04	0.08	103	-0.56	0.58
Dev Aggression to AF	mean RP	INT	-0.06	0.03	16	-1.94	0.07
		SEX	-0.06	0.04	16	-1.53	0.14

AF = adult females; all tables follow this convention.

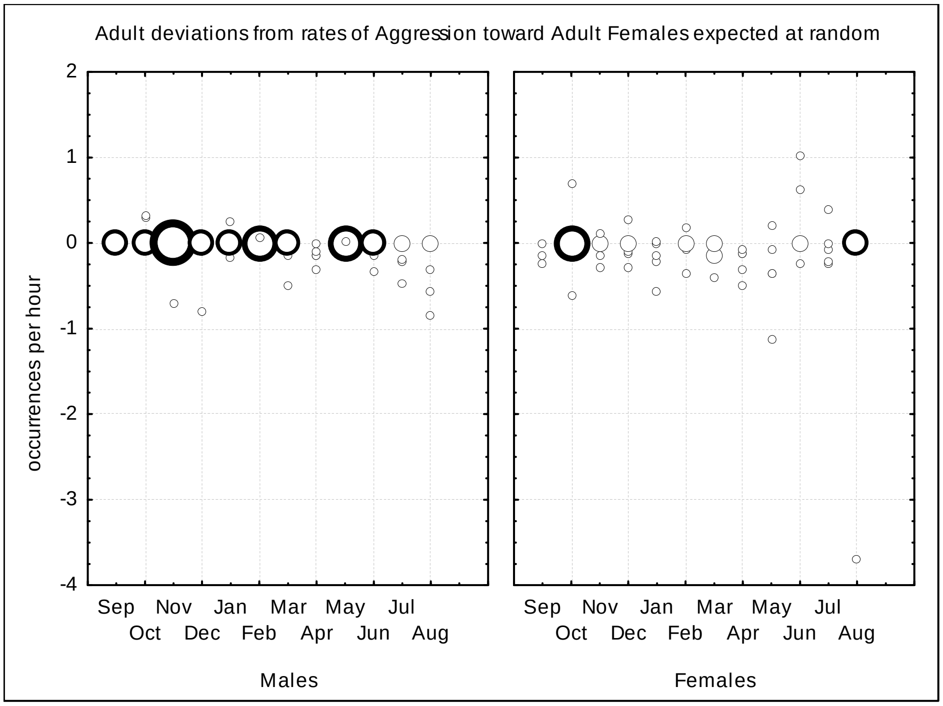


Fig. 4-2. Deviations from expected rates of aggression toward adult females.

It is surprising to see aggression by adult males toward adult females at all. Further investigation reveals that there were only eight observed instances of aggression directed by adult males toward adult females, and half of those instances were committed by a single male (263 from orange group). These aggressive events were not disproportionately directed at young females, but they were disproportionately directed at females who had not yet had an infant, which has been documented previously [Sauther et al. 1999]. It is possible that the three aggressive events directed at parous females by males were recording errors. Indicating "receipt" of a behavior by the focal individual required an extra keystroke, and it is possible that some of these data points represent a failure to register that keystroke—essentially, a typo. However, I do not think that this explains every aggressive event exhibited by adult males toward adult females, as I recall being surprised (rarely, but on more than one occasion) by witnessing aggression by male 263 toward group females. Nevertheless, this behavior was rare.

Aggression toward Adult Males

An LMEM could not be fit, but the best fit mean RP model indicates no sex difference in the deviations from rates of aggression toward adult males expected at random, and no evidence of bias of adult aggression either toward or away from adult males (Table 4-4, Figure 4-3).

TABLE 4-4. RP model parameter estimates for deviations from expected rates of aggression toward adult males.

Variable	Model	Effect	est	SE	DF	t	p
Dev Aggression to AM	mean RP	INT	0.00	0.02	16	0.19	0.85
		SEX	-0.05	0.03	16	-1.66	0.12

AM = adult males; all tables follow this convention.

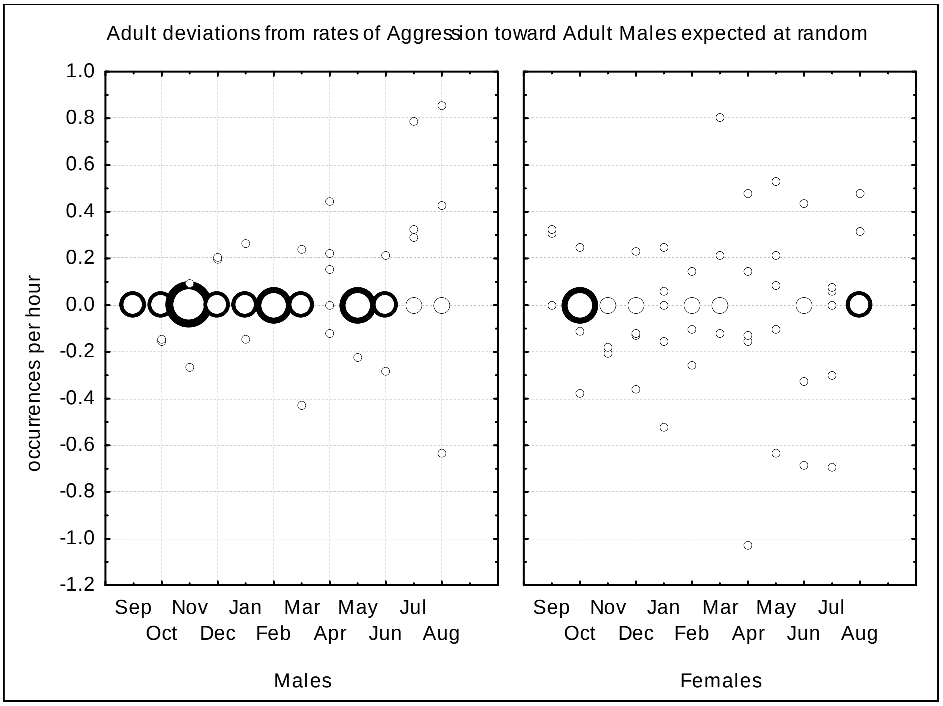


Fig. 4-3. Deviations from expected rates of aggression toward adult males.

Aggression toward Juvenile Females

Juveniles are those in the cohort that were 12-23 months old during this study. An LMEM could not be fit, but according to the best fit mean RP model, there is no sex difference in the deviations from rates of aggression toward juvenile females expected at random, and no evidence of bias of adult aggression either toward or away from juvenile females (Table 4-5, Figure 4-4.).

TABLE 4-5. RP model parameter estimates for deviations from expected rates of aggression toward juvenile females.

Variable	Model	Effect	est	SE	DF	t	p
Dev Aggression to JF	mean RP	INT	-0.01	0.00	16	-1.33	0.20
		SEX	-0.01	0.01	16	-1.42	0.18

JF = juvenile females; all tables follow this convention.

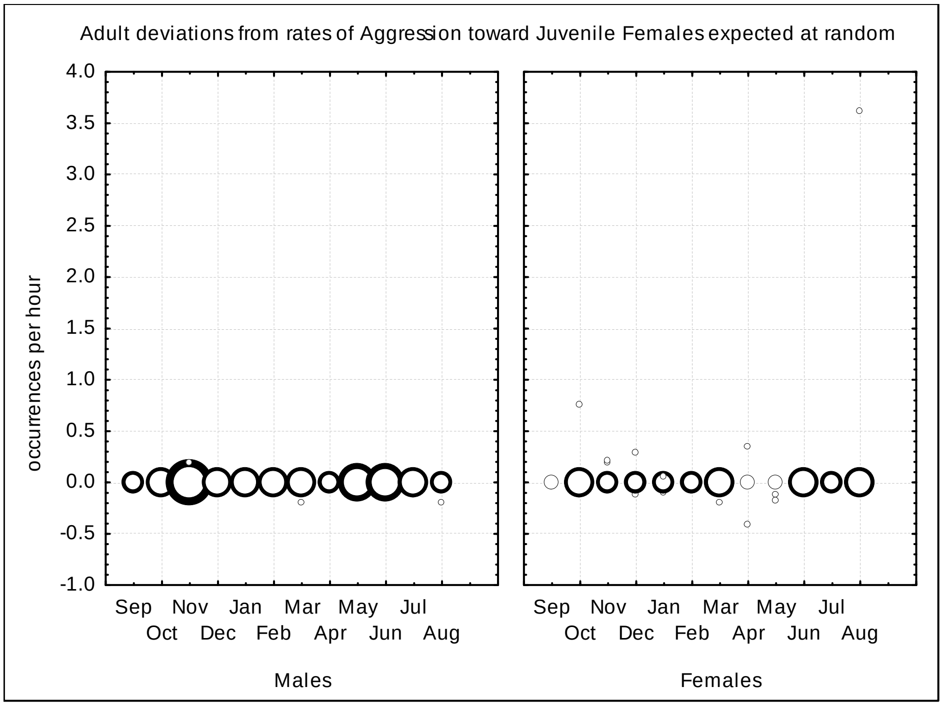


Fig. 4-4. Deviations from expected rates of aggression toward juvenile females.

Aggression toward Juvenile Males

There is no sex difference in bias of aggression toward juvenile males according to either the best fit random intercept LMEM or means RP models, and no evidence that adults bias their aggression either toward or away from juvenile males (Table 4-6, Figure 4-5).

TABLE 4-6. LMEM model parameter estimates for deviations from expected rates of aggression toward juvenile males.

Variable	Model	Effect	est	SE	DF	t	p
Dev Aggression to JM	random int. LMEM	INT	-0.01	0.03	16	-0.45	0.66
		SEX	0.02	0.04	103	0.66	0.51

JM = juvenile males; all tables follow this convention.

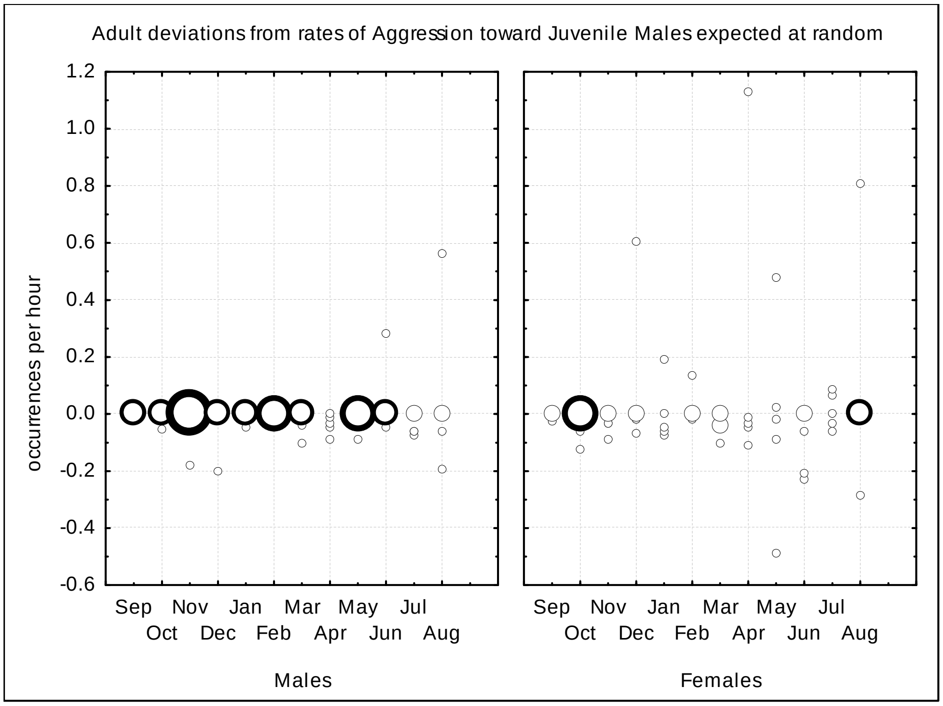


Fig. 4-5. Deviations from expected rates of aggression toward juvenile males.

Aggression toward Infants

Infants were the cohort individuals that were 0-11 months old during this study. Aggression toward this cohort was not analyzed separately according to sex because, after the first few months of study, the infant mortality pattern across study groups resulted in several female infants, but only a single male infant, being available to focal adults for social interaction. There is no sex difference in the deviations from rates of aggression toward infants expected at random according to either the best fit random intercepts LMEM or the mean RP models, and no evidence of bias of adult aggression either toward or away from infants (Table 4-7, Figure 4-6).

TABLE 4-7. Model parameter estimates of deviations from expected rates of aggression toward infants.

Variable	Model	Effect	est	SE	DF	t	p
Dev Aggression to INFs	random int. LMEM	INT	-0.02	0.03	16	-0.68	0.50
		SEX	0.03	0.04	103	0.85	0.40
	mean RP	INT	-0.02	0.01	16	-1.40	0.18
		SEX	-0.02	0.02	16	-1.40	0.18

INFs= infants; all tables follow this convention.

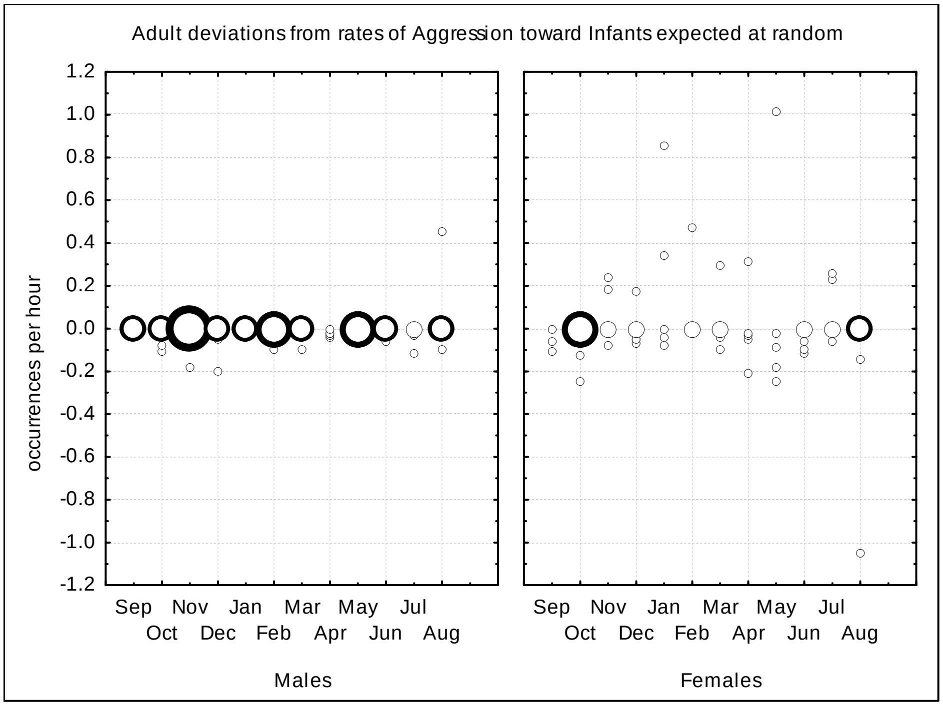


Fig. 4-6. Deviations from expected rates of aggression toward infants.

Non-aggressive dominance

Non-aggressive dominance in this study is the behavior “supplant”. This is not an overtly aggressive behavior and requires no physical contact, but, like taking priority of access to food while subordinate animals wait, it is an overt expression of dominance.

Rates of supplanting others

According to the best fit LMEM, there is a significant sex difference in mean rates of supplants, with adult females supplanting others more often than do adult males. The best fit mean RP model indicates a trend toward higher rates of supplants by adult females (Table 4-8, Figure 4-7).

TABLE 4-8. Model parameter estimates for rates of supplanting others.

Variable	Model	Effect	est	SE	DF	t	p
Supplant	random int. LMEM	INT	0.18	0.06	16	2.88	0.01*
		SEX	0.20	0.09	103	2.37	0.02*
	mean RP	INT	0.16	0.04	16	3.81	0.002*
		SEX	0.11	0.06	16	1.78	0.09†

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

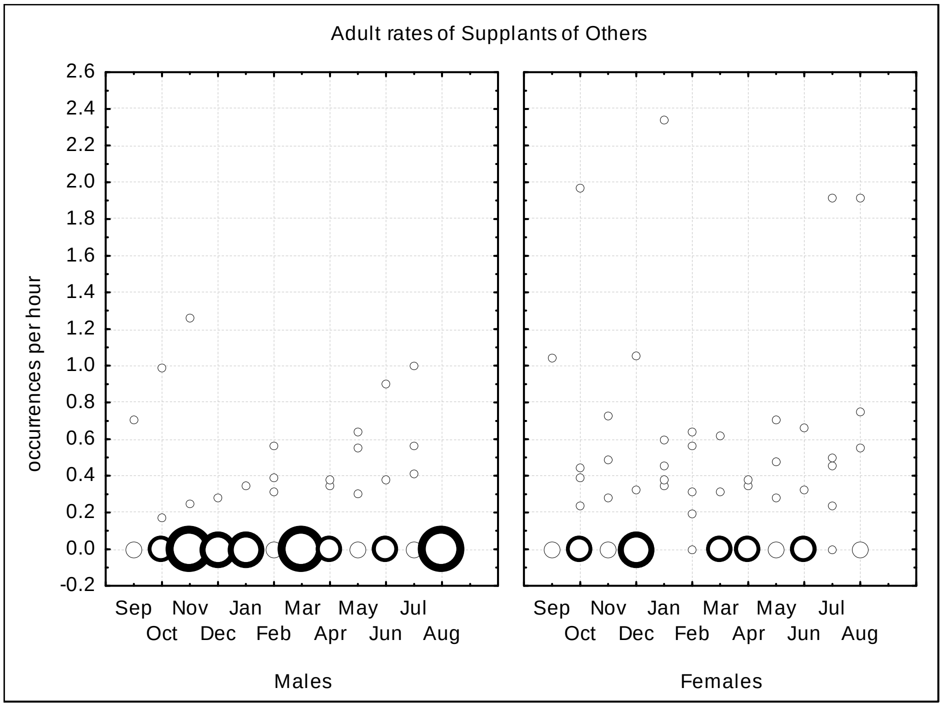


Fig. 4-7. Adult rates of supplanting others.

As with aggressive behavior, considering supplants toward all others may obscure patterns of supplanting of specific age/sex classes. Given female dominance in this species, it is probable that adult males and females target different age/sex classes with their expression of dominance. Therefore, adult sex deviations from rates of supplants expected if adults directed their supplants randomly across all available group members were also examined.

Supplanting Adult Females

An LMEM could not be fit. According to the best fit mean RP model, there is no sex difference in the deviations from rates of supplanting adult females expected at random, but a significant bias against supplanting adult females by both sexes (Table 4-9, Figure 4-8).

TABLE 4-9. RP model parameter estimates for deviations from expected rates of supplanting adult females.

Variable	Model	Effect	est	SE	DF	t	p
Dev Supplant AF	mean RP	INT	-0.05	0.02	16	-3.20	0.006*
		SEX	0.03	0.02	16	1.64	0.12

$* p \leq 0.05$

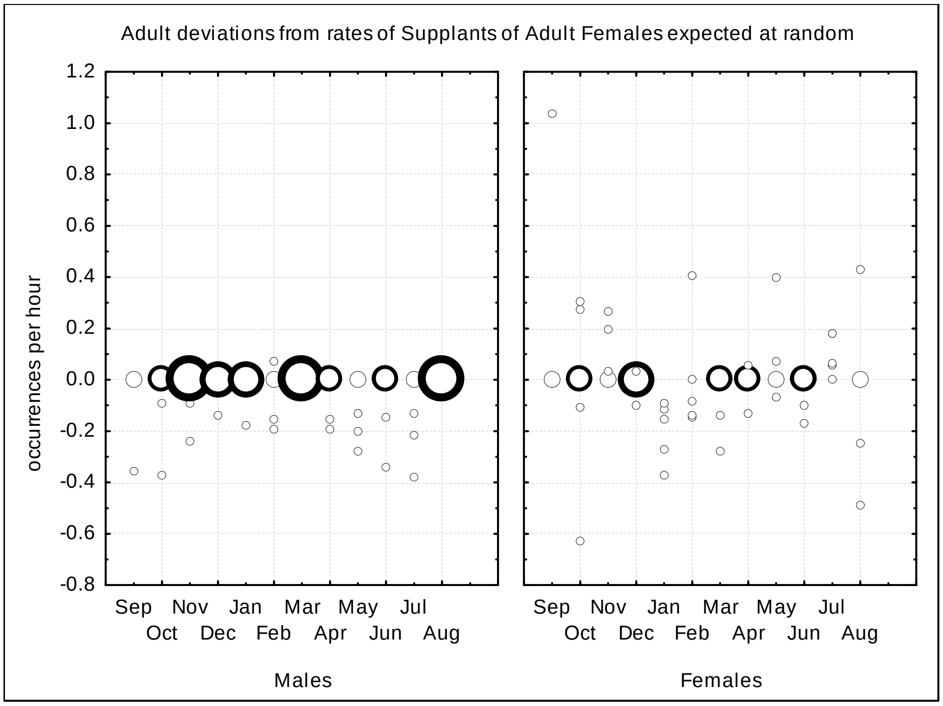


Fig. 4-8. Deviations from expected rates of supplants of adult females.

Supplanting Adult Males

An LMEM could not be fit. According the best fit mean RP model, adults differ significantly in their deviations from expected rates of supplanting adult males, with adult males biasing their expression of supplants more heavily toward adult males than adult females do. This significant sex difference justifies investigating the bias in rates of supplanting adult males for each sex independently. The best fit mean RP models indicate that adult males supplant adult males significantly more often than expected at random, but that adult females tend to supplant adult males less often than expected at random (Table 4-10, Figure 4-9).

TABLE 4-10. RP model parameters estimates of deviations from expected rates of supplanting adult males.

Variable	Model	Effect	est	SE	DF	t	p
Dev Supplant AM	mean RP	INT	0.07	0.02	16	3.54	0.003*
		SEX	-0.06	0.03	16	-2.39	0.03*
AF (only) Dev Supplant AM	mean RP	INT	-0.03	0.02	9	-1.80	0.10†
AM (only) Dev Supplant AM	mean RP	INT	0.10	0.02	7	4.05	0.005*

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

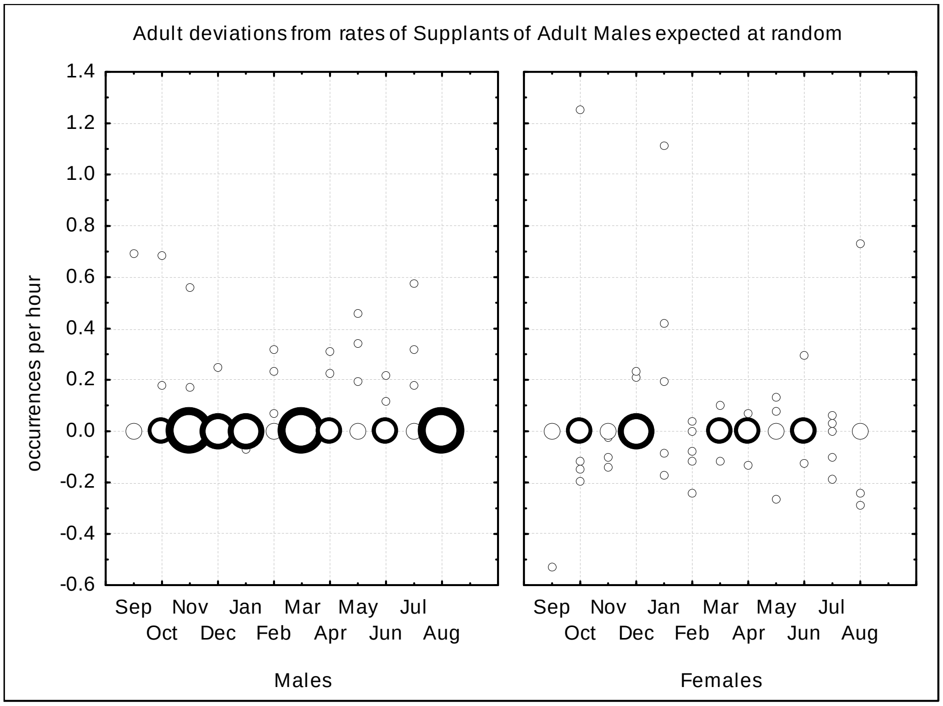


Fig. 4-9. Deviations from expected rates of supplanting adult males.

Supplanting Juvenile Females

Adults were only observed to supplant juvenile females on three occasions. All were exhibited by adult females, but the rarity of this behavior obviates the possibility of a significant sex difference. An LMEM could not be fit. As expected, according the best fit mean RP model, there is no sex difference in the deviations from rates of supplanting juvenile females expected at random, but both sexes supplant juvenile females significantly less often than expected (Table 4-11, Figure 4-10).

TABLE 4-11. RP model parameter estimates of deviations from expected rates of supplanting juvenile females.

Variable	Model	Effect	est	SE	DF	t	p
Dev	mean RP	INT	-0.01	0.00	16	-2.93	0.01*
Supplant JF		SEX	0.01	0.01	16	1.32	0.21

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

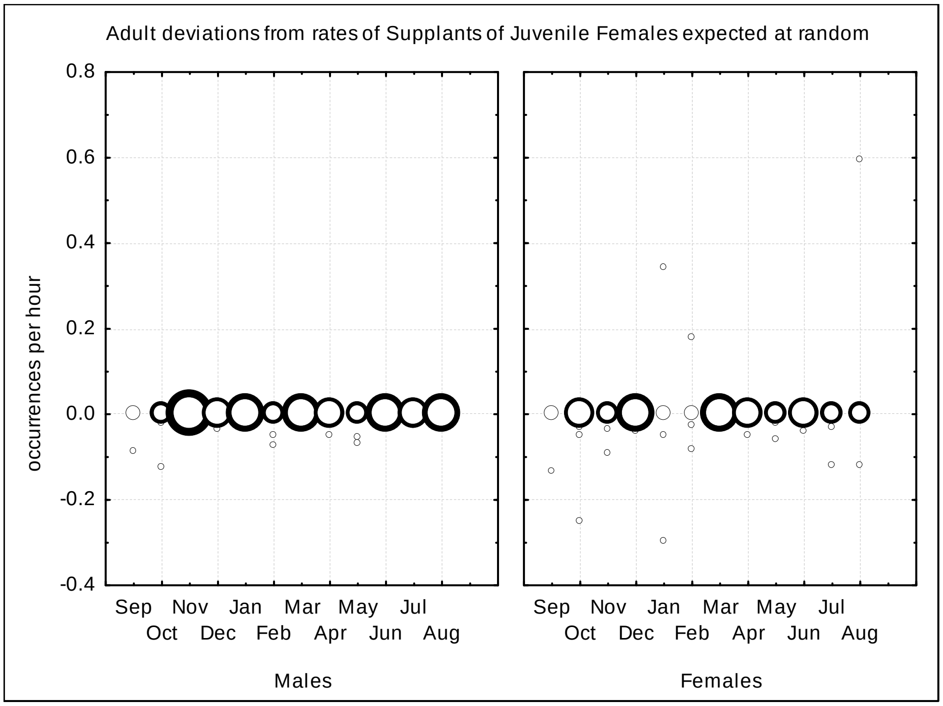


Fig. 4-10. Deviations from expected rates of supplants of juvenile females.

Supplanting Juvenile Males

According the best fit random intercepts LMEM and mean RP model, there is no sex difference in the deviations from rates of supplanting juvenile males expected at random, and no evidence for a bias either toward or away from supplanting juvenile males (Table 4-12, Figure 4-11).

TABLE 4-12. Model parameter estimates of deviations from expected rates of supplants of juvenile males.

Variable	Model	Effect	est	SE	DF	t	p
Dev Supplant JM	random int. LMEM	INT	-0.01	0.01	16	-1.02	0.32
		SEX	0.01	0.01	103	0.59	0.56
	mean RP	INT	-0.01	0.01	16	-1.65	0.12
		SEX	-0.01	0.01	16	-1.31	0.21

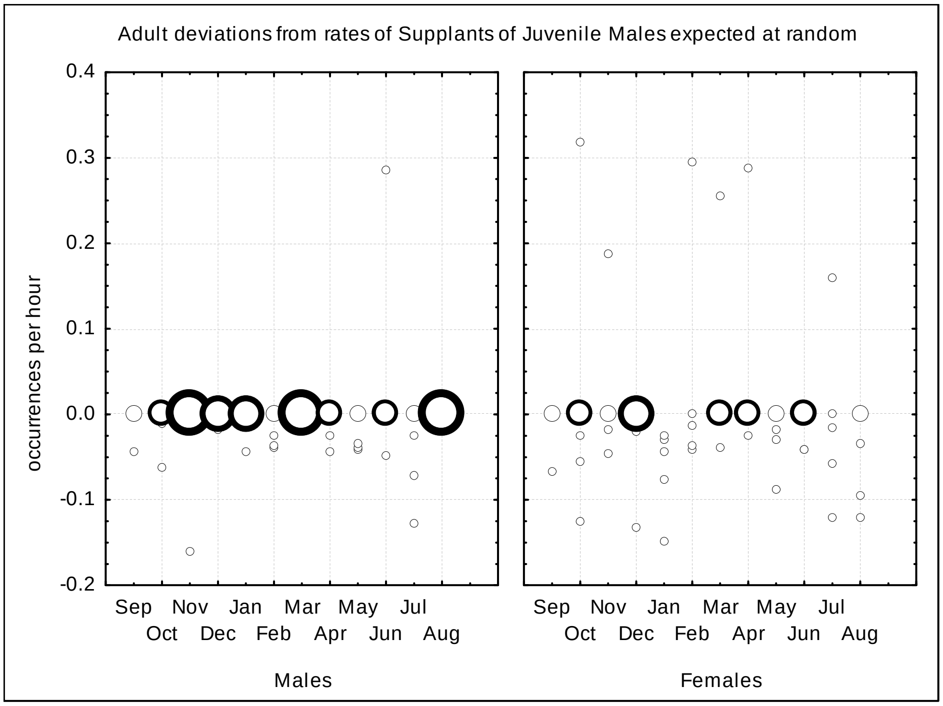


Fig. 4-11. Deviations from expected rates of supplants of juvenile males.

Supplanting Infants

According the best fit mean RP model, there is no sex difference in the deviations from rates of supplanting infants expected at random, but adults supplant infants less often than expected at random (Table 4-13, Figure 4-12).

TABLE 4-13. RP model parameter estimates of deviations from expected rates of supplants of infants.

Variable	Model	Effect	est	SE	DF	t	p
Dev	mean RP	INT	-0.02	0.00	16	-3.40	0.004*
Supplant INFs		SEX	0.00	0.01	16	-0.70	0.50

* $p \leq 0.05$

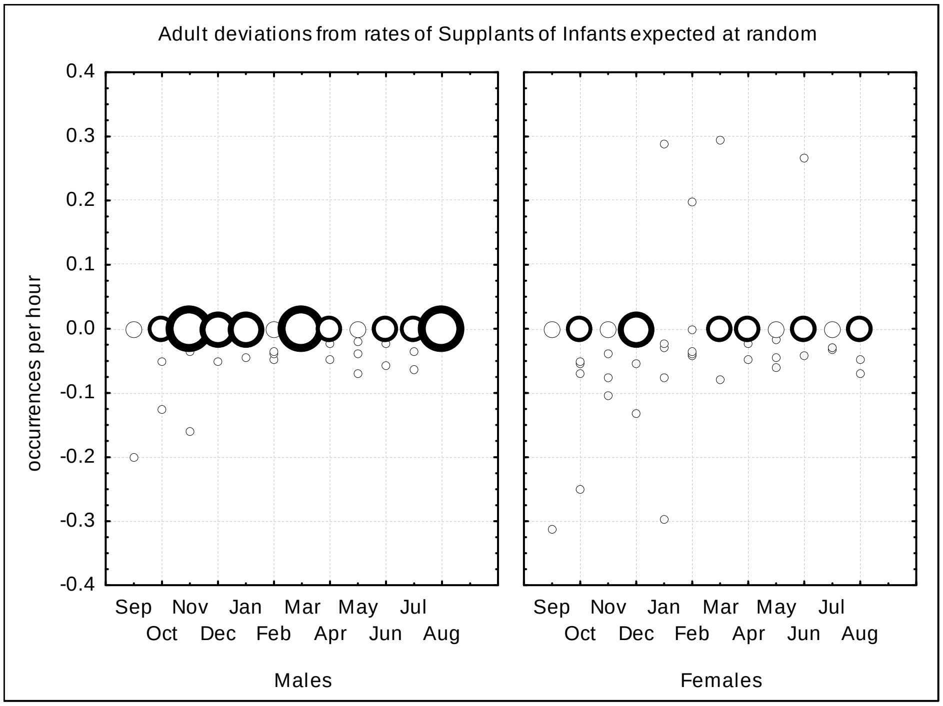


Fig. 4-12. Deviations from expected rates of supplants of infants.

Avoidance

Avoidance is a low-intensity submissive behavior in which a subordinate individual changes position in order to preclude interaction with a dominant individual. In that regard, "avoid" is a submissive behavior intrinsic to the focal individual rather than a response to an extrinsic behavior directed at the focal individual, as is the act of being supplanted by another individual.

Rates of Avoidance of Others

According to the best fit random intercepts LMEM and mean RP models, there is no significant difference between adult male and adult female rates of avoidance of others overall (Table 4-14, Figure 4-13).

TABLE 4-14. Model parameter estimates of rates of avoidance of others.

Variable	Model	Effect	est	SE	DF	t	p
Avoidance	random int. LMEM	INT	0.32	0.08	16	3.88	0.001*
		SEX	-0.09	0.12	103	-0.79	0.43
	mean RP	INT	0.03	0.04	16	0.59	0.57
		SEX	0.04	0.06	16	0.72	0.48

* $p \leq 0.05$

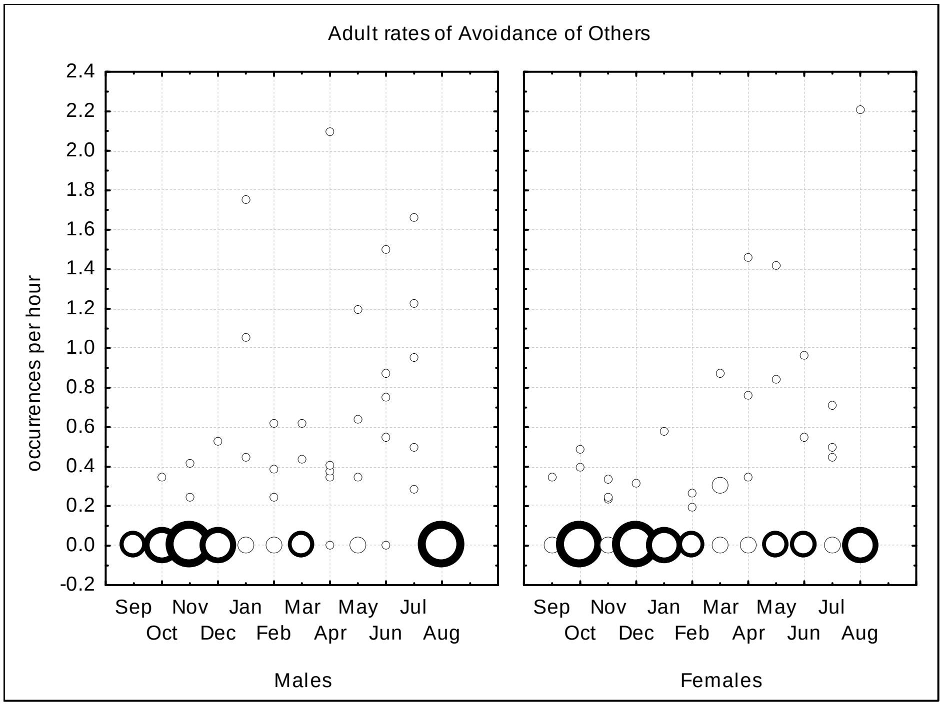


Fig. 4-13. Adult rates of avoidance of others.

Adult deviations from rates of avoidance of adult females expected at random

There is no sex difference in adult deviations from expected rates of avoidance of adult females at random according to the best fit random intercepts LMEM and mean RP models, and no evidence that adults avoid adult females more or less than expected at random (Table 4-15, Figure 4-14).

TABLE 4-15. Model parameter estimates of deviations from expected rates of avoidance of adult females.

Variable	Model	Effect	est	SE	DF	t	p
Dev Avoid AF	random int. LMEM	INT	0.03	0.06	16	0.53	0.60
		SEX	0.11	0.08	103	1.36	0.18
	mean RP	INT	-0.01	0.03	16	-0.51	0.61
		SEX	0.05	0.04	16	1.34	0.20

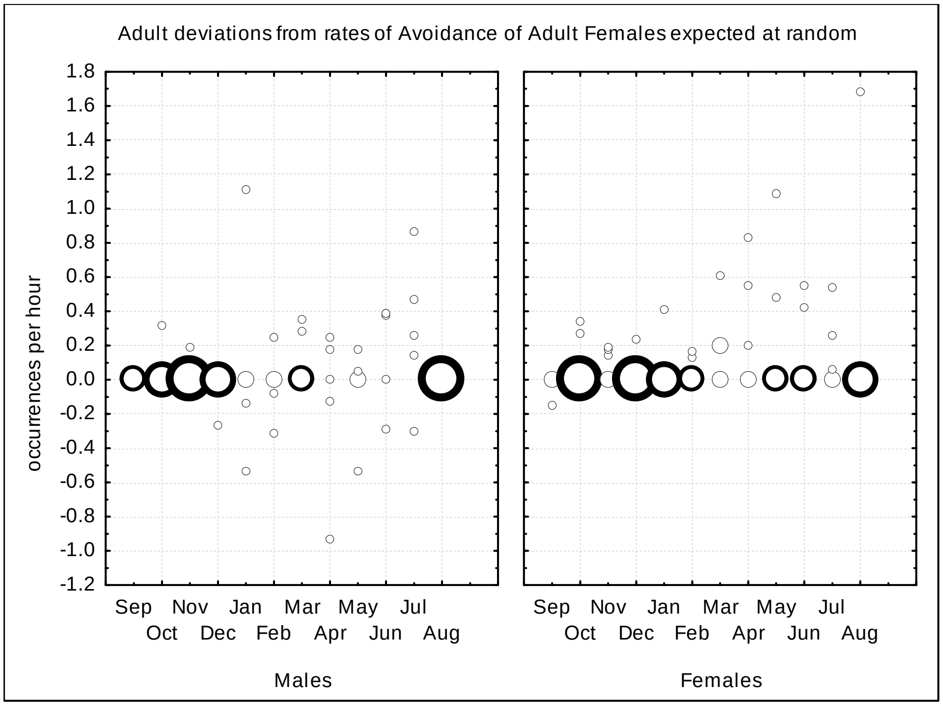


Fig. 4-14. Deviations from expected rates of avoidance of adult females.

Adult deviations from rates of avoidance of adult males expected at random

The best fit random intercepts LMEM and mean RP models indicate no sex difference in the deviations from rates of avoidance of adult males expected at random, and no evidence that adults avoid adult males at non-random rates (Table 4-16, Figure 4-15).

TABLE 4-16. Model parameter estimates of deviations from expected rates of avoidance of adult males.

Variable	Model	Effect	est	SE	DF	t	p
Dev Avoid AM	random int. LMEM	INT	0.03	0.05	16	0.54	0.59
		SEX	-0.10	0.07	103	-1.57	0.12
	mean RP	INT	-0.02	0.02	16	-1.50	0.15
		SEX	-0.02	0.02	16	-0.87	0.40

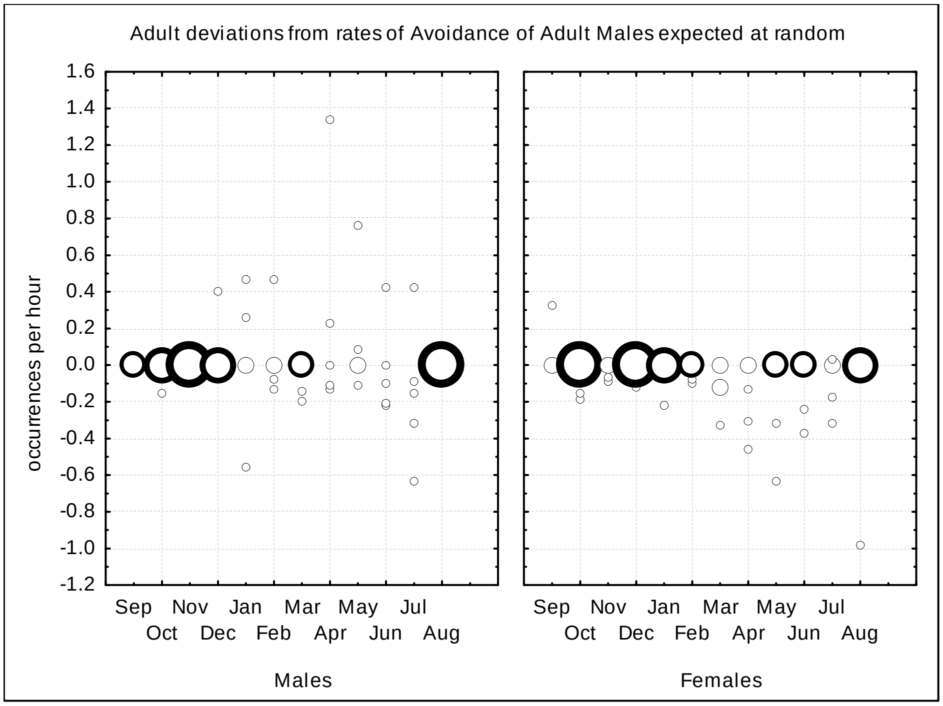


Fig. 4-15. Deviations from expected rates of avoidance of adult males.

Adult rates of avoidance of juvenile females

Adults were never observed to avoid juvenile females (Figure 4-16).

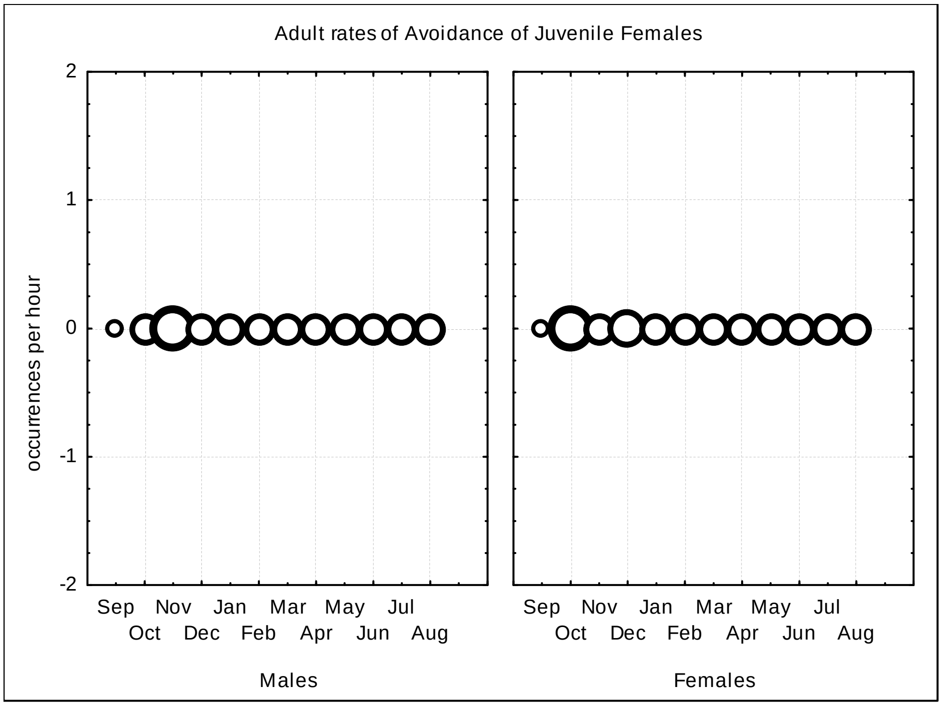


Fig. 4-16. Adult rates of avoidance of juvenile females.

Adult rates of avoidance of juvenile males

Only one adult male was ever observed to avoid a juvenile male. Both occasions of this behavior involved the same adult male/juvenile male dyad. The rarity of this behavior precludes the possibility of a statistically significant sex difference (Figure 4-17).

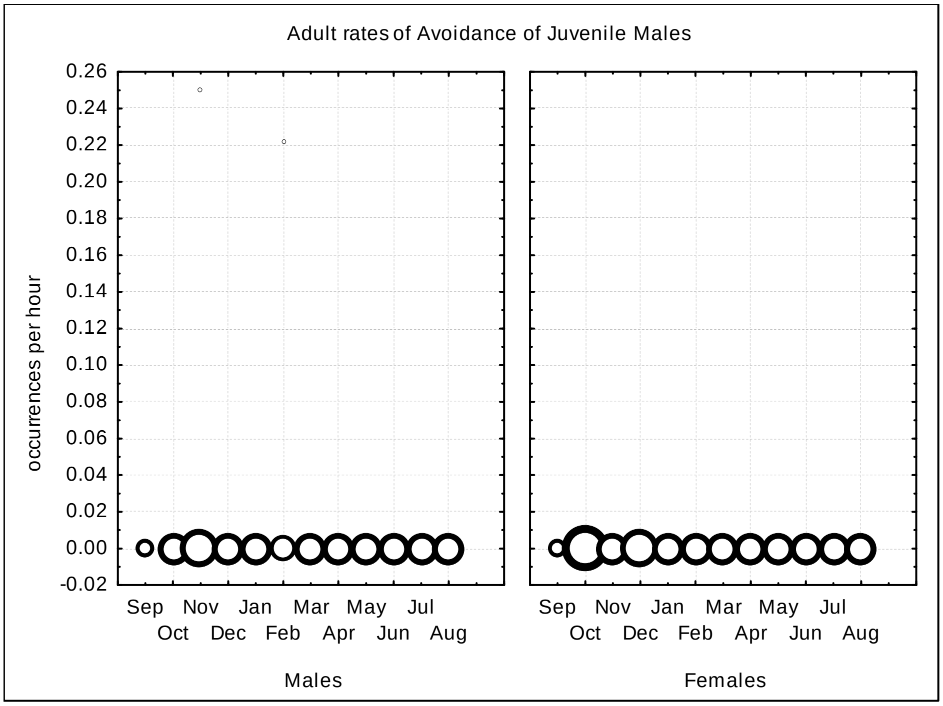


Fig. 4-17. Adult rates of avoidance of juvenile males.

Adult rates of avoidance of infants

One adult male was observed to avoid one infant female on one occasion when the infant female was nearly a year old. The infant female involved was a particularly precocious infant of the dominant female in the group who had learned early on that if she persistently, vocally protested her treatment by other individuals, her mother or another high ranking female would eventually come to her aid. The rarity of this behavior precludes the possibility of a statistically significant sex difference (Figure 4-18).

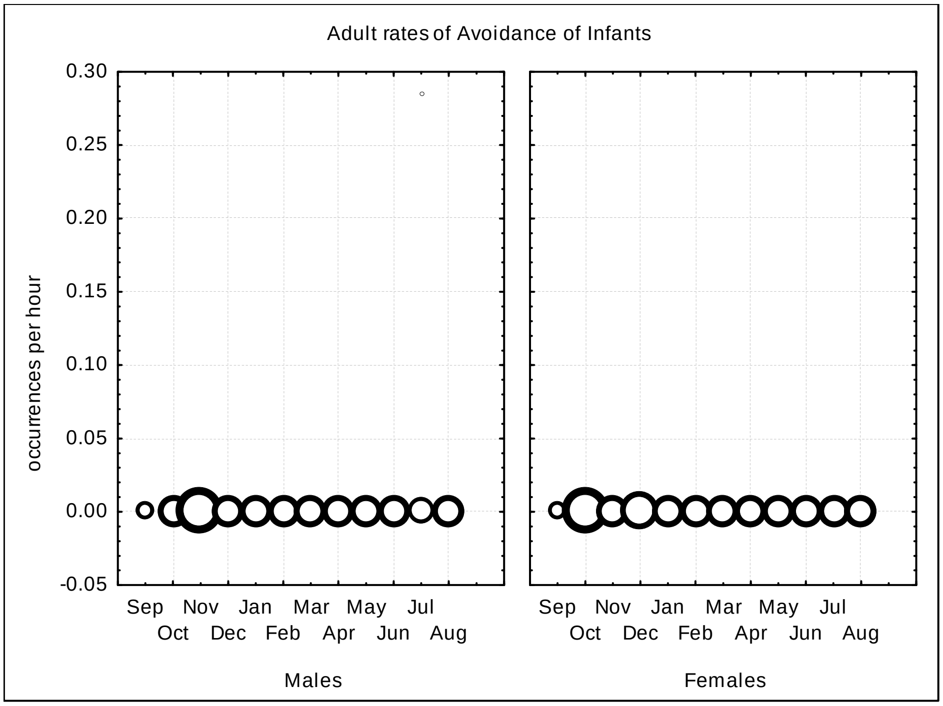


Fig. 4-18. Adult rates of avoidance of infants.

Fear

Fear is represented by the behavior "flee", which is a much more extreme and energetically costly form of submission than all others.

Rates of Fear of Others

While the boxplots of adult rates of fear of others suggest an increase through time, the scatterplots of individual data points do not suggest such a pattern. The best fit LMEM and RP models are a random intercepts model and mean model, respectively. They indicate no significant sex difference in the expression of fear of others (Table 4-17, Figure 4-19).

TABLE 4-17. Model parameter estimates of rates of fear of others.

Variable	Model	Effect	est	SE	DF	t	p
Fear	random int. LMEM	INT	0.41	0.11	16	3.60	0.002*
		SEX	-0.10	0.16	103	-0.64	0.53
	mean RP	INT	0.15	0.04	16	3.72	0.002*
		SEX	-0.09	0.06	16	-1.57	0.14

* $p \leq 0.05$

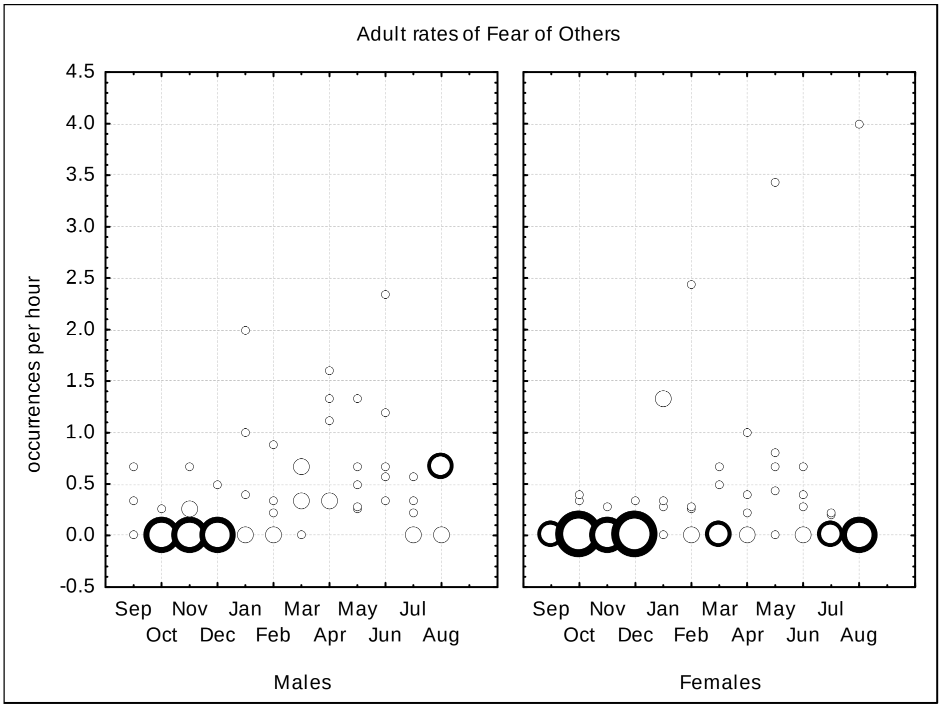


Fig. 4-19. Adult rates of fear of others.

As with all other agonistic behaviors, sex differences in the expression of fear toward specific age/sex classes may be present.

Fear of Adult Females

The best fit random intercepts LMEM and mean RP models indicate no sex difference in the deviations from rates of fear of adult females expected at random. But according to the best fit random intercepts LMEM, adults of both sexes fear adult females more often than expected at random. In contrast, the best fit mean RP model indicates that both sexes express fear of adult females as expected at random (Table 4-18, Figure 4-20). A qualitative examination of individual ordinary least-squares (OLS) regressions suggest that most individuals tend to express fear of adult females a bit more than expected at random, but the effect does not seem to be very strong (Figure 4-21). I therefore accept a conservative interpretation that adults of both sexes express fear of adult females as expected at random.

Note that the individual OLS regressions do not include samples from individuals who were sampled for only one month, and therefore under-represent the data that are actually used by the LMEM and RP models. They do not appropriately account for within-subject correlation, and they are not used in any of the analyses presented herein. LMEM uses maximum-likelihood methods to estimate individual slopes and intercepts, and RP models do not consider individual slopes and intercepts. Individual OLS regressions are only used here as a way to qualitatively assess and visualize individual longitudinal trends, as suggested by Singer and Willett [2003].

TABLE 4-18. Model parameter estimates of deviations from expected rates of fear of adult females.

Variable	Model	Effect	est	SE	DF	t	p
Dev Fear of AF	random int. LMEM	INT	0.16	0.07	16	2.14	0.05*
		SEX	0.02	0.10	103	0.19	0.85
	mean RP	INT	0.03	0.03	16	1.06	0.31
		SEX	0.00	0.04	16	-0.06	0.95

* $p \leq 0.05$

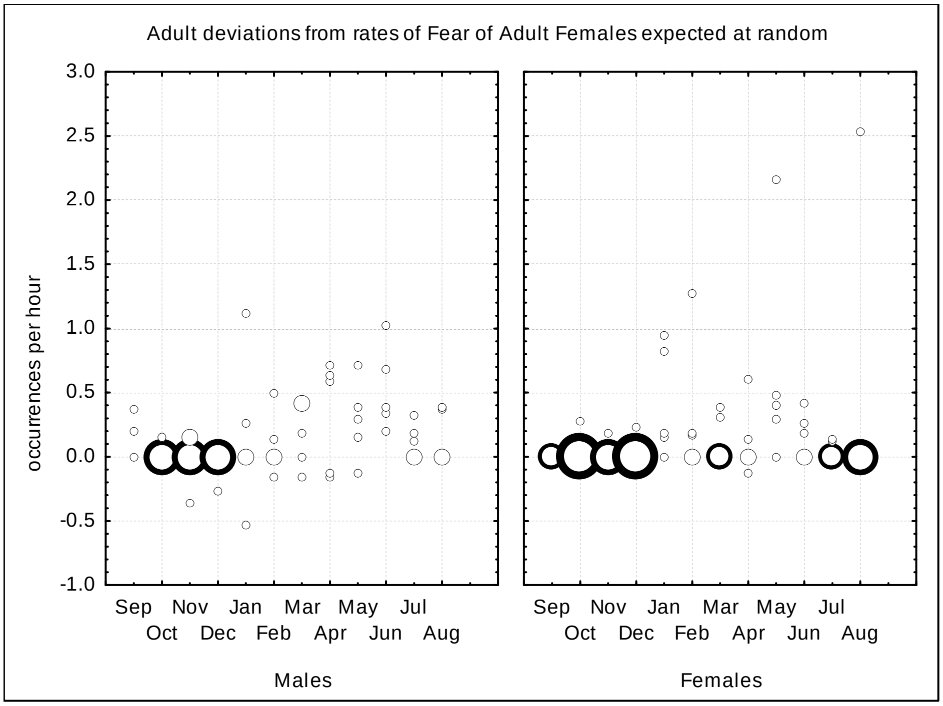


Fig. 4-20. Deviations from expected rates of fear of adult females.

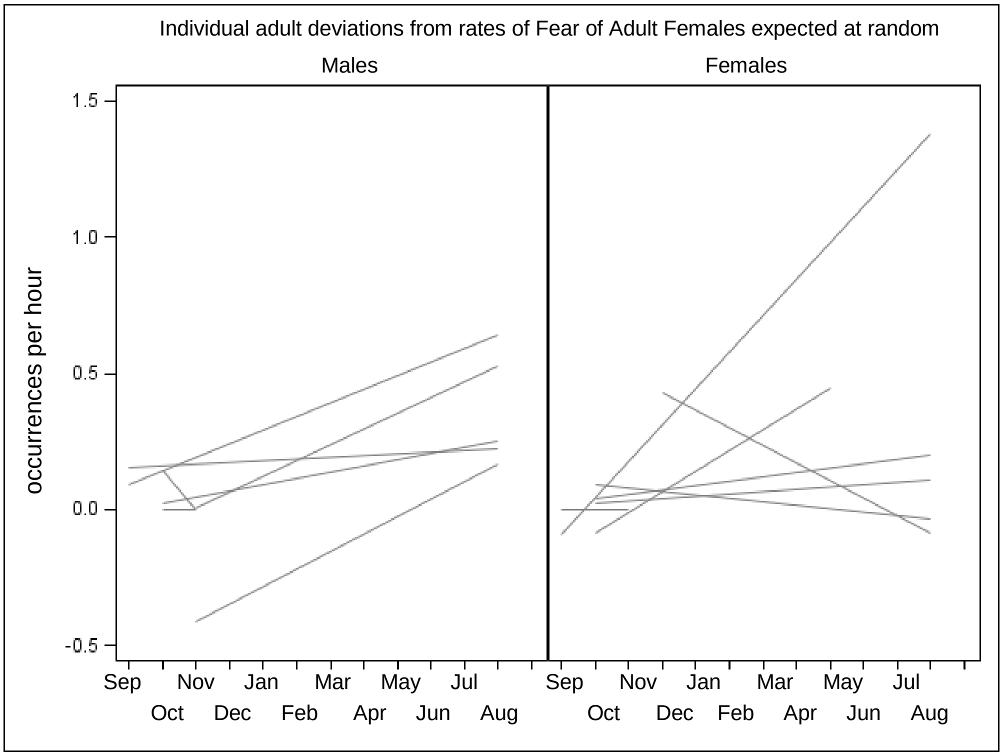


Fig. 4-21. Individual OLS regressions of deviations from expected rates of fear of adult females.

Fear of Adult Males

Both the best fit random intercepts LMEM and RP model indicate no sex difference in deviations from expected rates of fear of adult males at random, but that adults of both sexes fear adult males less often than expected at random (Table 4-19, Figure 4-22).

TABLE 4-19. Model parameter estimates of deviations from expected rates of fear of adult males.

Variable	Model	Effect	est	SE	DF	t	p
Dev Fear of AM	random int. LMEM	INT	-0.10	0.04	16	-2.46	0.03*
		SEX	-0.01	0.06	103	-0.11	0.91
	mean RP	INT	-0.04	0.01	16	-2.91	0.01*
		SEX	0.01	0.02	16	0.75	0.46

* $p \leq 0.05$

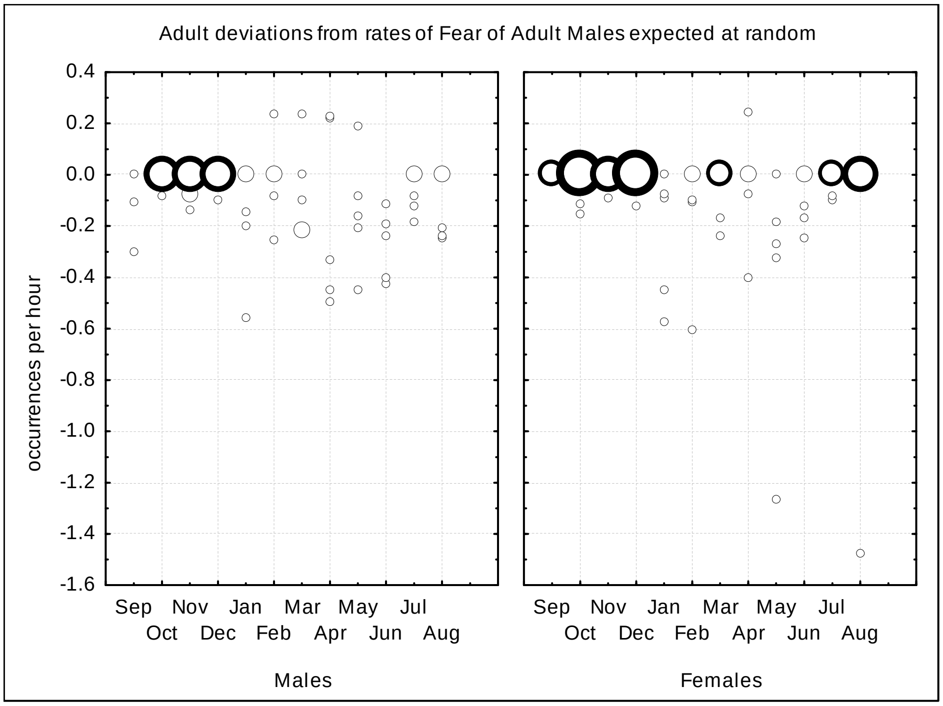


Fig. 4-22. Deviations from expected rates of fear of adult males.

Fear of Juvenile Females, Juvenile Males, and Infants

Adults were never observed to fear juvenile females, juvenile males, or infants.

Discussion – Agonism

The following tables summarize tests of adult sex differences in agonistic behavior, and tests of adult patterns of bias in their agonistic behavior toward particular age/sex classes. Only statistically significant results are presented; empty cells represent results of no statistical significance. In general, adults exhibit few sex differences in their expression of agonistic behavior (Table 4-20). They are limited to: adult females exhibiting more aggression (Table 4-21), adult females supplanting others more often (Table 4-21), and males concentrating their supplanting behavior on other adult males while females did not (Table 4-21). These results are consistent with expectations for a female dominant species, as are other results (that are not sex-typed), such as both sexes exhibiting more fear of adult females, fewer supplants of adult females, and less fear of adult males than expected at random. It should be noted that although females are more aggressive than males on average, there is a great deal of overlap and a high degree of inter- and intra-individual variation in both overall rates of agonism and overt aggression throughout the year.

Qualitatively, it appears that there may be a tendency for female aggression to increase at the end of the observation year (Figure 4-1). If so, this could be due to the fact that the rainy season has ended by that time and resource availability during that season declines (Figure 4-23). Increased intra-group aggression during times of resource uncertainty is consistent with data from captive experimentation [Rosenblum 1987].

TABLE 4-20. Summary of sex differences in overall rates of agonism.

Intrinsic Agonistic Behavior	Sex Difference	Time effects	
Aggression	♀ +	·	·
Supplant	♀ +	·	·
Avoid	·	·	·
Fear	·	·	·

For Sex Difference:
+ indicates significantly more than the opposite sex;
· indicates no significant difference.
For Time effects:
· indicates no temporal effect.

TABLE 4-21. Summary of sex differences in bias of agonism toward each partner age/sex class.

Intrinsic Agonistic Bias	Partner type	Sex-typed bias		Time effects	
Aggression	AF	·	·	·	·
Aggression	AM	·	·	·	·
Aggression	JF	·	·	·	·
Aggression	JM	·	·	·	·
Aggression	INFs	·	·	·	·
Supplant	AF	♀ –	♂ –	·	·
Supplant	AM	·	♂ +	·	·
Supplant	JF	♀ –	♂ –	·	·
Supplant	JM	·	·	·	·
Supplant	INFs	♀ –	♂ –	·	·
Avoid	AF	·	·	·	·
Avoid	AM	·	·	·	·
Fear	AF	♀ +	♂ +	·	·
Fear	AM	♀ –	♂ –	·	·

For Sex-typed bias:
+ indicates significantly more than expected at random;
– indicates significantly less than expected at random;
· indicates no significant difference from that expected at random.
For Time effects:
· indicates no temporal effect.

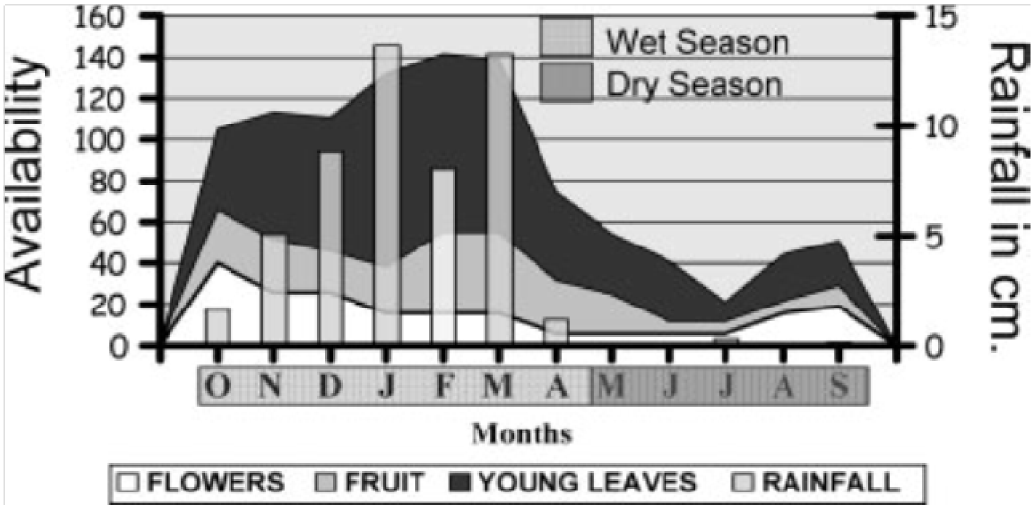


Fig. 4-23. Annual resource availability and precipitation at Beza Mahafaly Special Reserve [Sauther and Cuozzo 2009].

AFFILIATION

Grooming

Grooming is the only overt form of affiliation in *Lemur catta* besides play, of which adults engage in very little. The amount of time spent grooming another individual includes the amount of time spent allogrooming and mutual grooming with that individual.

Time spent grooming

The best fit random intercepts LMEM indicates a significant sex difference in the amount of time adults spend engaged in grooming others, but the best fit mean intercept response profile model does not (Table 4-22, Figure 4-24). Plots of individual OLS regressions are somewhat suggestive that, on average, adult females may spend more time grooming than adult males (Fig. 4-25). Plots of individual yearly means are clearly suggestive that, as a group, adult females spend more time on average over the course of the year grooming others (Fig. 4-26). Taken together, these results suggest that adult females spend more time grooming others than adult males, but remain inconclusive. Because I generally prefer the results of LMEMs to RP models, I tentatively accept the interpretation that adult females spend more time grooming others than adult males, but not that there is a great deal of variation in grooming times as well as overlap between the sexes.

There is one non-completer male and one non-completer female that have very unusual individual OLS regressions, suggesting that they are outliers (Figure 4-27). But the individual values at each month belonging to those individuals are not outlying and they should not, therefore, unduly influence either type of analysis (the random intercepts LMEM does not consider inter-individual variation in slopes).

TABLE 4-22. Model parameter estimates of time spent grooming others.

Variable	Model	Effect	est	SE	DF	t	p
Grooming	random int. LMEM	INT	0.84	0.18	16	4.57	0.0003*
		SEX	0.53	0.26	103	2.03	0.05*
	mean RP	INT	0.56	0.14	16	4.09	0.0009*
		SEX	0.11	0.19	16	0.60	0.56

* p ≤ 0.05

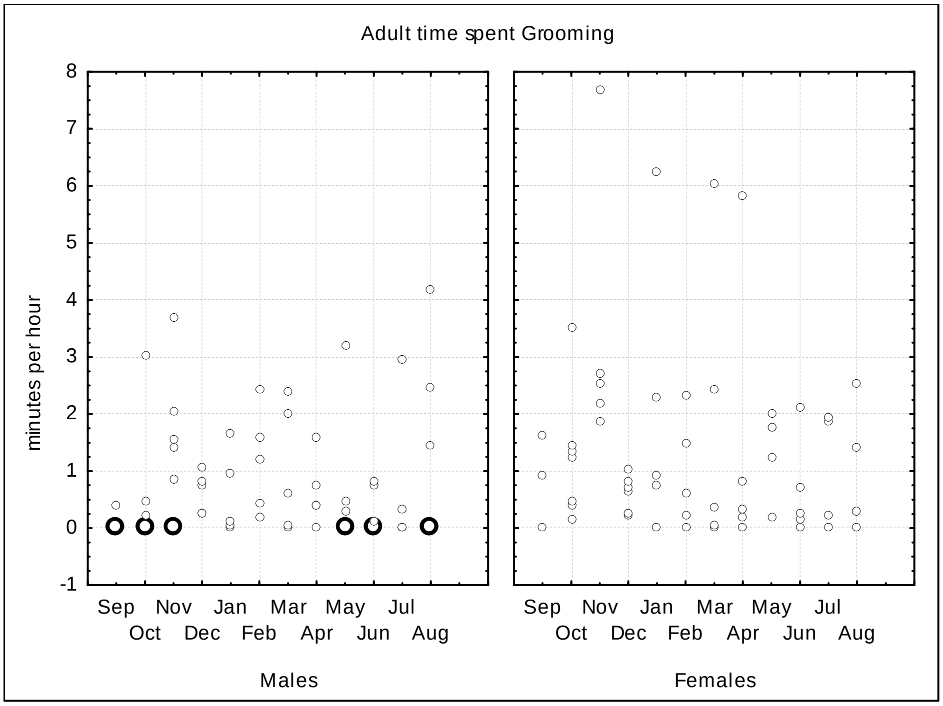


Fig. 4-24. Adult time spent grooming others.

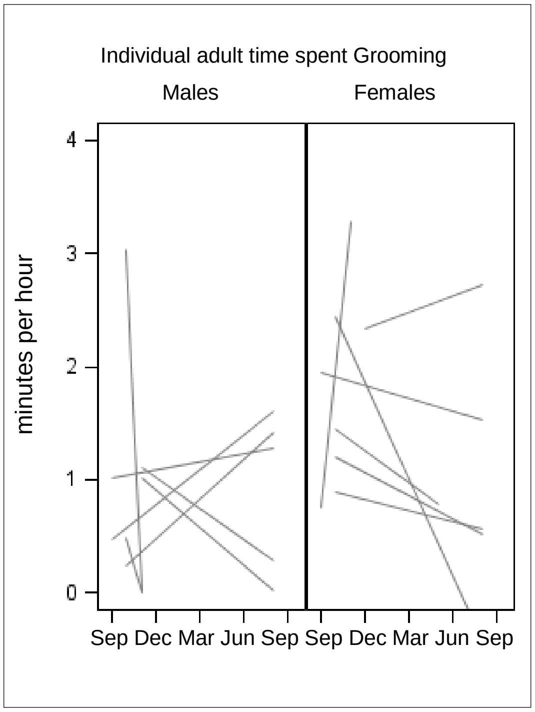
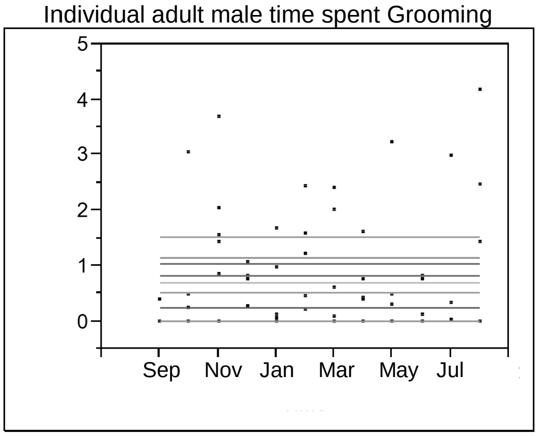


Fig. 4-25. Ordinary least squares regressions of individual time spent grooming others.



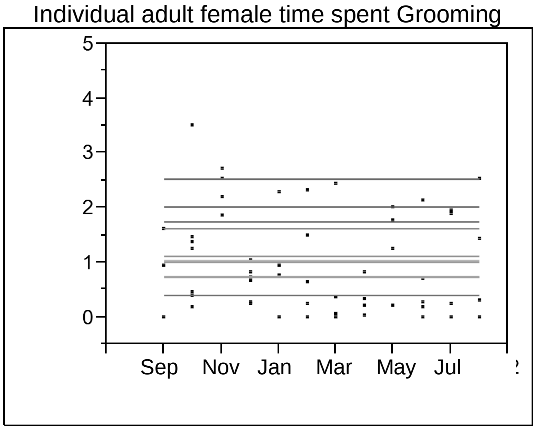
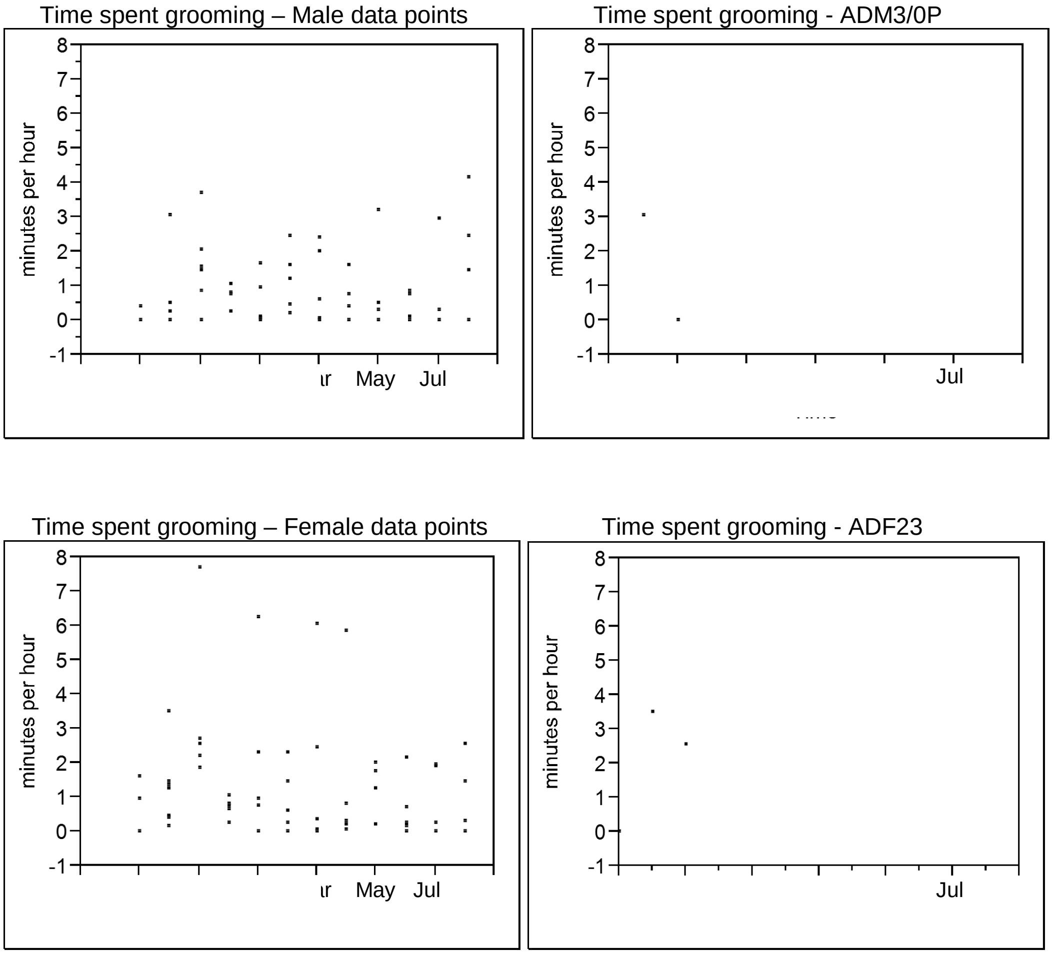


Fig. 4-26. Individual annual means of time spent grooming others. Dots represent individual monthly means; lines represent individual annual means. All figures of this type follow these conventions.


Time spent grooming – Male data points

Time spent grooming - ADM3/0P

Time spent grooming – Female data points

Time spent grooming - ADF23

Fig. 4-27. Individual adult time spent grooming: males (upper left); male outlier (upper right); females (lower left); female outlier (lower right).

Grooming Adult Females

According to the best fit random intercepts LMEM and RP models, there is no significant sex difference in the deviations from time spent grooming adult females expected if individuals' grooming were randomly distributed across all available group members and no indication that adults bias their grooming time toward or away from adult females (Table 4-23, Figure 4-28). In order to control for any differences in overall time spent grooming, the following analyses of grooming time are of deviations from expectations of grooming time per age/sex class if an individual's grooming were distributed randomly across all group members.

TABLE 4-23. Model parameter estimates of deviations from expected time spent grooming adult females.

Variable	Model	Effect	est	SE	DF	t	p
Dev Groom AF	random int. LMEM	INT	0.05	0.06	16	0.74	0.47
		SEX	0.07	0.09	103	0.74	0.46
	mean RP	INT	0.04	0.07	16	0.65	0.52
		SEX	0.06	0.10	16	0.64	0.53

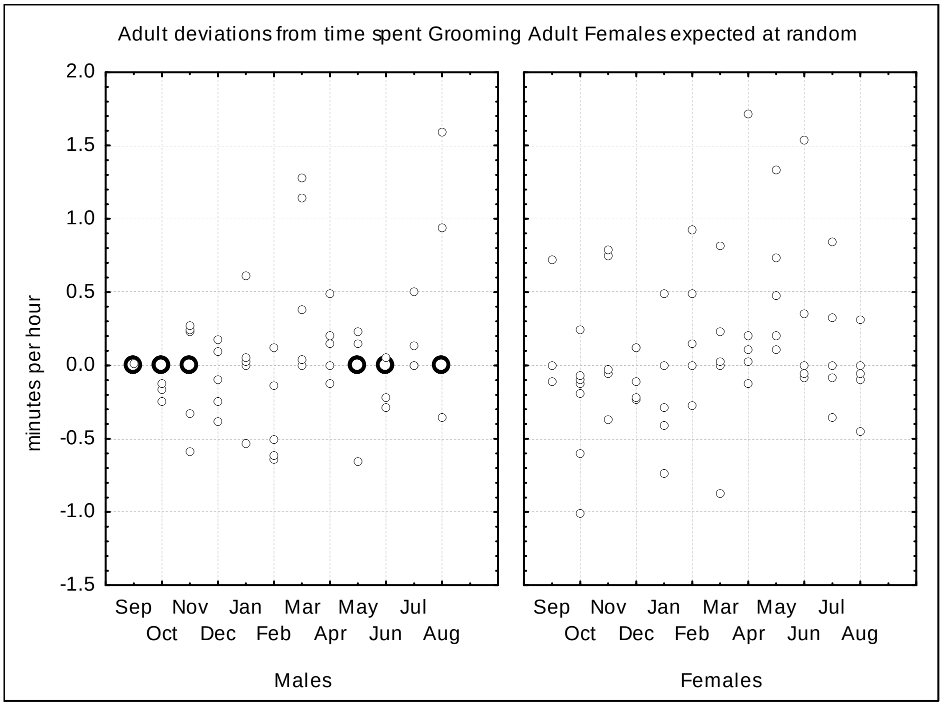


Fig. 4-28. Deviations from expected time spent grooming adult females.

Grooming Adult Males

According to both the best fit random intercepts LMEM and mean RP model, there is a significant sex difference in the deviations from time spent grooming adult males expected at random, in which adult females bias their grooming time away from adult males more than adult males do (Table 4-24, Figure

4-29). When analyzed separately by sex, both the best fit random intercepts LMEM and mean RP model indicate that adult females spend significantly less time grooming adult males than expected at random, while the best fit RP model indicates that adult males groom adult males as expected at random (Table 4-24).

TABLE 4-24. Model parameter estimates of deviations from expected time spent grooming adult males.

Variable	Model	Effect	est	SE	DF	t	p
Dev Groom AM	random int. LMEM	INT	0.02	0.07	16	0.26	0.80
		SEX	-0.38	0.10	103	-3.76	0.0003*
	mean RP	INT	-0.04	0.04	16	-0.98	0.34
		SEX	-0.20	0.06	16	-3.28	0.005*
AF Dev Groom AM	random int. LMEM	INT	-0.36	0.08	9	-4.46	0.002*
	mean RP	INT	-0.23	0.04	9	-6.21	0.0002*
AM Dev Groom AM	mean RP	INT	-0.02	0.01	7	-1.60	0.15

* $p \leq 0.05$

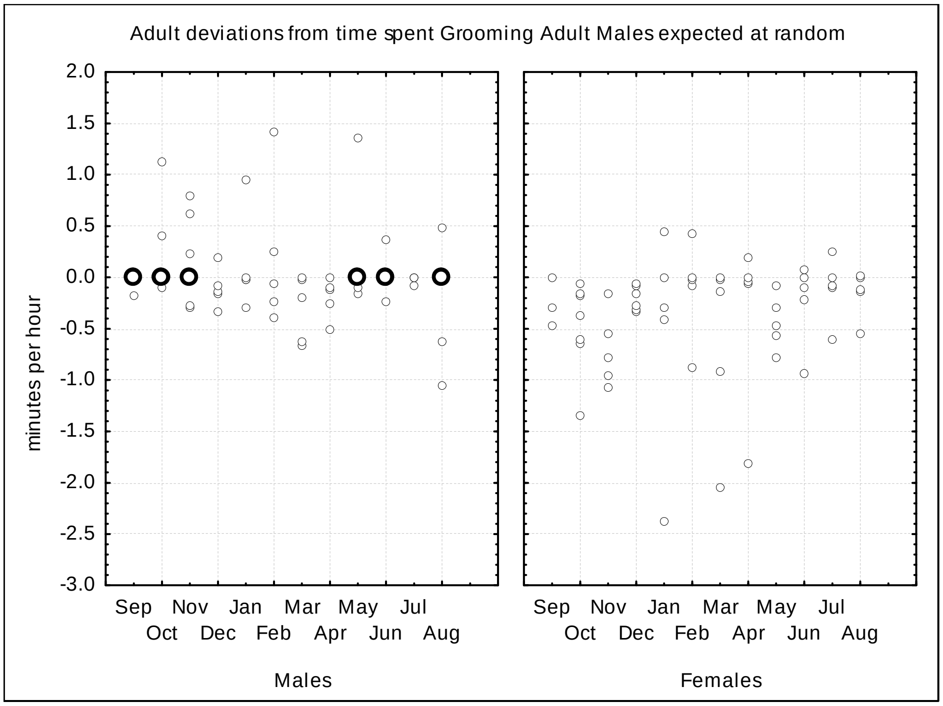


Fig. 4-29. Deviations from expected time spent grooming adult males.

Grooming Juvenile Females

There is no significant sex difference in deviations from grooming time focused on juvenile females expected at random according to the best fit random intercepts LMEM and mean RP models (Table 4-25, Figure 4-30). The best fit mean RP model indicates that adults spend less time grooming juvenile females than expected at random, but the best fit random intercepts LMEM finds no difference from random expectation (Table 4-25).

TABLE 4-25. Model parameter estimates of deviations from expected time spent grooming juvenile females.

Variable	Model	Effect	est	SE	DF	t	p
Dev Groom JF	random int. LMEM	INT	-0.04	0.03	16	-1.40	0.18
		SEX	-0.02	0.04	103	-0.43	0.67
	mean RP	INT	-0.03	0.01	16	-2.37	0.03*
		SEX	0.01	0.02	16	0.93	0.37

$* p \leq 0.05$

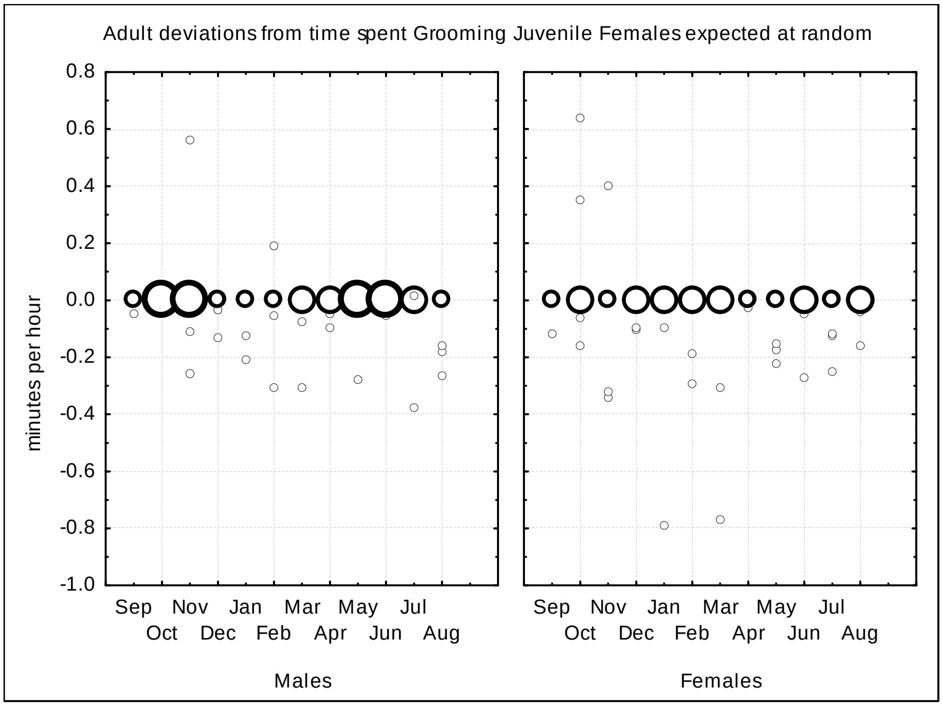


Fig. 4-30. Deviations from expected time spent grooming juvenile females.

Grooming Juvenile Males

An LMEM could not be fit. As with adult grooming of juvenile females, there is no significant sex difference in deviations from expected at random in time spent grooming juvenile males according to the best fit RP model, but both sexes of adults spend less time grooming juvenile males than expected at random (Table 4-26, Figure 4-31).

TABLE 4-26. RP model parameter estimates of deviations from expected rates of grooming juvenile males.

Variable	Model	Effect	est	SE	DF	t	p
Dev Groom JM	mean RP	INT	-0.02	0.01	16	-2.47	0.03*
		SEX	-0.01	0.01	16	-0.97	0.35

* $p \leq 0.05$

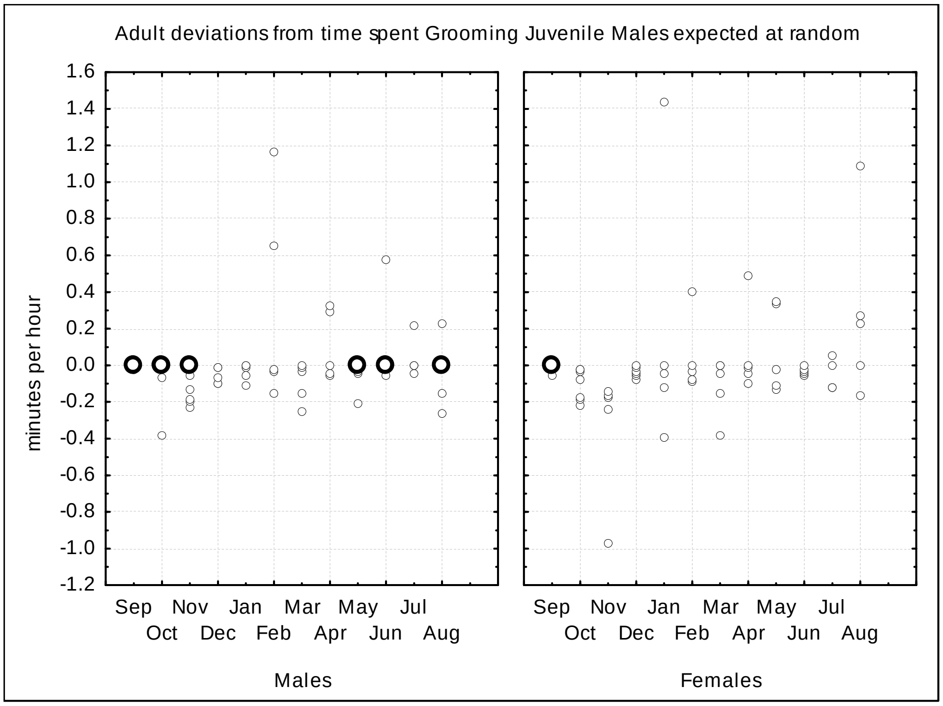


Fig. 4-31. Deviations from expected time spent grooming juvenile males.

Grooming Infants

Recall that adult females are those without dependent infants, such that these analyses are of adult females grooming infants not their own. Analyses of the deviations from time spent grooming infants expected at random are unclear. An LMEM could not be fit. The best fitting mean and linear RP models indicate no sex difference in deviations from time spent grooming infants expected at random, but the less well-fitting quadratic RP model indicates a significant sex difference, a significant time^2 effect, and significant sex*time interaction and sex*time^2 interaction (Table 4-27, Figure 4-32). In this model, females bias their grooming more toward infants than males, but their grooming bias toward infants decreases with time and increases very slightly with time^2.

Separate analyses by sex do not clarify the issue (Table 4-27). According to the best fit random intercepts LMEM, adult males do not bias their grooming toward or away from infants, but according to the best fit mean RP model, they groom infants significantly less than expected at random. According to the best fit mean RP model, adult females groom infants significantly less than expected at random, although very slightly. An examination of the individual OLS regressions and individual yearly means does not support the interpretation that females, on average, groom infants less than expected at random (Figure 4-33). Indeed, the scatterplots of deviations from expected values at random (Figure 4-32), the plots of individual OLS regressions (Figure 4-33), and the yearly mean values of those deviations (Figure 4-34) all suggest that adult males and adult females do have different patterns of deviations from values of grooming infants expected at random. At least some adult females appear to strongly biasing their grooming time toward infants in the first half of the year, but return to levels expected at random during the second half. Perhaps a better model to describe the underlying pattern present here would be some sort of discontinuous change model, but such models are too complex to fit to these particular data.

TABLE 4-27. Model parameter estimates of deviations from expected time spent grooming infants.

Variable	Model	Effect	est	SE	DF	t	p
Dev Groom INFs	mean RP	INT	-0.04	0.02	16	-2.51	0.02*
		SEX	0.00	0.02	16	0.06	0.95
	linear RP	INT	-0.04	0.06	16	-0.62	0.54
		SEX	0.04	0.09	16	0.47	0.64
		TIME	0.00	0.01	101	-0.02	0.98
		SEX*TIME	0.00	0.01	101	-0.47	0.64
	quad RP	INT	0.02	0.12	16	0.18	0.86
		SEX	0.38	0.17	16	2.21	0.04*
		TIME	-0.02	0.03	99	-0.67	0.50
		SEX*TIME	-0.10	0.05	99	-2.24	0.03*
		$TIME^2$	0.00	0.00	99	0.73	0.47
		$SEX*TIME^2$	0.01	0.00	99	2.13	0.04*
AM Dev Groom INFs	random int. LMEM	INT	-0.02	0.03	7	-0.87	0.41
	mean RP	INT	-0.03	0.01	7	-3.17	0.02*
AF Dev Groom INFs	mean RP	INT	-0.04	0.01	9	-2.78	0.02*

* $p \leq 0.05$

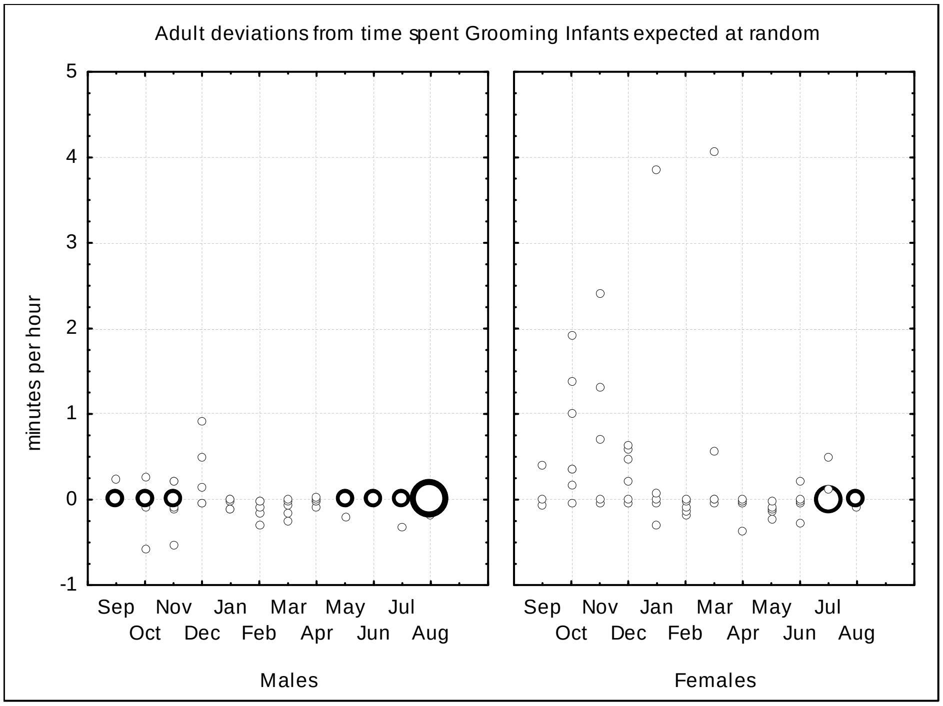


Fig. 4-32. Deviations from expected time spent grooming infants.

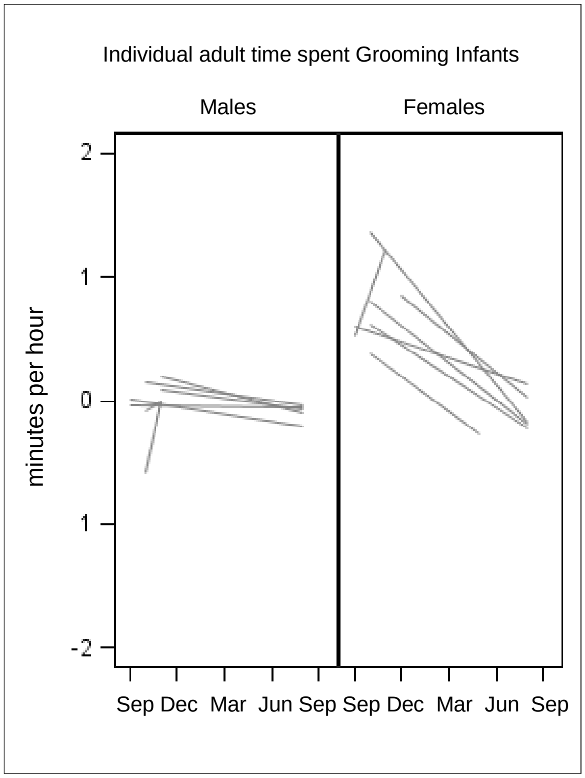
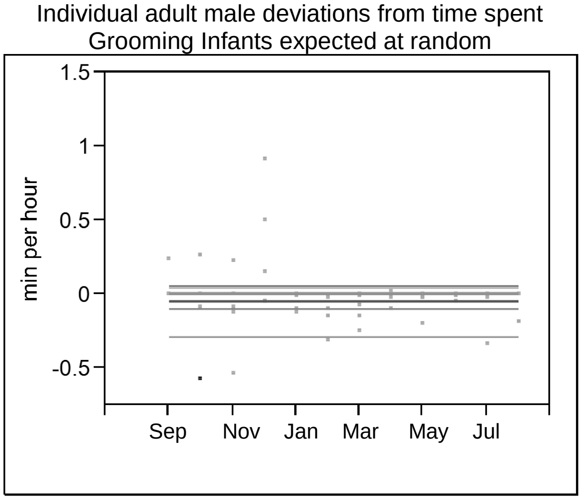


Fig. 4-33. Ordinary least squares regressions of individual time spent grooming infants.

Individual adult male deviations from time spent Grooming Infants expected at random



Individual adult female deviations from time spent Grooming Infants expected at random

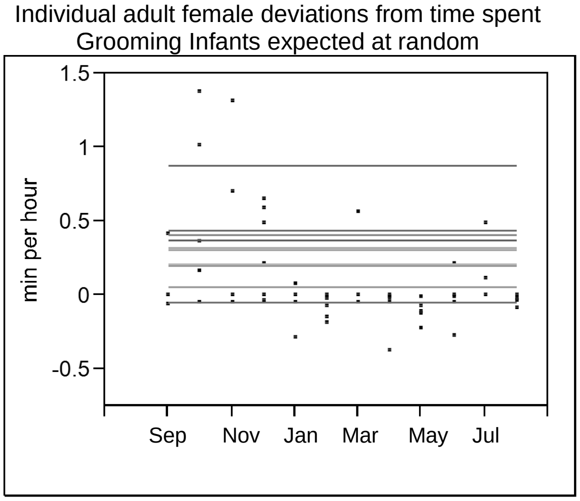


Fig. 4-34. Individual annual mean values of deviations from expected time spent grooming infants.

In cases where overall time engaged in a behavior differs between the sexes, it is not useful to examine raw time engaged in that behavior with particular age/sex classes, because those times are not controlled in any way for overall sex differences. Here, because the results of some grooming analyses are unclear (including overall time grooming), analyses of raw time spent grooming particular age/sex classes may help to clarify grooming biases.

According to all best fit analyses of absolute time spent grooming others (rather than deviations from expectations at random), there are no sex differences in absolute grooming time directed toward particular age sex/classes except with respect to infants. Adult females groom non-filial infants significantly more than adult males do, but less as infants age (Table 4-28). In fact, many adult females spend no time grooming infants from January onward (Figure 4-35).

TABLE 4-28. Model parameter estimates of absolute time spent grooming others, by age/sex class.

Variable	Model	Effect	est	SE	DF	t	p
Time Groom AF	random int. LMEM	INT	0.40	0.11	16	3.50	0.003*
		SEX	0.18	0.16	103	1.13	0.26
	mean RP	INT	0.15	0.07	16	2.18	0.04*
		SEX	-0.02	0.09	16	-0.19	0.85
Time Groom AM	random int. LMEM	INT	0.27	0.07	16	4.10	0.0008*
		SEX	-0.14	0.09	103	-1.52	0.13
	mean RP	INT	0.28	0.07	16	3.79	0.002*
		SEX	-0.15	0.10	16	-1.44	0.17
Time Groom JF	mean RP	INT	0.02	0.02	16	1.27	0.22
		SEX	0.02	0.03	16	0.71	0.49
Time Groom JM	mean RP	INT	0.07	0.04	16	1.87	0.08†
		SEX	0.03	0.05	16	0.57	0.57
Time Groom INFs	linear RP	INT	0.14	0.11	16	1.29	0.22
		SEX	1.02	0.16	16	6.55	<.0001*
		TIME	-0.02	0.01	101	-1.32	0.19
		SEX*TIME	-0.12	0.02	101	-6.44	<.0001*

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

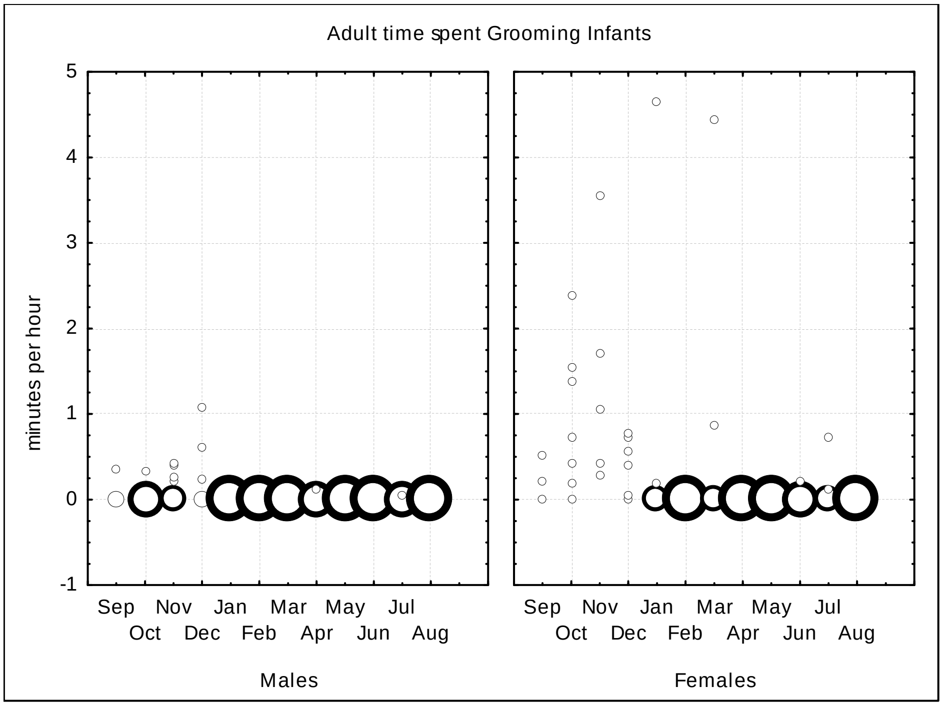


Fig. 4-35. Adult absolute time spent grooming infants.

Summary and Discussion – Grooming

The following tables summarize tests of adult sex differences in affiliative behavior, and tests of adult patterns of bias in their affiliative behavior toward particular age/sex classes. Only statistically significant results are presented; empty cells represent results of no statistical significance. Equivocal results are indicated with a question mark (?).

Some analyses indicate that adult females groom more than adult males overall (Table 4-29). What is clear is that adult females bias their grooming away from adult males and toward infants (but only toward infants when infants are young), while adult males do not. These results, combined with the uncertainty about whether adult females groom more than adult males overall, suggests that any sex difference in overall time spent grooming is probably driven mostly by higher time spent grooming infants by adult females. Interestingly, other than a female preference for young infants, adults of both sexes groom subadults very little, and adult females groom members of the infant cohort very little after they are 5-6 months old (Table 4-30). Although I refer to them here as “infants” for clarity (because analyses were performed on the cohort across the entire year), members of the infant cohort are technically no longer infants after approximately 6 months old, when they are weaned and transition to juvenility. In other words, only actual infants are of interest to non-maternal adult females. Adult females exhibit no particular interest in grooming non-filial juveniles of any age, regardless of whether they are young (members of that year’s infant cohort) or old (members of the previous year’s infant cohort).

It is possible that individual females preferred particular infants as grooming partners, that those particular infants left the sample due to disappearance, and that this explains the temporal pattern apparent in adult female grooming of non-filial infants. Further testing of this dataset may be able to address this alternative explanation. However, previous research indicates that mother-infant pairs are of great interest to other group members, more so than either infants or mothers alone [Nakamichi and Koyama 2000], so I suspect that the real effect captured here is that adult females lose interest in infants once they are fully independent.

TABLE 4-29. Summary of sex differences in overall time spent grooming.

Intrinsic affiliative behavior	Sex Difference	Time effects	
Grooming overall	♀ + ?	·	·

Sex difference: + significantly greater
? equivocal result
· no difference
Time effects: · no effect

TABLE 4-30. Summary of sex differences in bias of grooming of each partner age/sex class.

Intrinsic Affiliative Bias	Partner type	Sex-typed bias		Time effects	
Grooming	AF	·	·	·	·
Grooming	AM	♀ –	·	·	·
Grooming	JF	·	·	·	·
Grooming	JM	·	·	·	·
Grooming	INFs	♀ +	·	♀ –	·

Sex-typed bias: + significantly more than expected at random
– significantly less than expected at random
· no difference from expected at random
Time effects: – decrease with time
· no effect

PROXIMITY PATTERNS

One way in which adults have been suggested to differ by sex is in their proximity patterns [Pereira 2002]. It is uncertain whether proximity patterns can fairly be considered intrinsic patterns of association, given that proximity is at least theoretically determined by all individuals' spacing choices. However, it is also not clear that it should be considered extrinsic to the individual, as the individual should be at least partially in control of its proximity to others. Global measures of proximity are investigated here with the acknowledgement that they may not be fully intrinsically determined. If important sex differences are found, future work can focus on disentangling responsibility for those sex-typed patterns.

Proximity patterns here are quantified along two dimensions—average number of individuals in proximity per scan and average time (number of scans) spent in proximity. These measures are derived from instantaneous data in which proximity to all group members within 3 meters was recorded. These measures are irrespective of activity and reflect only spatial relationships to others.

Number of neighbors in proximity

Neighbors in Contact

An LMEM could not be fit. A qualitative examination of the boxplots and scatterplots of the data suggests that there are some interesting temporal trends within each sex, but the best fit RP model according the AICc is a mean RP model, and independent analyses by sex also are best fit by random intercepts and mean models (Table 4-31). Regardless, both the best fit mean RP model and the next best-fitting linear RP model indicate a significant sex difference in the average number of neighbors in contact per scan, with females having more neighbors in contact per scan than males (Table 4-31, Figure 4-36). Additionally, the linear RP model finds a significant sex*time interaction effect, in which the sex difference decreases through time (Table 4-31). An investigation of the individual OLS regressions for this variable indicates an outlying non-completer female (#23) who has high numbers of neighbors in contact per scan but who left the dataset due to having an infant (Figure 4-37). It is possible that this individual's values are high due to her pregnant condition and that she does not well-represent non-maternal females' patterns of proximity at this time. But this female was not removed from this or subsequent analyses for several reasons. First, only the second of her three monthly values was outlying (Figure 4-38), and several other females who did not have unusually high numbers of neighbors also left the sample due to having an infant, suggesting that there is nothing about the pre-parturient state that induced her high numbers of neighbors in one month. Second, removing her from the analysis does not change the results (Table 4-32), indicating that she, alone, is not responsible for the significant sex difference here.

TABLE 4-31. Model parameter estimates of number of neighbors in contact.

Variable	Model	Effect	est	SE	DF	t	p
# neighbors in contact	mean RP	INT	0.06	0.01	16	4.28	0.0006*
		SEX	0.05	0.02	16	2.71	0.02*
# neighbors in contact	linear RP	INT	0.03	0.03	16	0.92	0.37
		TIME	0.01	0.00	101	1.36	0.18
		SEX	0.14	0.04	16	3.27	0.005*
		SEX*TIME	-0.02	0.01	101	-2.22	0.03*
# neighbors in contact AF	random int. LMEM	INT	0.22	0	9.00	4.42	0.002*
	mean RP	INT	0.05	0	9.00	4.54	0.001*
# neighbors in contact AM	mean RP	INT	0.03	0	7.00	5.14	0.001*

* $p \le 0.05$

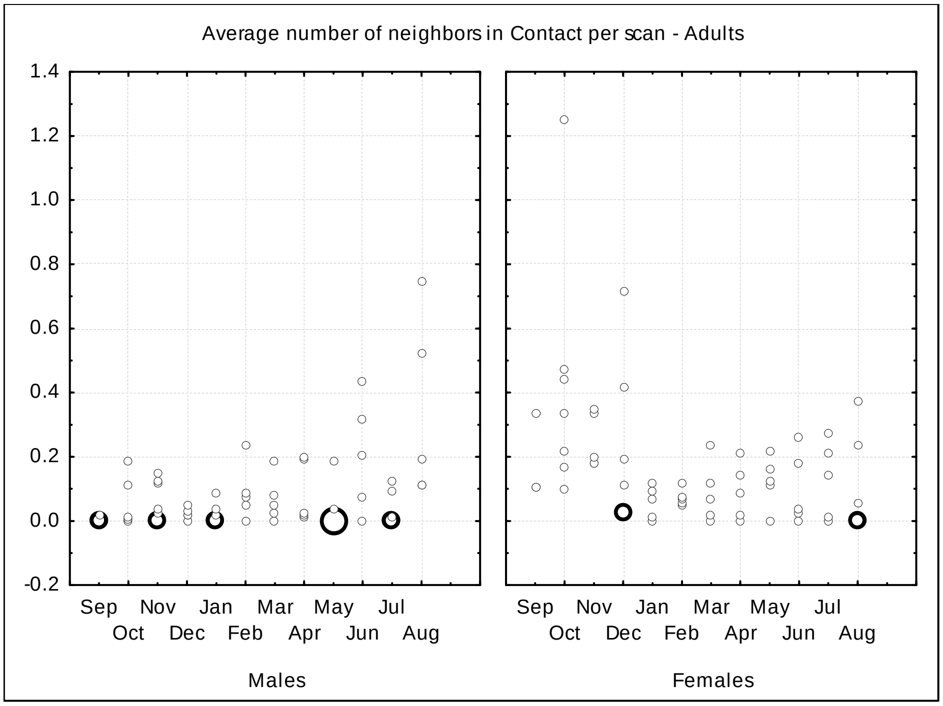


Fig. 4-36. Adult average number of neighbors in contact per scan.

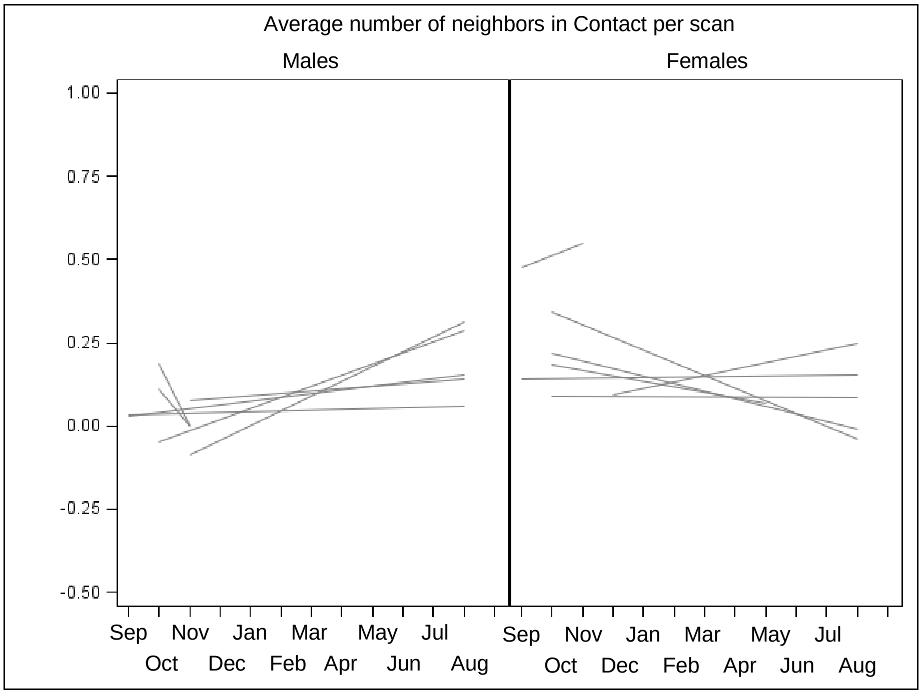
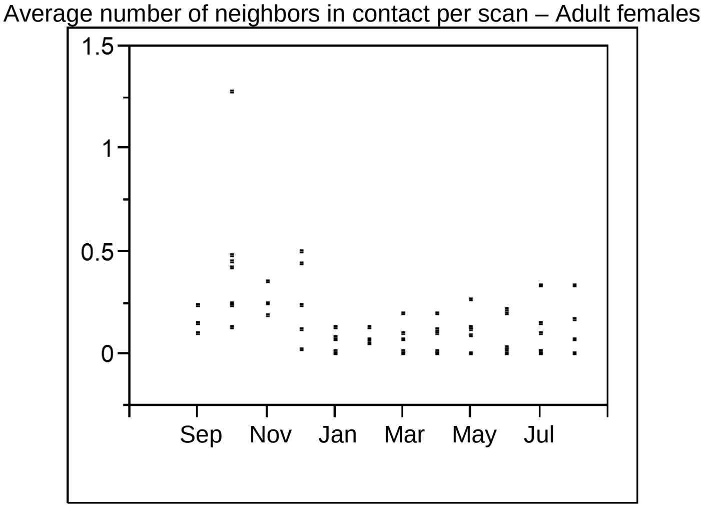


Fig. 4-37. Individual ordinary least squares regressions of number of neighbors in contact per scan.



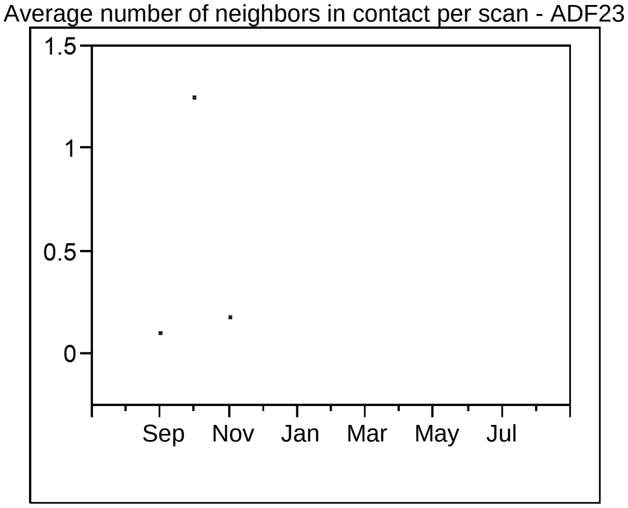


Fig. 4-38. Adult female average number of neighbors in contact per scan (top) and values from an outlying female (below).

TABLE 4-32. RP model parameter estimates of number of neighbors in contact with adults with individual ADF23 removed from the analysis.

Variable	Model	Effect	est	SE	DF	t	p
# neighbors in contact	mean RP	INT	0.06	0.01	16	4.28	0.0006*
		SEX	0.05	0.02	16	2.71	0.02*
# neighbors in contact - ADF23	mean RP	INT	0.06	0.01	15	4.07	0.001*
		SEX	0.06	0.02	15	2.88	0.01*

* $p \leq 0.05$

Neighbors within Reach

The best fit random intercepts LMEM indicates a significant sex difference in the average number of neighbors within reach, with females having more neighbors within reach than males (Table 4-33, Figure 4-39). The best fitting mean RP model indicates no sex difference. As in most instances of disagreement between the LMEM and RP models, I preferentially accept the LMEM results because this type of analysis at least partially accounts for inter-individual differences.

TABLE 4-33. Model parameter estimates of number of neighbors in reach.

Variable	Model	Effect	est	SE	DF	t	p
# neighbors in reach	random int. LMEM	INT	0.10	0.16	16	0.61	0.55
		SEX	0.52	0.22	103	2.37	0.02*
	mean RP	INT	0.08	0.03	16	3.05	0.008*
		SEX	-0.06	0.04	16	-1.68	0.11

* $p \leq 0.05$

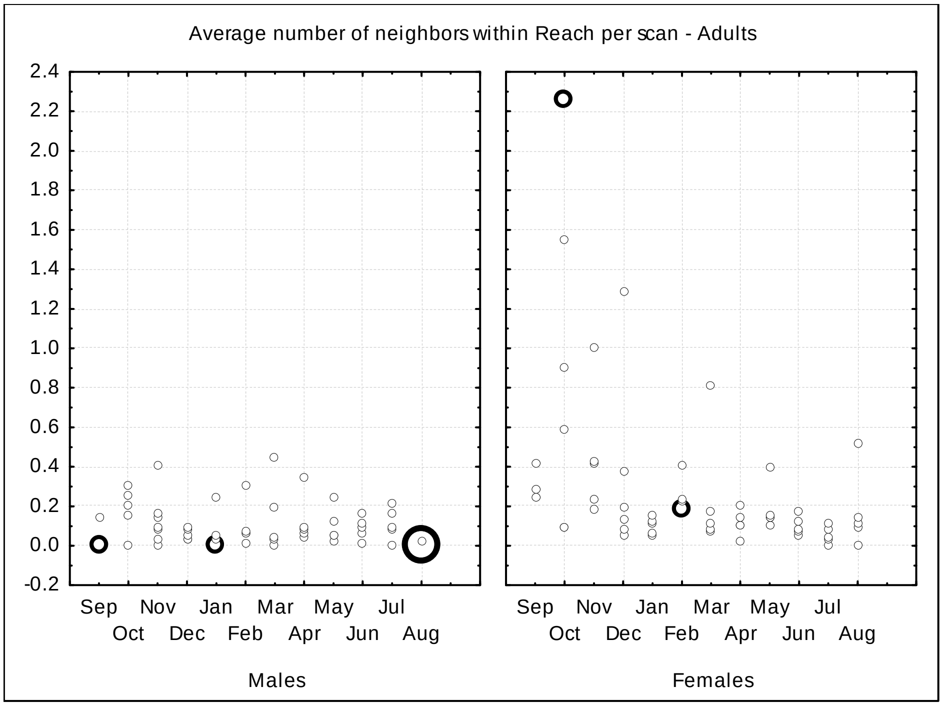


Fig. 4-39. Average number of neighbors within reach.

Neighbors in 3m

Both the best fit random intercepts LMEM and mean RP models indicate a significant sex difference in the average number of neighbors within 3m, in which adult females, on average, have more neighbors within 3m than adult males (Table 4-34, Figure 4-40).

TABLE 4-34. Model parameter estimates of number of neighbors within 3 meters.

Variable	Model	Effect	est	SE	DF	t	p
# neighbors in 3m	random int. LMEM	INT	1.73	0.14	16	12.19	<.0001*
		SEX	0.72	0.20	103	3.63	0.0004*
	mean RP	INT	1.50	0.10	16	14.78	<.0001*
		SEX	0.50	0.14	16	3.51	0.003*

* $p \leq 0.05$

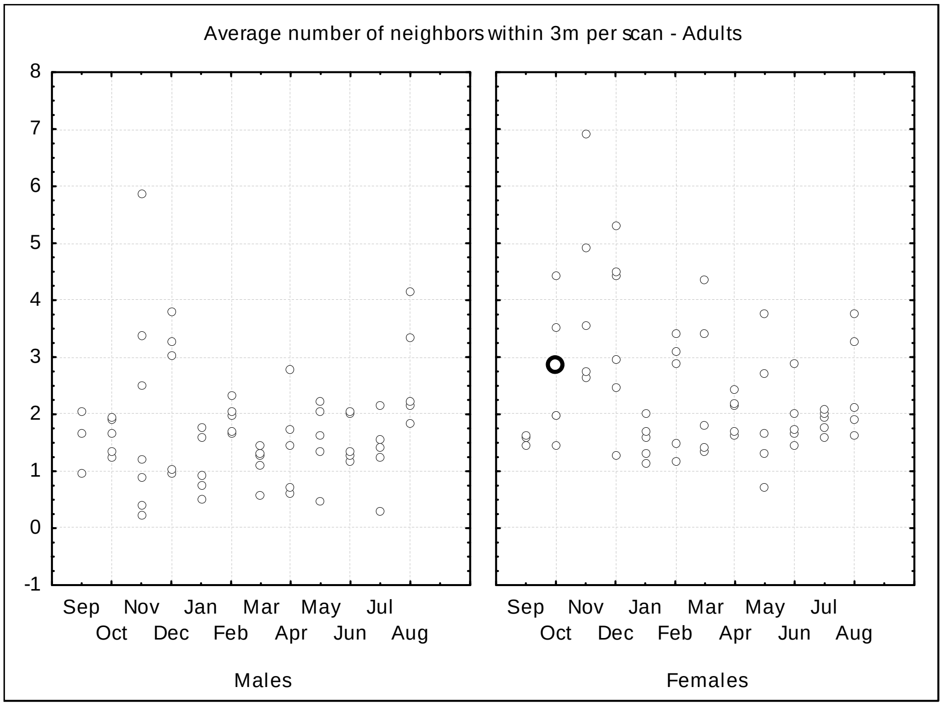


Fig. 4-40. Average number of neighbors within 3 meters.

Time in proximity

Time in Contact with Others

An LMEM could not be fit. The best fit linear RP model indicates a significant sex difference in the number of scans per hour spent in contact, with females spending more time in contact with others than males, as well as a significant sex*time interaction in which this sex difference decreases through time (Table 4-35). Analyses by sex indicate that this is due to an increase in contact time for adult males as the year progresses. Qualitatively, it appears that there are complex temporal patterns of time spent in contact for adult females that are not well-captured by these analyses (Figure 4-41).

TABLE 4-35. Model parameter estimates of time in contact with others.

Variable	Model	Effect	est	SE	DF	t	p
Time in contact	linear RP	INT	0.44	0.43	16	1.01	0.33
		SEX	2.63	0.61	16	4.28	0.0006*
		TIME	0.14	0.07	101	1.89	0.06†
		TIME*SEX	-0.32	0.11	101	-3.03	0.003*
AF Time in contact	mean RP	INT	1.50	0.20	9	7.35	<.0001*
AM Time in contact	linear RP	INT	0.16	0.11	7	1.44	0.19
		TIME	0.15	0.03	51	4.59	<.0001*

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

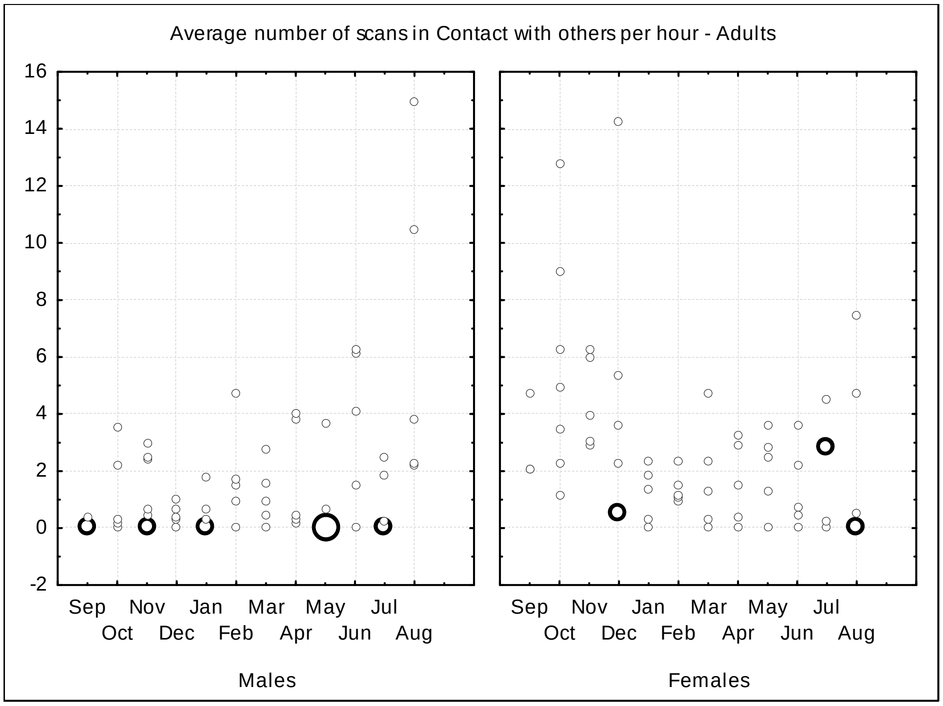


Fig. 4-41. Average time in contact with others.

Time within Reach of Others

The most complex LMEM that could be fit was a random intercepts LMEM, which indicates a significant sex difference in time spent within reach of others, with females spending more time within reach of others than males (Table 4-36). The best fit linear RP model also indicates a significant sex difference with females spending more time within reach of others overall, and a significant sex*time interaction (Table 4-36). Analyses by sex indicate that this is because adult females spend a great deal more time within reach of others at the beginning of the observation year, but less as the observation year progresses, while males exhibit no temporal change (Table 4-36, Figure 4-42).

TABLE 4-36. Model parameter estimates of time spent in reach of others.

Variable	Model	Effect	est	SE	DF	t	p
Time in reach	random int. LMEM	INT	1.54	1.20	16	1.29	0.22
		SEX	4.39	1.62	103	2.72	0.008*
	linear RP	INT	1.72	0.58	16	2.96	0.009*
		SEX	4.10	0.84	16	4.88	0.0002*
		TIME	0.00	0.07	101	0.00	1.00
		TIME*SEX	-0.43	0.10	101	-4.46	<.0001*
AF Time in reach	linear LMEM	INT	7.35	1.43	9	5.14	0.0006*
		TIME	-0.31	0.10	50	-3.05	0.004*
	linear RP	INT	6.06	0.61	9	10.00	<.0001*
		TIME	-0.47	0.08	50	-6.15	<.0001*
AM Time in reach	random int. LMEM	INT	1.62	0.28	7	5.70	0.0007*
	mean RP	INT	1.61	0.31	7	5.26	0.001*

* p ≤ 0.05; † 0.05 < p ≤ 0.10

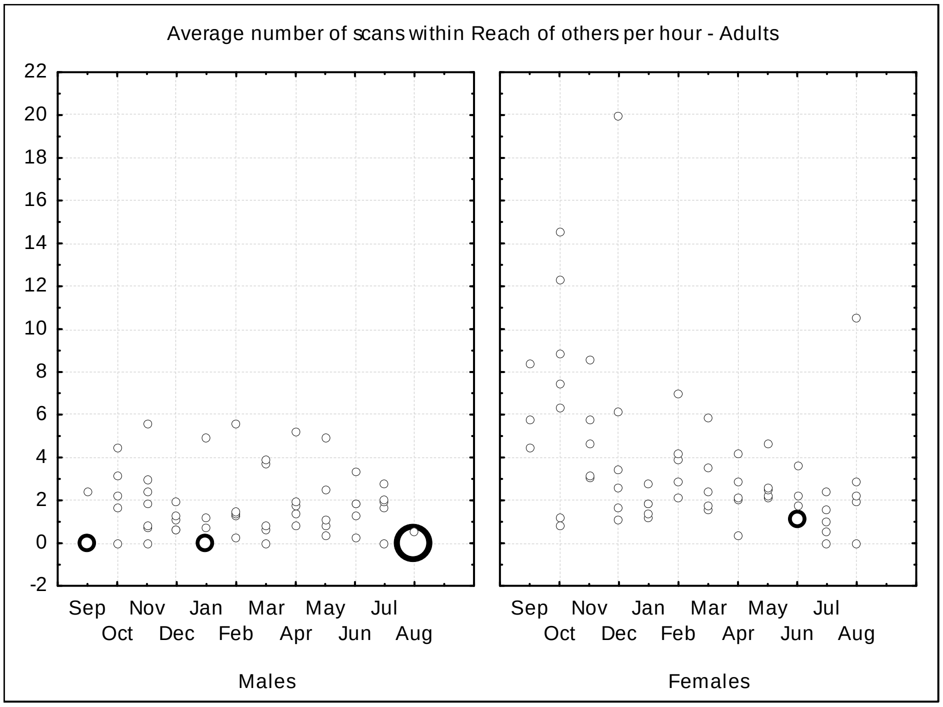


Fig. 4-42. Average time within reach of others.

Time within 3m of Others

The best fit quadratic LMEM indicates that females tend to spend more time within 3m of others than males (Table 4-37). There is also a tendency for both sexes to spend more time within 3m of others as the observation year progressed. These results were confirmed by the best fit linear RP model, which indicated significant positive effects of sex (females) and time on the amount of time spent within 3m of others (Table 4-37, Figure 4-43).

TABLE 4-37. Model parameter estimates of number of time within 3 meters of others.

Variable	Model	Effect	est	SE	DF	t	p
Time in 3m	quad LMEM	INT	11.87	1.58	16	7.50	<.0001*
		SEX	3.82	2.18	87	1.75	0.08†
		TIME	-0.48	0.47	12	-1.02	0.33
		SEX*TIME	-0.08	0.67	87	-0.12	0.91
		$TIME^2$	0.07	0.04	87	1.87	0.07†
		$SEX*TIME^2$	-0.01	0.06	87	-0.10	0.92
	linear RP	INT	10.34	1.18	16	8.73	<.0001*
		SEX	4.00	1.63	16	2.45	0.03*
		TIME	0.35	0.12	101	2.89	0.005*
		TIME*SEX	-0.10	0.17	101	-0.58	0.56

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

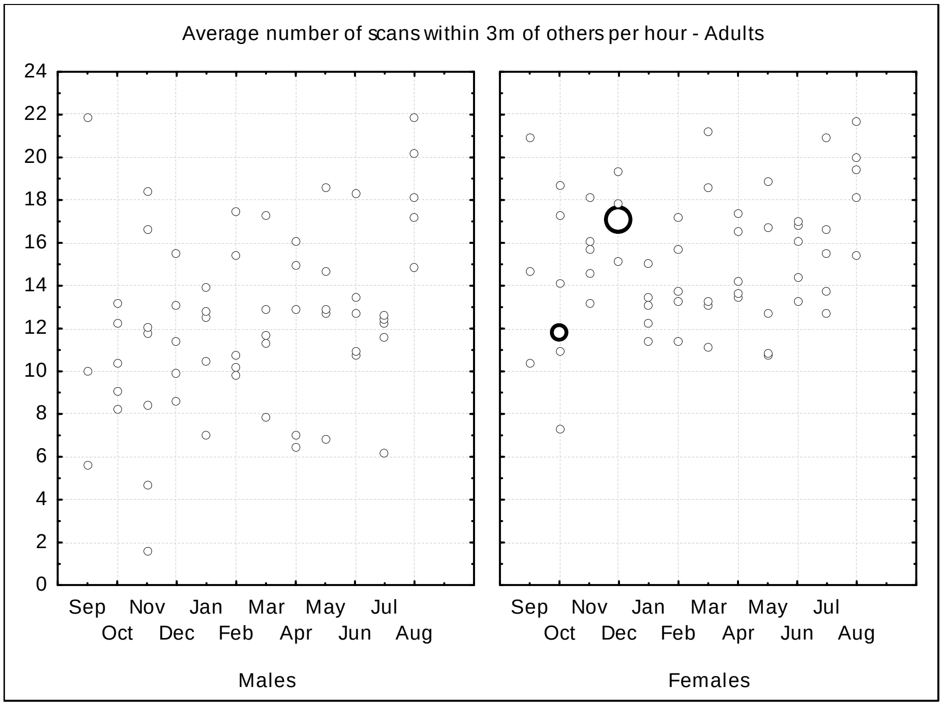


Fig. 4-43. Average time within 3 meters of others.

Time within 5m of others (inclusive)

This measure is all-inclusive. If an individual had no neighbors within 5m, it was considered not to have any neighbors at all. Both the best fit linear LMEM and RP models indicate that females spend significantly more time than males within 5m of others, and that both sexes spend significantly more time within 5m of others as the observation year progressed (Table 4-38). In other words, adult males spend significantly more time alone than adult females, and both sexes spend less time alone as the observation year progresses (Figure 4-44).

TABLE 4-38. Model parameter estimates of number of time within 5 meters of others.

Variable	Model	Effect	est	SE	DF	t	p
Time in 5m	linear LMEM	INT	12.94	1.53	16	8.48	<.0001*
		SEX	4.86	2.08	89	2.34	0.02*
		TIME	0.62	0.12	12	5.24	0.0002*
		SEX*TIME	-0.24	0.17	89	-1.42	0.16
	linear RP	INT	12.90	1.60	16	8.07	<.0001*
		SEX	4.89	2.17	16	2.25	0.04*
		TIME	0.64	0.11	101	6.02	<.0001*
		TIME*SEX	-0.23	0.15	101	-1.50	0.14

* p ≤ 0.05

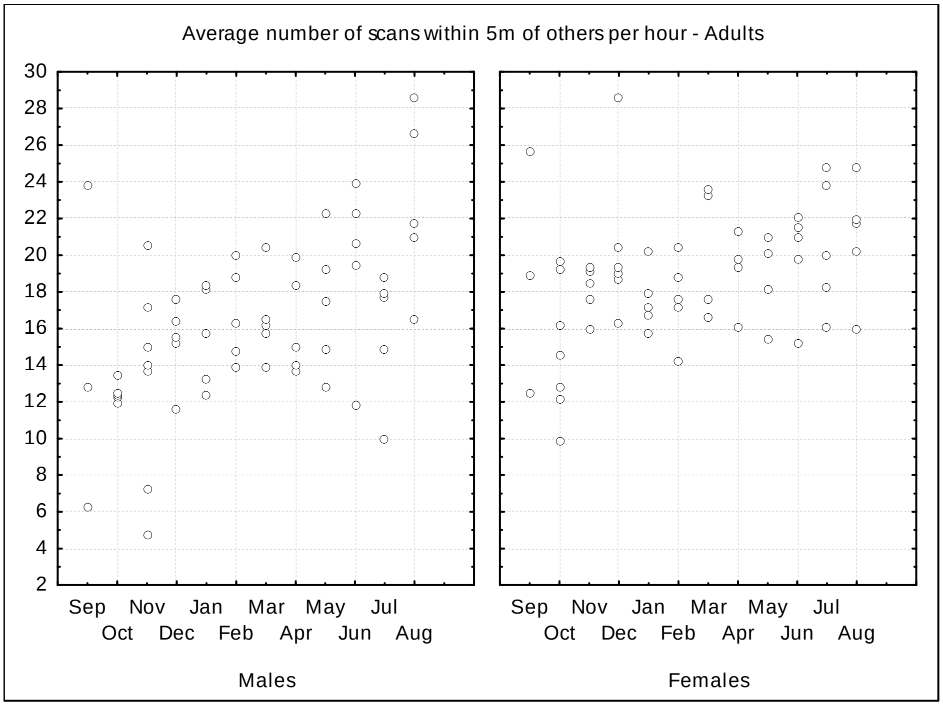


Fig. 4-44. Average time within 5 meters of others.

Deviations from random proximity to other age/sex classes

Given that females had more neighbors than males at all distances and spent more of their time in proximity to others at all distances, females were also more likely to be more often and in closer proximity to each age/sex class. To assess whether adults exhibited a bias toward or away from proximity to particular age sex classes, I calculated deviations from rates of proximity with each age/sex class expected at random given the amount of time an individual spent in proximity to others and conducted tests of sex differences in those deviations.

Contact with Adult Females

The best fit random intercepts LMEM indicates no sex difference in the deviations from rates of contact with adult females expected at random, but the best fit mean RP model indicates a significant sex difference, with females biasing their time more heavily toward contact with other females than do males (Table 4-39). Qualitatively, it appears that adult males and females have reversed patterning of bias toward contact time with adult females, with adult females showing a bias toward contact time with them at the beginning of the observation year that decreases with time and adult males showing a bias toward contact time with adult females at the end of the observation year (Figure 4-45). Analyses by sex bear this out—the best fit models for adult females indicate either that adult females bias their contact time toward adult females or that they bias their time toward adult females but that they do so less as time progresses, while adult males tend to bias their contact time slightly away from adult females overall (Table 4-39). Because a qualitative examination of the scatterplots and the analyses by sex are in concordance with the mean RP model, in this case I tentatively accept the results of the mean RP model that females spend significantly more of their contact time with adult females than adult males do.

TABLE 4-39. Model parameter estimates of deviations from expected time in contact with adult females.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in contact AF	random int. LMEM	INT	0.56	0.43	17	1.32	0.20
		TIME	-0.01	0.06	13	-0.09	0.93
	mean RP	INT	-0.08	0.10	16	-0.76	0.46
		SEX	0.34	0.14	16	2.40	0.03*
AF Dev Time in contact AF	linear LMEM	INT	1.46	0.58	9	2.50	0.03*
		TIME	-0.06	0.04	50	-1.68	0.10†
	mean RP	INT	0.31	0.10	9	3.08	0.01*
AM Dev Time in contact AF	mean RP	INT	-0.07	0.03	7	-2.13	0.07†

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

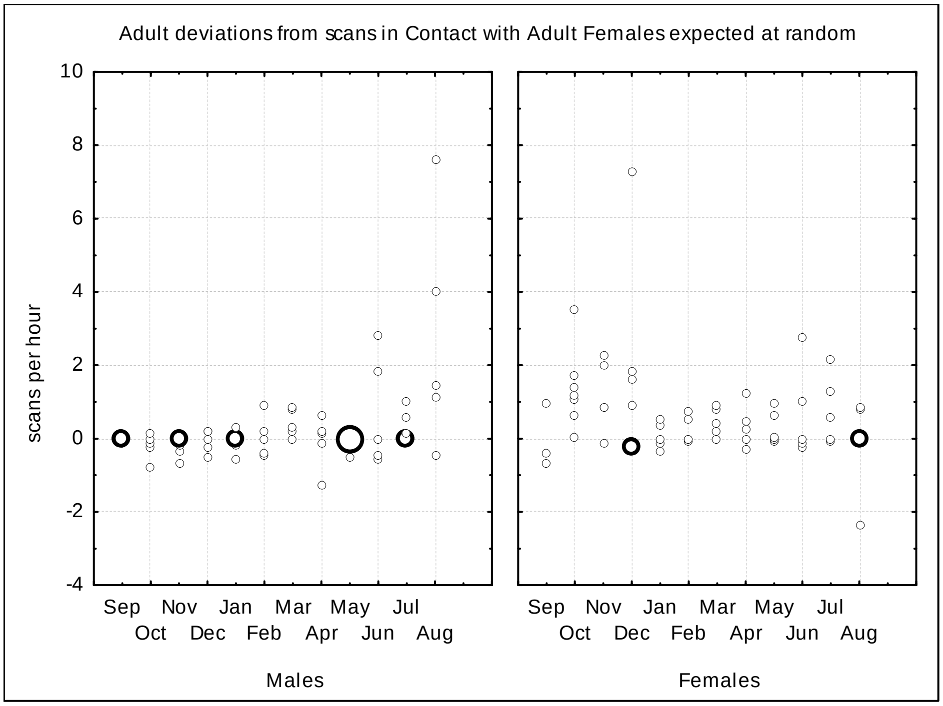


Fig. 4-45. Deviations from expected time spent in contact with adult females.

Within Reach of Adult Females

An LMEM could not be fit. The best fit mean RP model indicates no sex difference in bias toward or away from time spent within reach of adult females (Table 4-40). And, since the intercept is not significantly different from zero, there is also no evidence of bias exhibited toward or away from time spent within reach of adult females by either sex (Table 4-40, Figure 4-46).

TABLE 4-40. RP model parameter estimates of deviations from expected time spent in reach of adult females.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in reach AF	mean RP	INT	-0.11	0.09	16	-1.24	0.23
		SEX	0.20	0.13	16	1.56	0.14

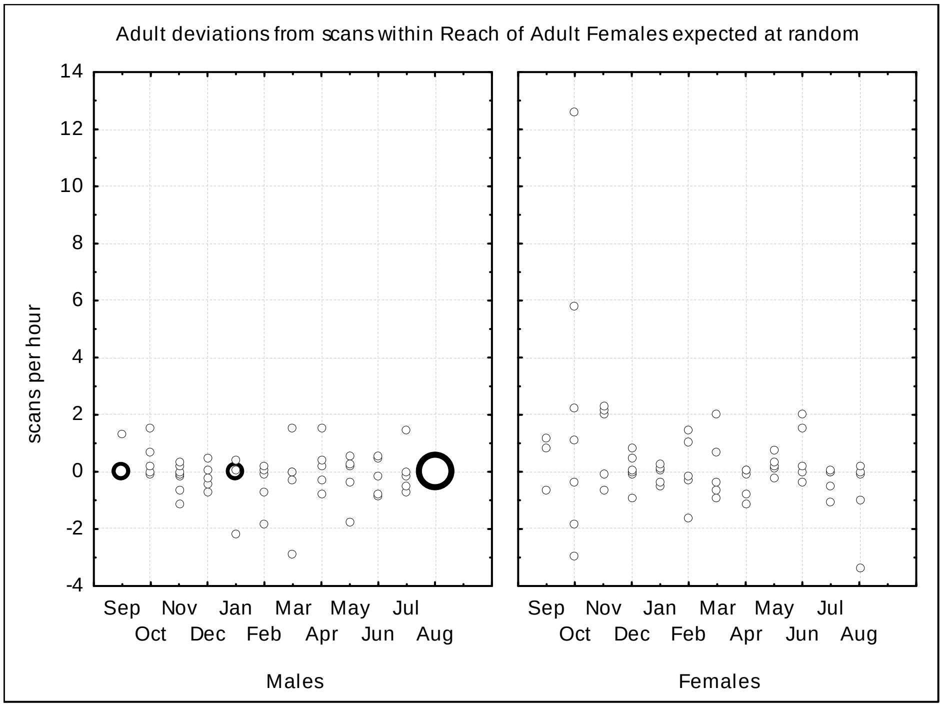


Fig. 4-46. Deviations from expected time spent in reach of adult females.

Within 3m of Adult Females

The best fit linear LMEM indicates that adult females bias their time within 3m of others significantly more heavily toward other females than do adult males (Table 4-41). The best fit linear RP model suggests that adult females tend to bias their time within 3m of others more heavily toward other females than do adult males. Both models indicate a sex*time interaction effect, with females biasing their time within 3m of others less heavily toward adult females as the study year progressed. Analyses by sex indicate that adult females spend significantly more time than expected at random within 3m of other adult females at the beginning of the observation year, but that the effect decreases significantly through time, whereas males spend time within 3m of adult females as expected at random (Table 4-41, Figure 4-47).

TABLE 4-41. Model parameter estimates of deviations from expected time spent within 3 meters of adult females.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in 3m AF	linear LMEM	INT	0.37	1.33	16	0.28	0.78
		SEX	4.05	1.84	89	2.21	0.03*
		TIME	0.11	0.17	12	0.66	0.52
		SEX*TIME	-0.51	0.24	89	-2.14	0.04*
	linear RP	INT	0.20	0.97	16	0.20	0.84
		SEX	2.68	1.36	16	1.96	0.07†
		TIME	-0.02	0.11	101	-0.21	0.83
		TIME*SEX	-0.39	0.16	101	-2.44	0.02*
AF Dev Time in 3m AF	linear LMEM	INT	4.79	1.13	9	4.24	0.002*
		TIME	-0.42	0.17	50	-2.52	0.02*
	linear RP	INT	4.68	1.18	9	3.97	0.003*
		TIME	-0.42	0.17	50	-2.49	0.02*
AM Dev Time in 3m AF	random int. LMEM	INT	0.94	0.92	7	1.03	0.34
	mean RP	INT	0.93	0.98	7	0.96	0.37

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

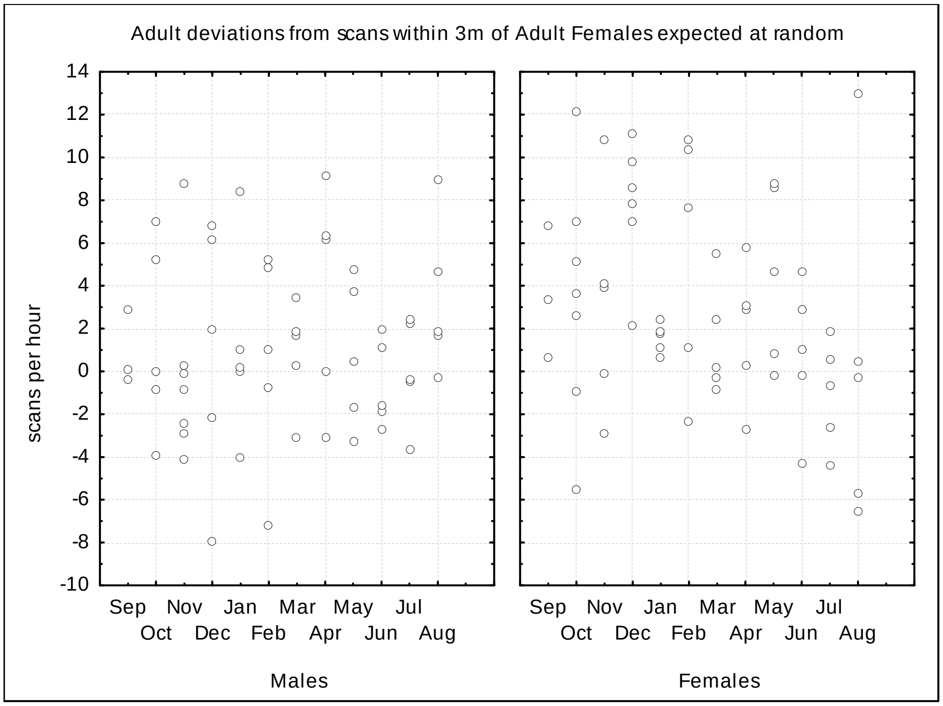


Fig. 4-47. Deviations from expected time spent within 3 meters of adult females.

Contact with Adult Males

The best fit random intercepts LMEM and mean RP models indicate that adult females bias their time spent in contact much more strongly away from adult males than do adult males (Table 4-42, Figure 4-48). Analyses by sex indicate that adult females spend significantly less time than expected at random in contact with adult males at the beginning of the observation year, but that their contact time with adult males becomes significantly less negatively biased through time, while adult males show the opposite pattern (Table 4-42). According to the best fit linear LMEM for adult males, adult males spend significantly more time in contact with adult males than expected at random at the beginning of the observation year, but this effect decreases significantly through time. The best fit mean RP model yields similar results, with adult males tending to be in contact with adult males more than expected at random at the beginning of the observation year but decreasing their bias toward contact time with adult males as time progressed (Table 4-42).

TABLE 4-42. Model parameters estimates of deviations from expected time spent in contact with adult males.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in contact AM	random int. LMEM	INT	0.00	0.30	16	0.02	0.99
		SEX	-1.13	0.41	103	-2.79	0.007*
	mean RP	INT	0.06	0.12	16	0.47	0.64
		SEX	-0.60	0.17	16	-3.57	0.002*
AF Dev Time in contact AM	linear LMEM	INT	-1.76	0.37	9	-4.73	0.001*
		TIME	0.13	0.05	50	2.74	0.009*
	mean RP	INT	-0.43	0.11	9	-4.06	0.003*
AM Dev Time in contact AM	linear LMEM	INT	0.55	0.24	7	2.34	0.05*
		TIME	-0.11	0.04	51	-3.11	0.003*
	linear RP	INT	0.17	0.08	7	2.07	0.08†
		TIME	-0.03	0.01	51	-2.72	0.009*

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

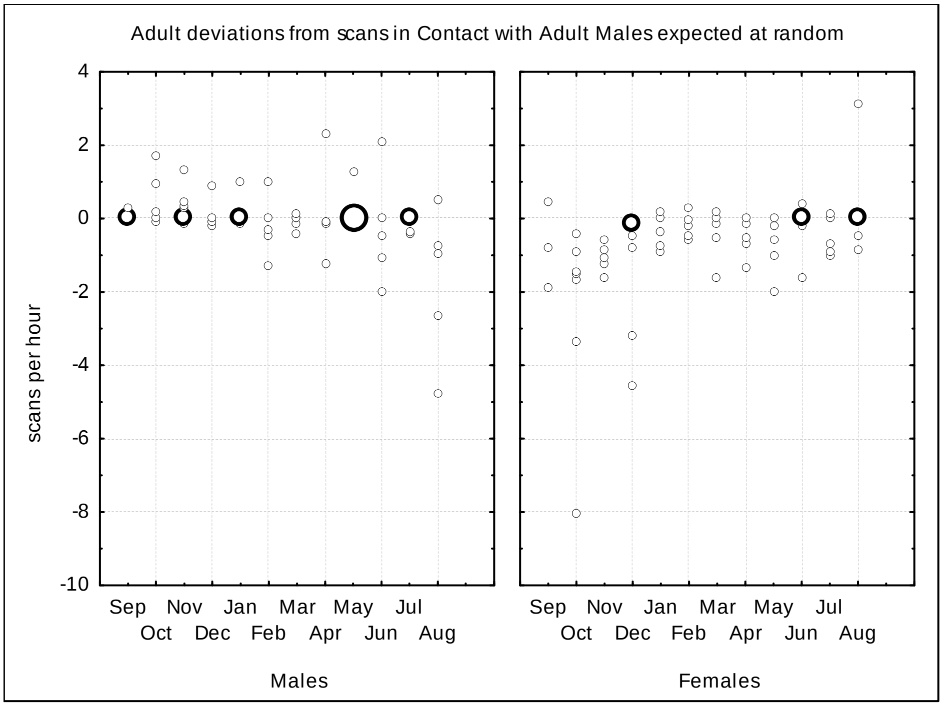


Fig. 4-48. Deviations from expected time spent in contact with adult males.

Within Reach of Adult Males

The best fit random intercepts LMEM and mean RP models indicate a significant sex difference in deviations from time spent within reach of adult males at random (Table 4-43, Figure 4-49), but in opposite directions. The LMEM indicates that females bias their time within reach of others substantially more strongly away from adult males than adult males do, while the best fit mean RP model suggests that females bias their time within reach of others slightly more strongly toward adult males than adult males do. These types of conflicts suggest poor model-fitting. Individual OLS regressions for this variable do not support an interpretation of adult females biasing their time within reach of others more strongly toward adult males than adult males do and reveal that there is a great deal more variation in this variable among females than there is among males (Figure 4-50). Analyses by sex indicate that adult males spend time within reach of other adult males as expected at random. For adult females, the best fit linear LMEM indicates that adult females spend less time than expected within reach of adult males at the beginning of the observation year, but tend to spend more time within reach of them as time progresses. In contrast, the best fit mean RP model indicates that adult females spend time within reach of adult males as expected at random, so the female pattern is uncertain. Because the two analyses of sex difference are in direct opposition, I accept the most conservative results suggested by the sex-specific analyses, which indicate no deviations from random expectations in time spent within reach of adult males, but note that, qualitatively, males exhibit hardly any deviation from random expectations with respect to time spent within reach of adult males, while females exhibit a great deal of inter- and intra-individual variation in this variable.

TABLE 4-43. Model parameter estimates of deviation from expected time spent within reach of adult males.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in reach AM	random int. LMEM	INT	-0.05	1.26	16	-0.04	0.97
		SEX	-3.47	1.70	103	-2.04	0.04*
	mean RP	INT	-0.20	0.15	16	-1.35	0.20
		SEX	0.42	0.20	16	2.09	0.05*
AF Dev Time in reach AM	linear LMEM	INT	-4.22	1.48	9	-2.84	0.02*
		TIME	0.17	0.09	50	1.87	0.07†
	mean RP	INT	0.21	0.15	9	1.45	0.18
AM Dev Time in reach AM	random int. LMEM	INT	-0.11	0.09	7	-1.19	0.27
	mean RP	INT	-0.06	0.04	7	-1.57	0.16

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

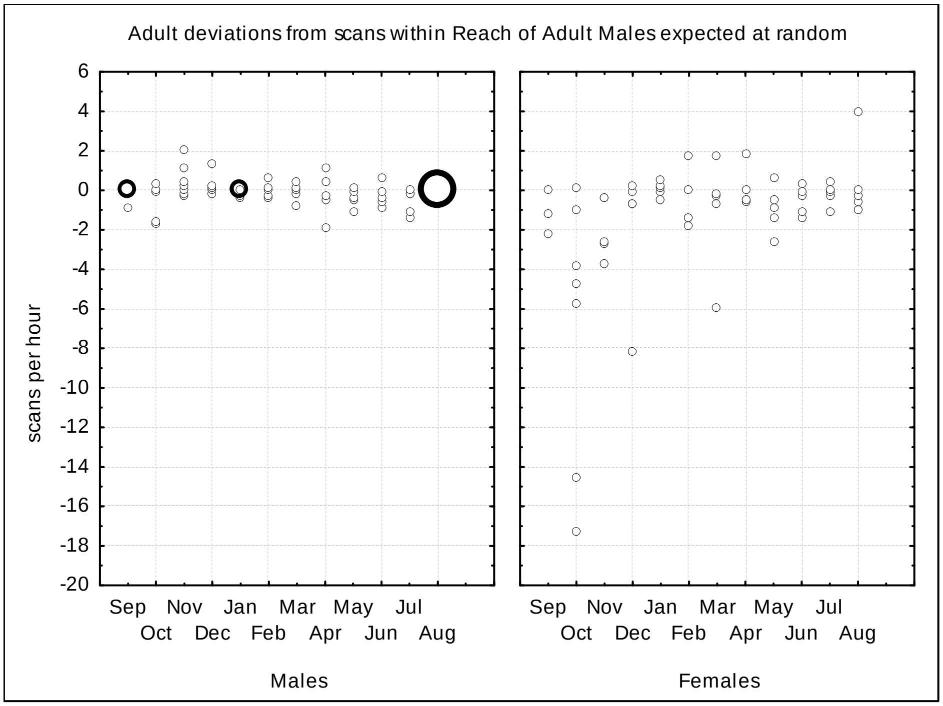


Fig. 4-49. Deviations from expected time spent within reach of adult males.

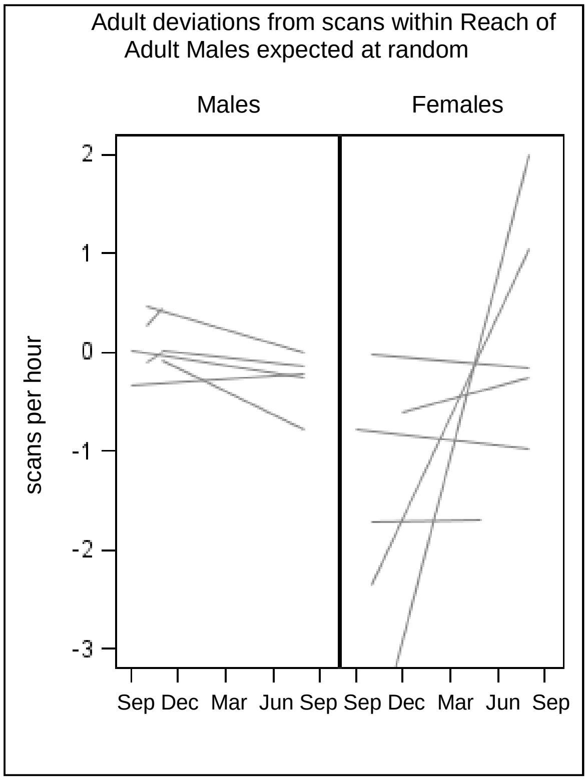


Fig. 4-50. Individual ordinary least squares regressions of deviations from expected time spent within reach of adult males.

Within 3m of Adult Males

The best fit linear LMEM and RP models both indicate a significant sex difference in which adult females bias their time within 3m of others more heavily away from adult males than do adult males, and the linear RP model indicates an additional time*sex interaction in which this sex difference is attenuated with time (Table 4-44). Analyses by sex indicate that adult females spend significantly and substantially less time than expected at random within 3m of adult males (Table 4-44, Figure 4-51). Analyses of males indicate that, if the main sex difference is attenuated with time, it is because males spend less of their time within 3m of others with adult males as time progresses (Table 4-44, Figure 4-51). Qualitative examination of the individual OLS regressions support that interpretation (Figure 4-52).

TABLE 4-44. Model parameter estimates of deviations from expected time spent within 3 meters of adult males.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in 3m AM	linear LMEM	INT	0.01	1.97	16	0.00	1.00
		SEX	-7.08	2.71	89	-2.62	0.01*
		TIME	-0.34	0.28	12	-1.24	0.24
		SEX*TIME	0.62	0.38	89	1.62	0.11
	linear RP	INT	-0.41	1.45	16	-0.28	0.78
		SEX	-6.64	2.02	16	-3.29	0.005*
		TIME	-0.28	0.18	101	-1.56	0.12
		TIME*SEX	0.61	0.25	101	2.39	0.02*
AF Dev Time in 3m AM	random int. LMEM	INT	-5.82	0.81	9	-7.21	<.0001*
AM Dev Time in 3m AM	linear LMEM	INT	-0.34	1.32	7	-0.26	0.80
		TIME	-0.28	0.14	51	-1.99	0.05*
	mean RP	INT	-2.40	0.56	7	-4.30	0.004*

* $p \leq 0.05$

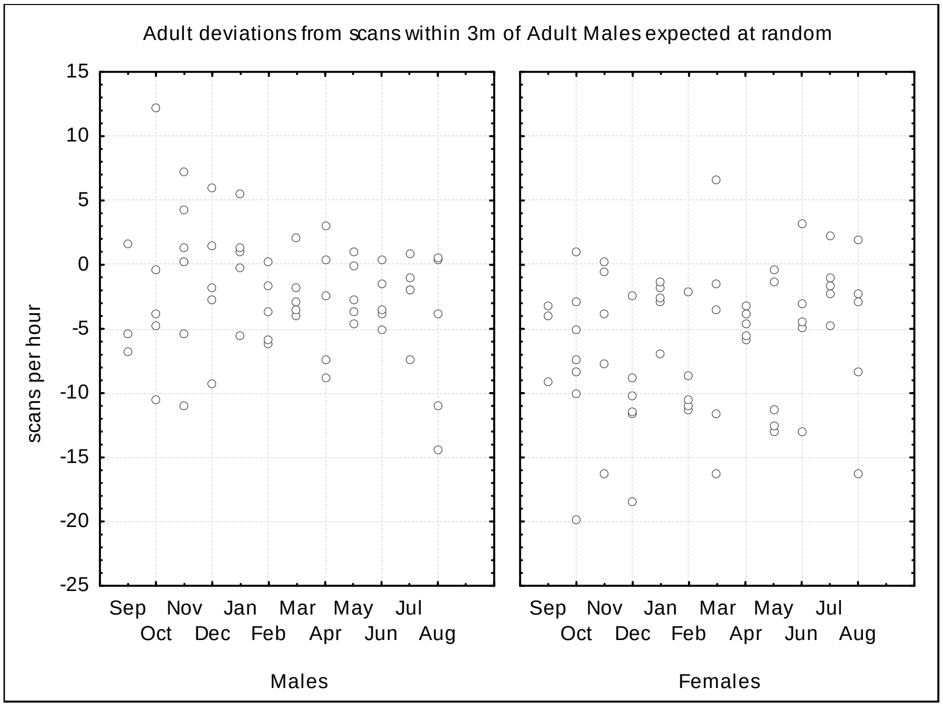


Fig. 4-51. Deviations from expected time spent within 3 meters of adult males.

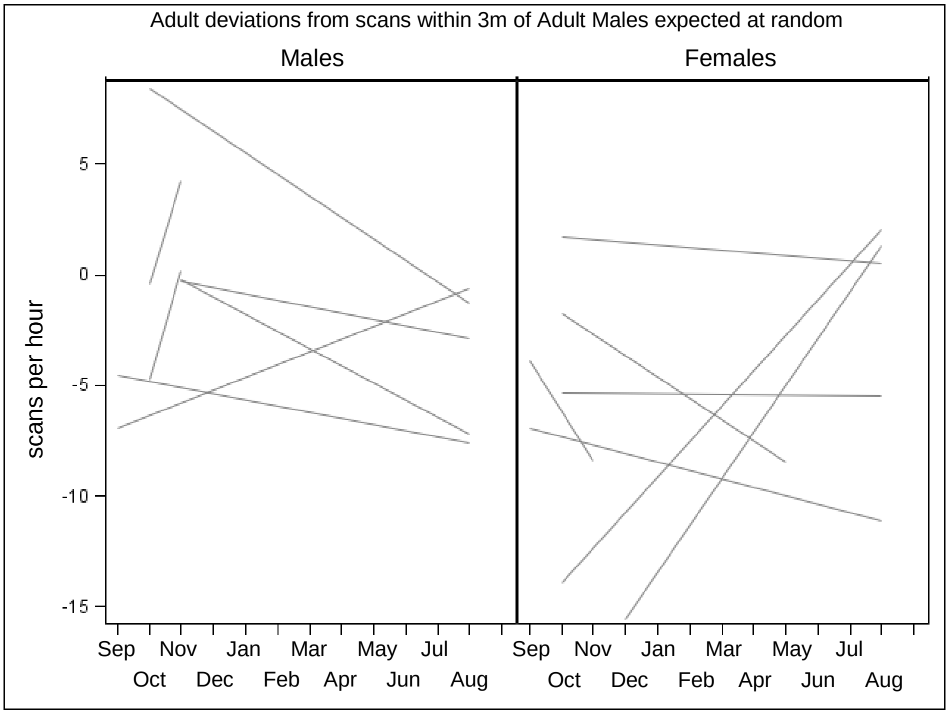


Fig. 4-52. Individual ordinary least squares regressions of deviations from expected time spent within 3 meters of adult males.

Contact with Juvenile Females

The best fit LMEM and RP models find no sex difference in bias toward or away from juvenile females in time spent in contact with others (Table 4-45, Figure 4-53). Adults may spend less of their contact time with juvenile females than expected at random, but this is only indicated by the mean RP model and not the random intercepts LMEM, so it is not definitively the case.

TABLE 4-45. Model parameter estimates of deviations from expected time spent in contact with juvenile females.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in contact JF	random int. LMEM	INT	-0.05	0.35	16	-0.15	0.88
		SEX	0.65	0.48	103	1.37	0.17
	mean RP	INT	-0.07	0.03	16	-2.12	0.05*
		SEX	-0.07	0.05	16	-1.52	0.15

* p ≤ 0.05

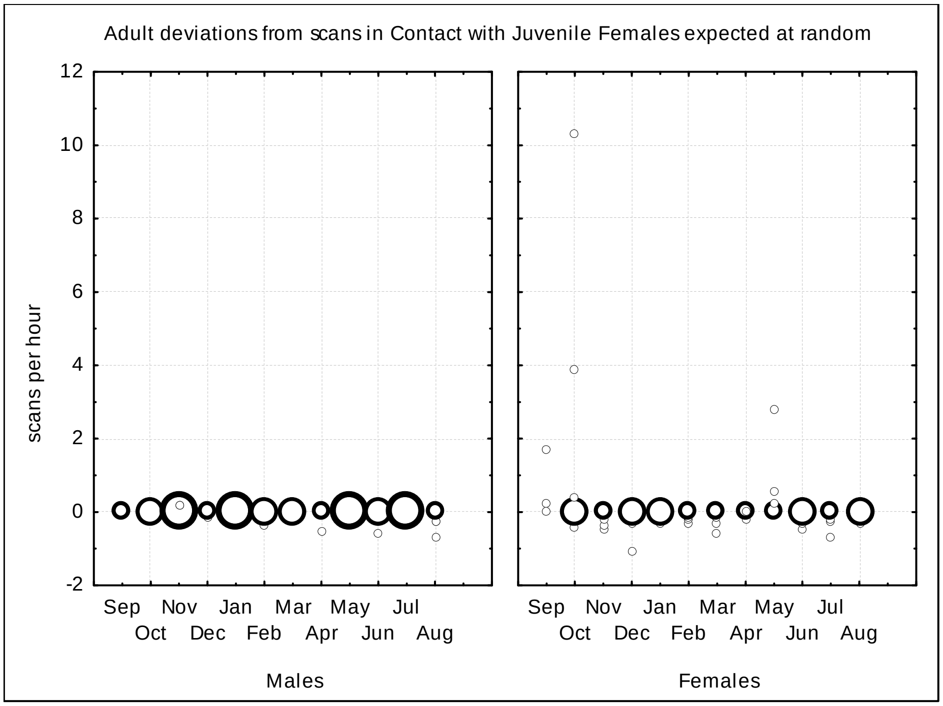


Fig. 4-53. Deviations from expected time spent in contact with juvenile females.

Within Reach of Juvenile Females

An LMEM could not be fit. The best fit mean RP model indicates no sex difference in bias toward or away from juvenile females in time spent within reach of others, but suggests that adults tend to spend slightly less time within reach of juvenile females than expected at random (Table 4-46, Figure 4-54).

TABLE 4-46. RP model parameter estimates of deviations from expected time spent within reach of juvenile females.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in reach JF	mean RP	INT	-0.05	0.03	16	-1.79	0.09†
		SEX	-0.02	0.04	16	-0.54	0.60

† $0.05 < p \leq 0.10$

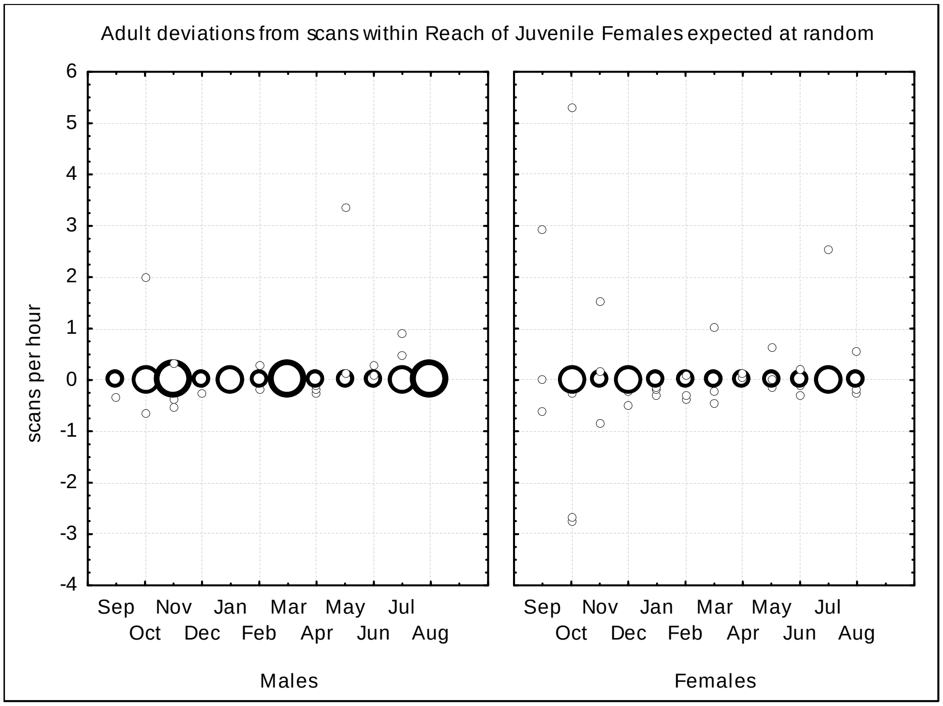


Fig. 4-54. Deviations from expected time spent within reach of juvenile females.

Within 3m of Juvenile Females

Neither the best fit random intercepts LMEM nor RP model suggest any difference from random allocation of time spent within 3m of juvenile females, as there is no sex difference and no difference from an intercept of zero (Table 4-47, Figure 4-55).

TABLE 4-47. Model parameter estimates of deviations from expected time spent within 3 meters of juvenile females.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in 3m JF	random int. LMEM	INT	0.03	0.26	16	0.11	0.91
		SEX	0.59	0.36	103	1.61	0.11
	mean RP	INT	0.04	0.27	16	0.14	0.89
		SEX	0.60	0.39	16	1.56	0.14

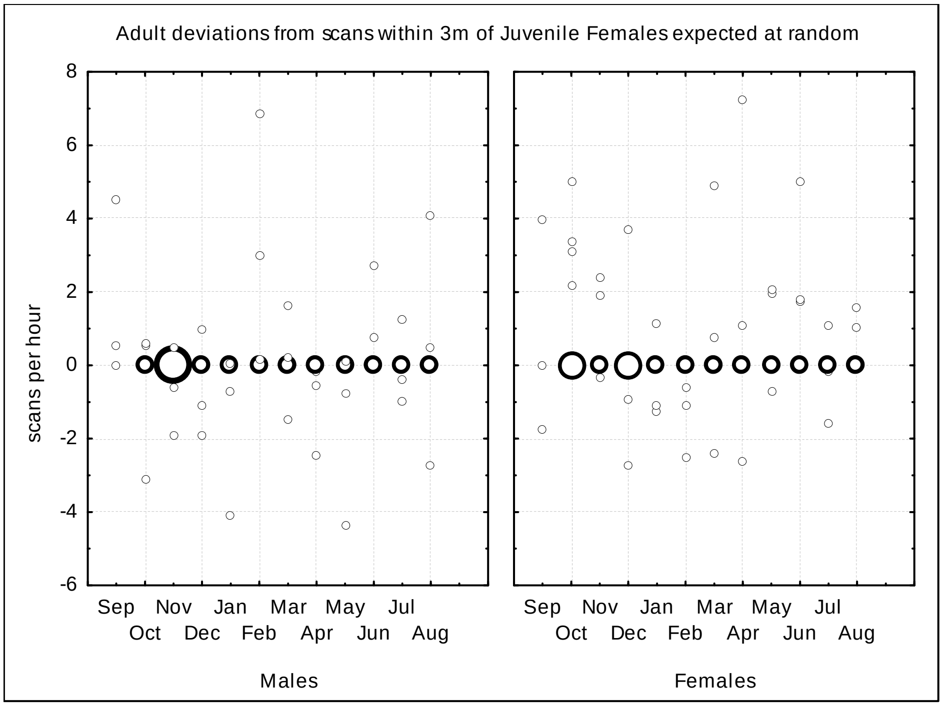


Fig. 4-55. Deviations from expected time spent within 3 meters of juvenile females.

Contact with Juvenile Males

An LMEM could not be fit. The best fit mean RP model indicates a tendency for adult females to spend less of their contact time with juvenile males than do adult males (Table 4-48). Analyses by sex indicate that both adult males and adult females spend less of their contact time with juvenile males than expected, adult females simply spend even less of it with juvenile males than do adult males (Figure 4-56).

TABLE 4-48. Model parameter estimates of deviations from expected time spent in contact with juvenile males.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in contact JM	mean RP	INT	-0.02	0.02	16	-1.00	0.33
		SEX	-0.06	0.03	16	-1.74	0.10†
AF Dev Time in contact JM	linear LMEM	INT	-0.28	0.08	9	-3.63	0.006*
		TIME	0.03	0.01	50	2.66	0.01*
	mean RP	INT	-0.06	0.03	9	-2.05	0.07†
AM Dev Time in contact JM	mean RP	INT	-0.04	0.01	7	-4.95	0.002*

* p ≤ 0.05; † 0.05 < p ≤ 0.10

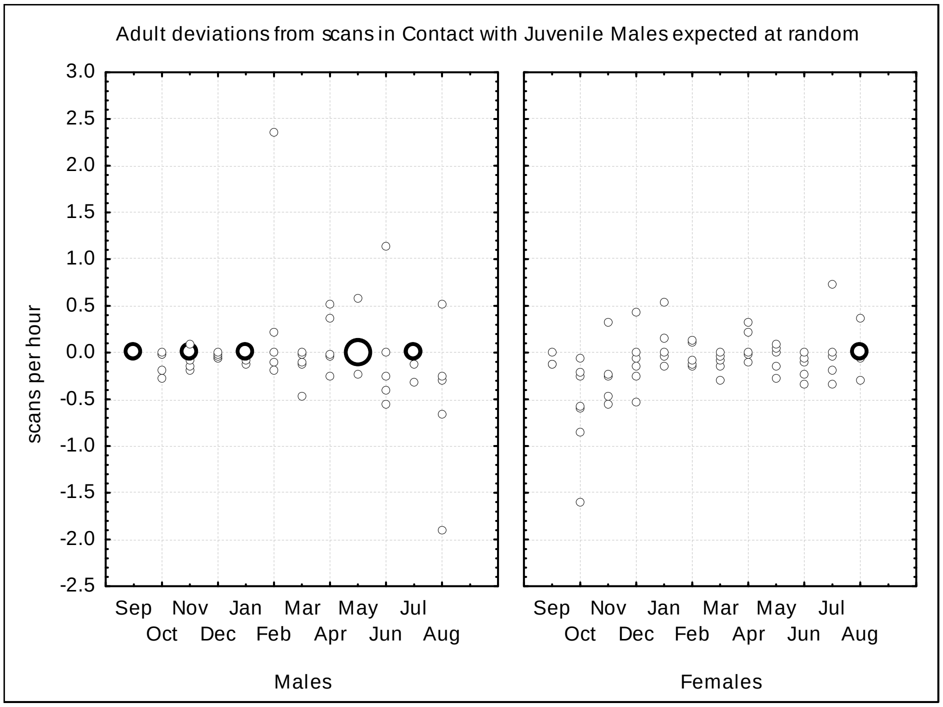


Fig. 4-56. Deviations from expected time spent in contact with juvenile males.

Within Reach of Juvenile Males

The linear LMEM indicates no significant sex difference, sex*time interaction or deviation from random expectation in bias in time spent within reach of others toward or away from juvenile males (Table 4-49). The best fit RP mean and linear models each suggest that females tend to bias their time within reach of others more strongly away from juvenile males than males do (Table 4-49, Figure 4-57). I preferentially accept the results of the linear LMEM because the LMEM accounts for inter-individual variation in intercepts and slopes, and because an examination of the individual OLS regressions does not support an interpretation of adult females spending less time than expected within reach of juvenile males (Figure 4-58). In general, adults do not bias their time spent within reach of others toward or away from juvenile males.

TABLE 4-49. Model parameter estimates of deviations from expected time spent within reach of juvenile males.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in reach JM	linear LMEM	INT	0.06	0.34	16	0.18	0.86
		SEX	-0.11	0.47	89	-0.23	0.82
		TIME	0.01	0.04	12	0.26	0.80
		SEX*TIME	0.00	0.05	89	0.08	0.93
	mean RP	INT	-0.08	0.06	16	-1.18	0.25
		SEX	-0.18	0.09	16	-1.97	0.07†

† $0.05 < p \leq 0.10$

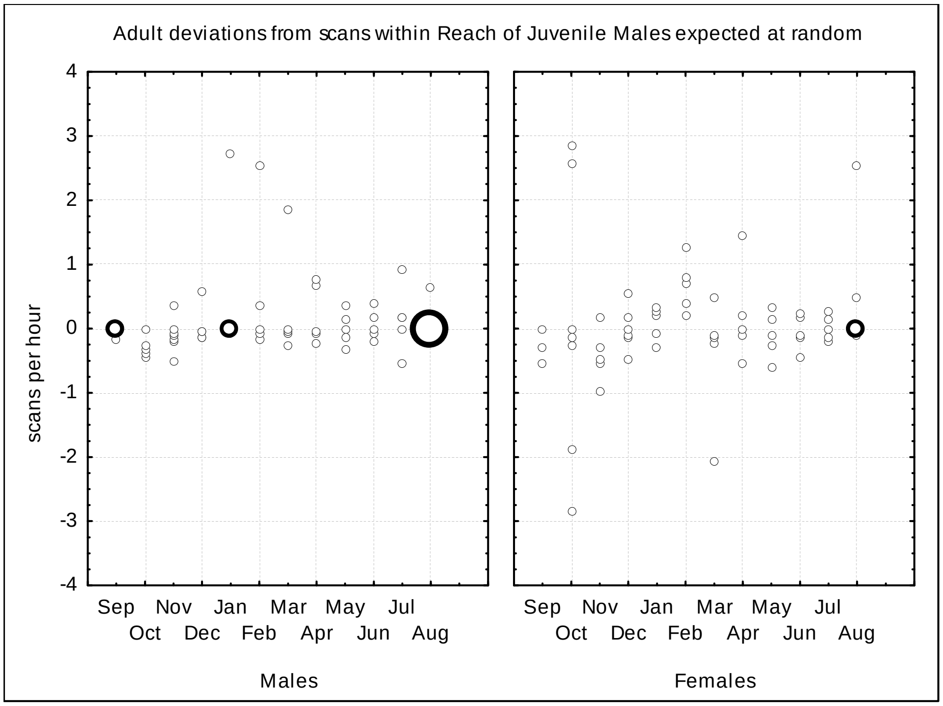


Fig. 4-57. Deviations from expected time spent within reach of juvenile males.

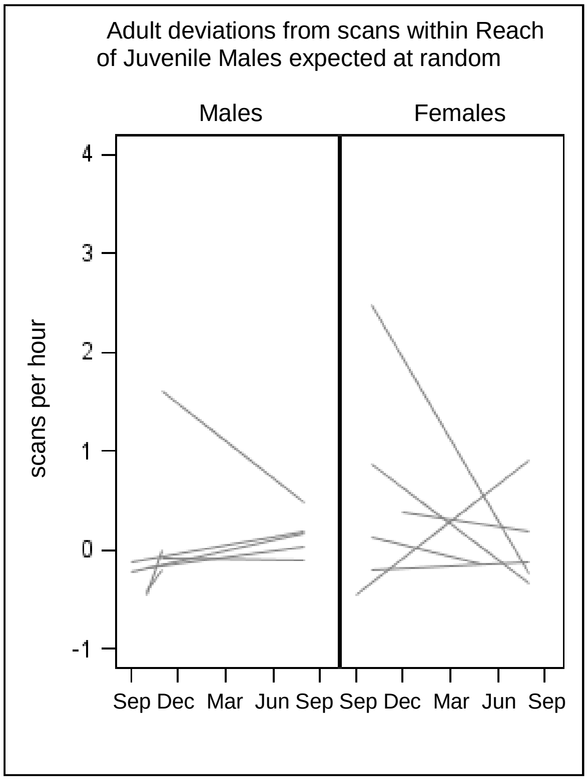


Fig. 4-58. Individual ordinary least squares regressions of deviations from expected time spent in contact with juvenile males.

Within 3m of Juvenile Males

The best fit LMEM was a random intercepts model that suggests adult females tend to bias their time within 3m of others more heavily toward juvenile males than do adult males (Table 4-50, Figure 4-59). The best fit linear RP model suggests a significant sex*time interaction, with females biasing their time within 3m of others more heavily toward juvenile males as the observation year progressed, but no significant sex difference or effect of time overall (Table 4-50). An investigation of the individual OLS regressions suggests that all females except one non-completer did spend more time within 3m of juvenile males as the year progressed, and, depending on the degree of this effect, it could appear as a significant effect of sex overall in a random intercepts LMEM that only quantifies overall sex difference and does not address temporal effects (Figure 4-60). Analyses by sex indicate that adult females begin the year within 3m of juvenile males at random rates, but tend to bias their time toward juvenile males as the year progresses, while adult males spend more time than expected within 3m of juvenile males overall. Therefore, in this case, I accept the results of the linear RP model—that adult males and females have different temporal patterns of time expenditure within 3m of juvenile males, if not differences in overall time expenditure with them.

TABLE 4-50. Model parameter estimates of deviations from expected time spent within 3 meters of juvenile males.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in 3m JM	random int. LMEM	INT	0.59	0.30	16	1.99	0.06†
		SEX	0.69	0.41	103	1.66	0.10†
	linear RP	INT	0.34	0.40	16	0.85	0.41
		TIME	0.04	0.04	101	1.06	0.29
		SEX	-0.19	0.56	16	-0.34	0.74
		TIME*SEX	0.19	0.06	101	3.33	0.001*
AF Dev Time in 3m JM	linear LMEM	INT	0.47	0.58	9	0.81	0.44
		TIME	0.16	0.08	50	1.91	0.06†
	linear RP	INT	0.47	0.60	9	0.78	0.46
		TIME	0.16	0.08	50	1.94	0.06†
AM Dev Time in 3m JM	mean RP	INT	0.60	0.22	7	2.78	0.03*

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

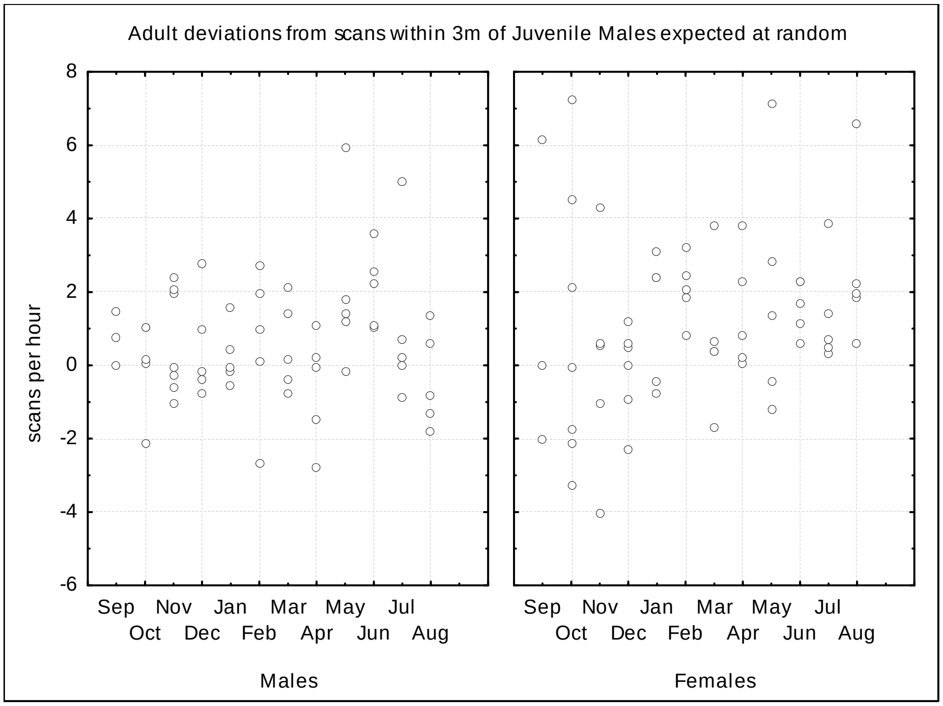


Fig. 4-59. Deviations from expected time spent within 3 meters of juvenile males.

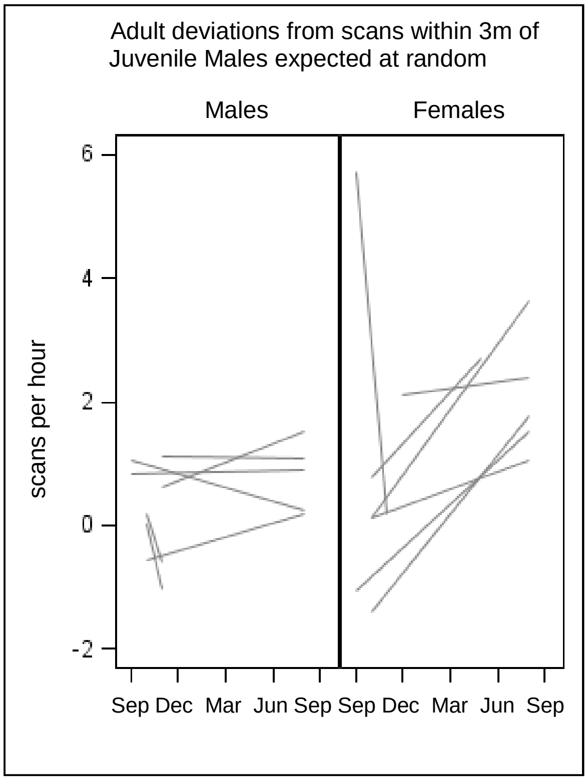


Fig. 4-60. Individual ordinary least squares regressions of deviations from expected time spent within 3 meters of juvenile males.

Contact with Infants

An LMEM could not be fit. The best fit mean RP model indicates that females bias their time in contact with others significantly more heavily toward infants than do males (Table 4-51). Analyses by sex indicate that adult females actually spend their contact time with infants as expected at random but that adult males spend significantly less time in contact with infants than expected at random (Figure 4-61). In other words, adult males bias their contact time away from infants significantly more heavily than adult females, who show no bias.

TABLE 4-51. Model parameter estimates of deviations from expected rates of contact with infants.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in contact INFs	mean RP	INT	-0.12	0.02	16	-5.51	<.0001*
		SEX	0.13	0.03	16	4.01	0.001*
AF Dev Time in contact INFs	random int. LMEM	INT	0.03	0.10	9	0.30	0.77
	mean RP	INT	-0.07	0.05	9	-1.61	0.14
AM Dev Time in contact INFs	mean RP	INT	-0.11	0.02	7	-5.87	0.0006*

* $p \leq 0.05$

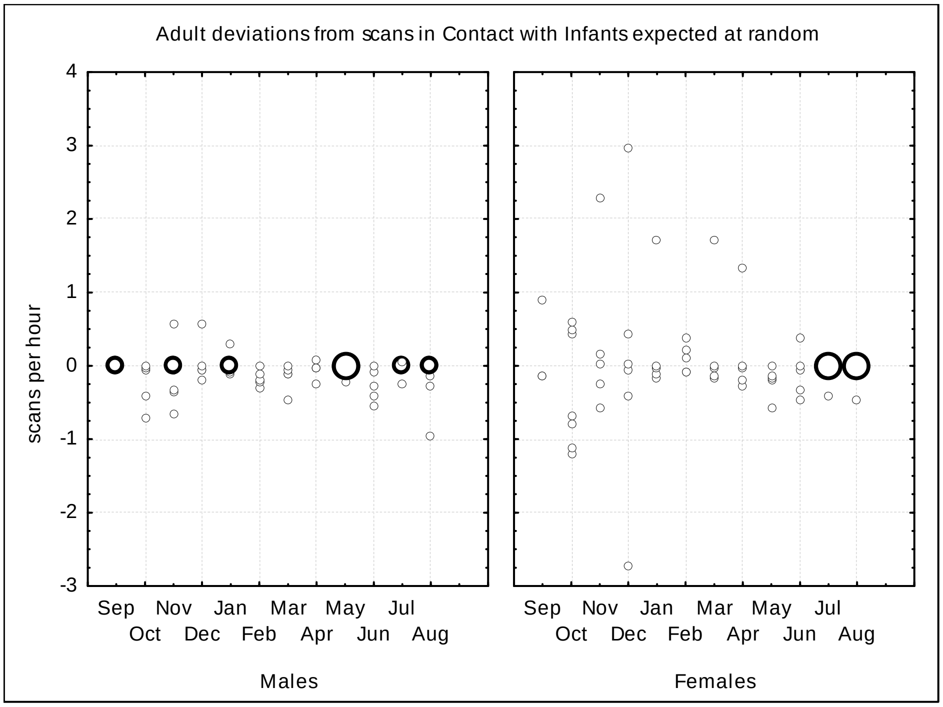


Fig. 4-61. Deviations from expected rates of contact with infants.

Within Reach of Infants

The most complex LMEM that could be fit was a random intercepts model that indicates that adult females bias their time within reach of others more strongly toward infants than adult males (Table 4-52, Figure 4-62). The best fit mean RP model finds no such sex difference. An examination of the OLS regressions for individuals suggests high adult female bias toward being within reach of young infants that tapers toward rates expected at random as infants age (Figure 4-63). Analyses by sex are not elucidatory. The best fit random intercepts LMEM for adult females indicates that they exhibit a bias toward infants in their time within reach of others, while the best fit mean RP model finds that they spend their time within reach of infants as expected at random. Males, also, do not exhibit a bias toward or away from infants with respect to time spent within reach of others. Due to these conflicting results, I accept the conservative conclusion that there is no clear evidence for any bias for adults of either sex toward or away from infants with respect to time spent within reach of others.

TABLE 4-52. Model parameter estimates of deviations from expected time spent within reach of infants.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in reach INFs	random int. LMEM	INT	-0.03	0.85	16	-0.04	0.97
		SEX	2.49	1.14	103	2.18	0.03*
	mean RP	INT	-0.01	0.07	16	-0.10	0.92
		SEX	-0.09	0.10	16	-0.92	0.37
AF Dev Time in reach INFs	random int. LMEM	INT	2.44	1.03	9	2.37	0.04*
	mean RP	INT	-0.04	0.06	9	-0.76	0.46
AM Dev Time in reach INFs	mean RP	INT	-0.02	0.01	7	-1.51	0.17

$* \ p \leq 0.05$

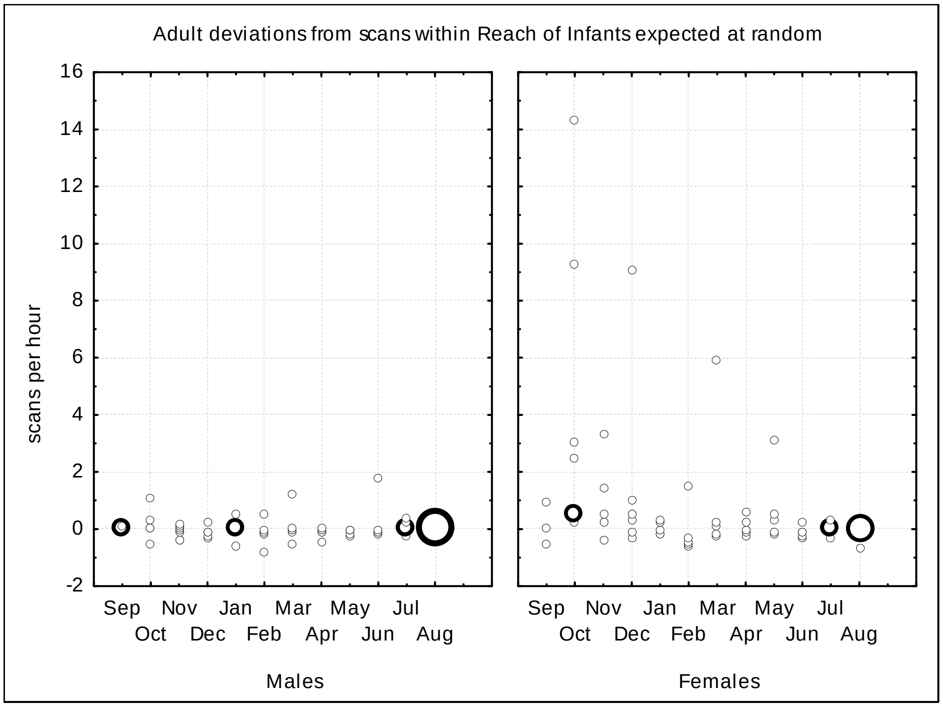


Fig. 4-62. Deviations from expected time spent within reach of infants.

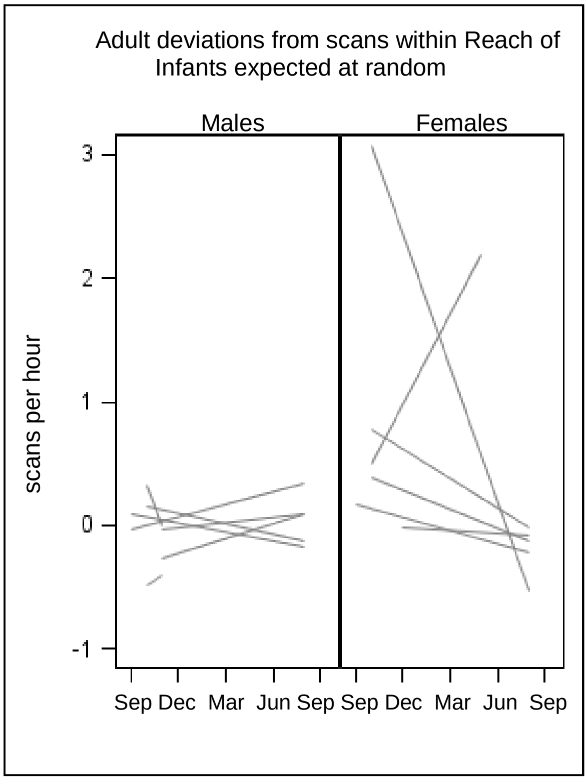


Fig. 4-63. Individual ordinary least squares regressions of deviations from expected time spent within reach of infants.

Within 3m of Infants

The best fit random intercept LMEM and mean RP models indicate no significant sex difference in bias toward or away from infants in time spent within 3m of others, nor any deviation from random expectation (Table 4-53, Figure 4-64).

TABLE 4-53. Model parameter estimates of deviations from expected time spent within 3 meters of infants.

Variable	Model	Effect	est	SE	DF	t	p
Dev Time in 3m INFs	random int. LMEM	INT	0.37	0.64	17	0.57	0.57
		TIME	0.10	0.09	13	1.05	0.31
	mean RP	INT	0.48	0.41	16	1.15	0.27
		SEX	0.82	0.58	16	1.43	0.17

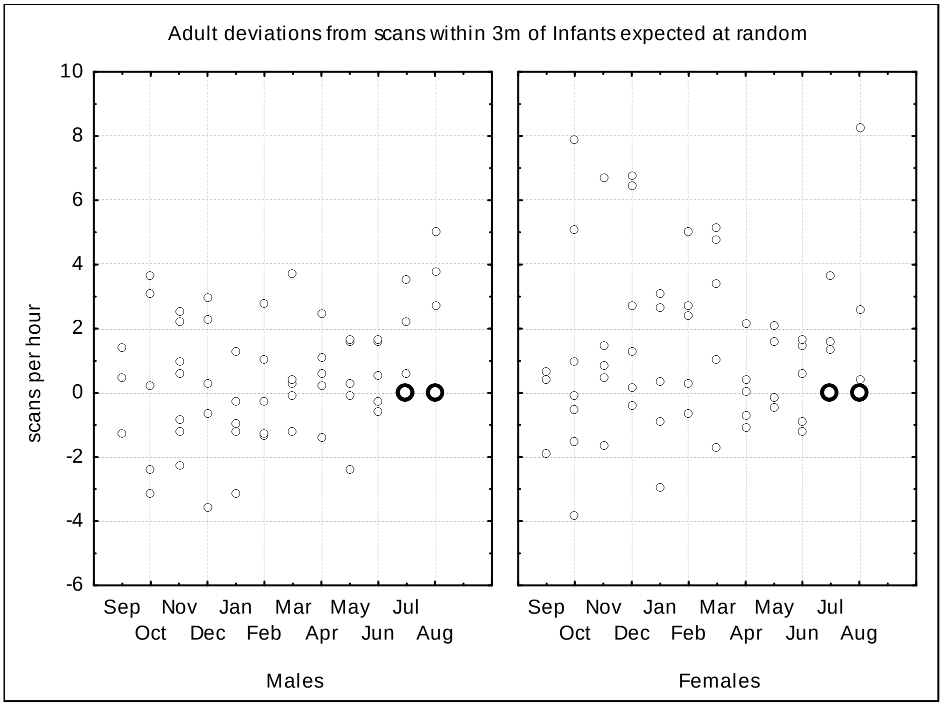


Fig. 4-64. Deviations from expected time spent within 3 meters of infants.

Summary and Discussion – Proximity

Tables 4-54 and 4-55 summarize tests of adult sex differences in proximity to others, and tests of adult patterns of bias in their proximity to particular age/sex classes. Only statistically significant results are presented; empty cells represent results of no statistical significance.

In terms of general measures of proximity, adult females are more spatially cohesive than adult males (Table 4-54). Adult females have more neighbors in proximity at all distances than do adult males and spend more time at all levels of proximity to other individuals. But, there are sex differences in the patterning of time in proximity throughout the year. Females decrease their time in very close proximity to others (in contact and within reach) and increase their time within 3m of others, suggesting that they become a bit less cohesive throughout the year. Adult males increase their time in contact and time within 3m of others throughout the year. Both sexes decrease the time they spend alone throughout the year. Additionally, it appears that these results oversimplify what may be more complex patterns of temporal change in proximity. Qualitatively, it appears that adult females have a quadratic changes in proximity through time rather than linear ones, beginning with high number of neighbors and lots of time spent in close proximity (in contact and within reach) at the beginning of the year that rapidly decrease and then gradually increase again toward the end of the year (Figures 4-65, 4-66, 4-67, 4-68).

The two spring mating pulses observed in 2009 are marked on Figures 4-65 through 4-68 by grey bars. It is reasonable to hypothesize that the increase in proximity measures for males late in the observation year stems from males working harder to maintain proximity to females during the mating season. This may also explain apparent (but statistically non-significant) increases in female proximity measures late in the observation year. Another reasonable conjecture regarding increased adult female proximity measures late in the observation year is that they are related to increased agonism late in the year as a result of decreasing resource availability (Figure 4-23). Future work may be able to test these conjectures. Adult, non-maternal female proximity patterns do seem to be strongly coincident with patterns of infant maturation in September through January.

TABLE 4-54. Summary of sex differences in global proximity measures.

Proximity measure	Sex Difference	Time effects	
Total # neighbors in contact	♀ +	·	·
Total # neighbors in reach	♀ +	·	·
Total # neighbors in 3m	♀ +	·	·
Time in contact with others	♀ +	·	♂ +
Time in reach of others	♀ +	♀ –	·
Time in 3m of others	♀ +	♀ +	♂ +
Time in 5m of others	♀ +	♀ +	♂ +

Sex difference: + significantly greater
Time effects: + increase with time
– decrease with time
· no effect

TABLE 4-55. Summary of sex differences in bias of proximity to each partner age/sex class.

Proximity measure	Partner type	Sex-typed bias		Time effect	
Time in contact	AF	♀ +	·	·	·
Time in reach	AF	·	·	·	·
Time in 3m	AF	♀ +	·	♀ –	·
Time in contact	AM	♀ –	♂ +	♀ +	♂ –
Time in reach	AM	·	·	·	·
Time in 3m	AM	♀ —	♂ –	·	♂ –
Time in contact	JF	·	·	·	·
Time in reach	JF	·	·	·	·
Time in 3m	JF	·	·	·	·
Time in contact	JM	♀ —	♂ –	·	·
Time in reach	JM	·	·	·	·
Time in 3m	JM	·	♂ +	♀ +	·
Time in contact	INFs	·	♂ –	·	·
Time in reach	INFs	·	·	·	·
Time in 3m	INFs	·	·	·	·

Sex-typed bias: + significantly more than expected at random
– significantly less than expected at random
— significantly less than –
· no difference from expected at random
Time effects: + increase with time
– decrease with time
· no effect

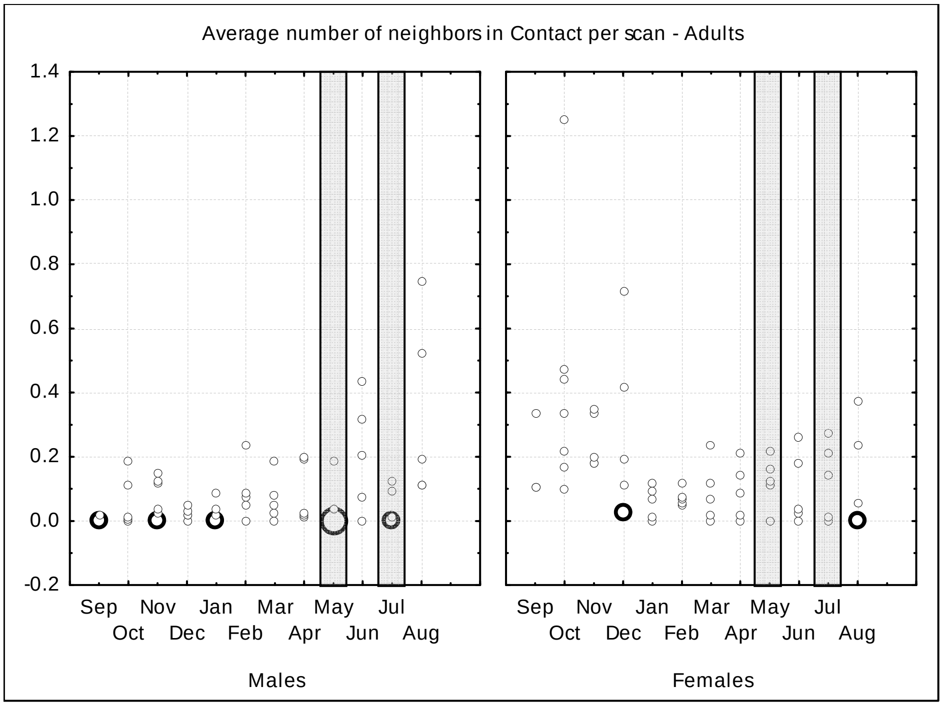


Fig. 4-65. Average numbers of neighbors in contact; grey bars indicate spring mating pulses in 2009.

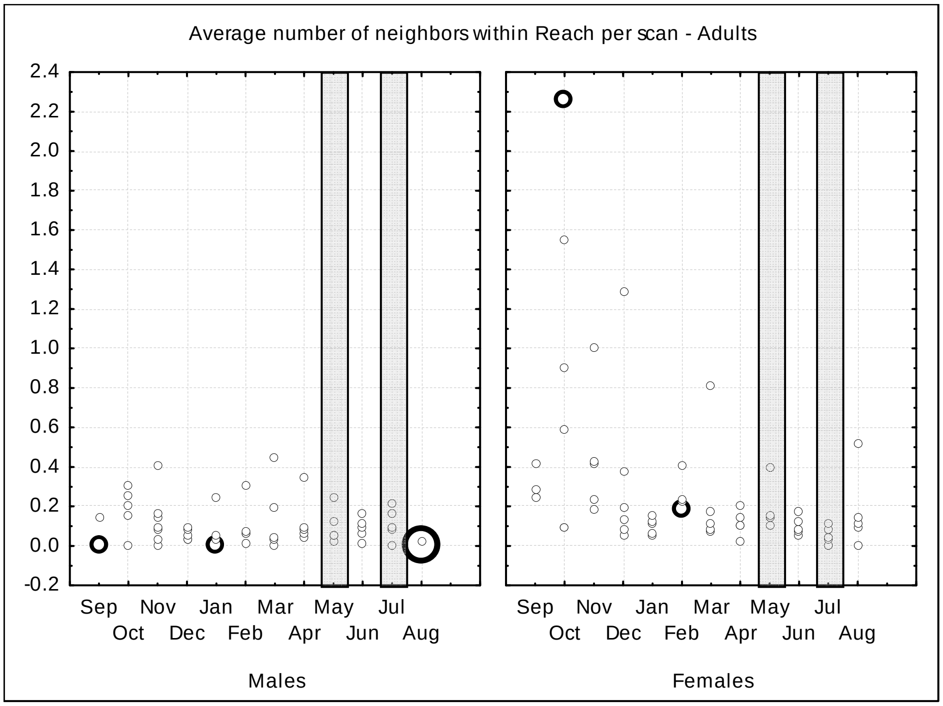


Fig. 4-66. Average numbers of neighbors in within reach; grey bars indicate spring mating pulses in 2009.

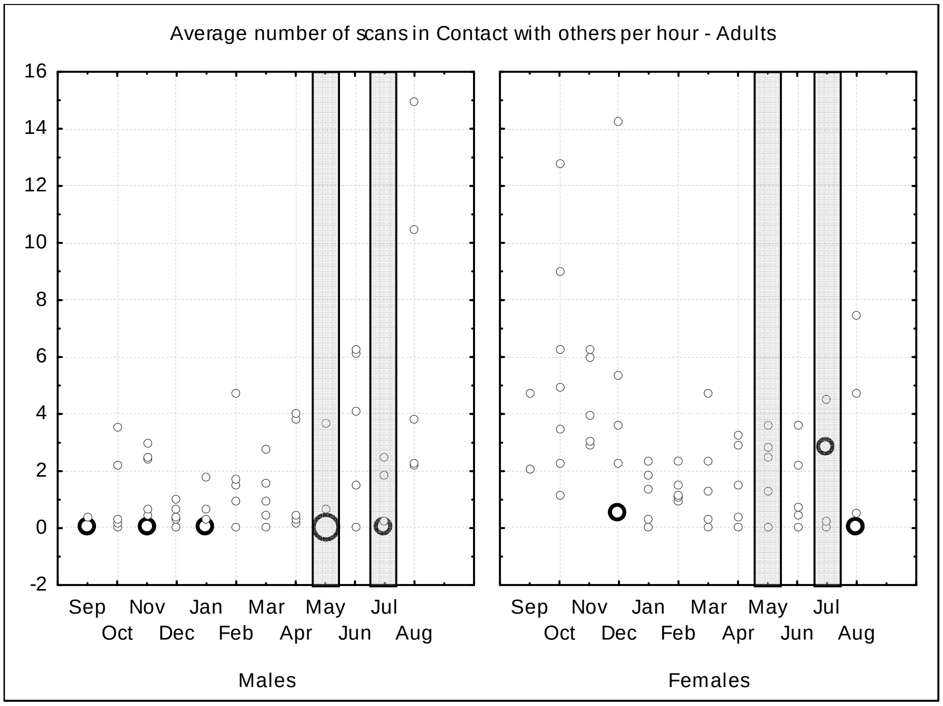


Fig. 4-67. Average amount of time spent in contact with others; grey bars indicate spring mating pulses in 2009.

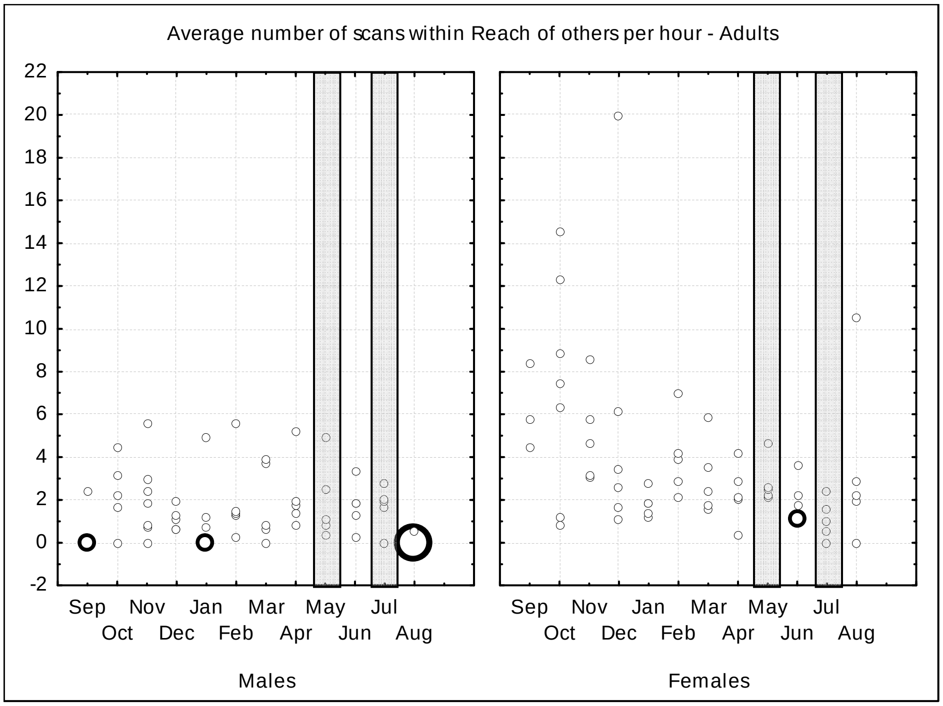


Fig. 4-68. Average amount of time spent within reach of others; grey bars indicate spring mating pulses in 2009.

In general, adult females spend more time in proximity with adult females and less time proximity to adult males than adult males. In other words, there is an overall pattern of spatial association with same-sex peers. Additionally, adult males do not spend much time in contact with subadults. Either they avoid subadults or subadults avoid them. Future work can address this point.

Adult patterns of time spent in contact with adult males reflects the yearly temporal patterns mentioned above (see Figure 4-42). When infants are young, adult females without infants bias their time in contact away from adult males because they are biasing it toward other adult females. From May through August, adult males begin to avoid other adult males, probably as a result of mating competition, while adult females bias their contact toward them, probably as a result of mating effort on the part of males that is tolerated by females during the mating season, or as a result of mating effort on the part of females. These analyses do not reveal whether focal females are targeting adult females with infants or just adult females in general when infants are young or whether adult males or adult females are responsible for maintaining the increased proximity between opposite-sex adults during the mating season, but future work will investigate these issues. Adult sex differences in patterns of proximity to juveniles are few and are not obviously relatable to temporal patterns of variation in resource availability or reproductive cyclicity. Notably, analyses for proximities of "contact" and "within reach" are not entirely duplicative, indicating that they may reliably reflect proximities that have different "value" to the animals.

INFANT INTEREST

The components of what I consider here as expressions of "infant interest" have already been discussed in other sections, but are revisited here in this section because sex differences in infant interest, in particular, characterize juvenile and adult primates of many species [*Papio cynocephalus ursinus*: Cheney 1978; *Alouatta palliata*: Clarke et al. 1998; *Cercopithecus mitis*: Cords et al. 2010, Förster and Cords 2005; *Alouatta seniculus*: Crockett and Pope 2002]. Two ways in which infant interest might be expressed are in grooming directed toward them and in maintenance of proximity to them.

Grooming

As previously indicated (Table 4-30), adult females groom infants more than adult males do, but only when infants are young.

Proximity

Adult females without infants of their own do not bias their time in contact with others toward non-filial infants in particular, but adult males bias their contact time away from infants (Table 4-51). Both measures of infant interest indicate that adult females are more interested in infants than adult males are, but it appears that adult males are disinterested in infants rather than that adult females are especially interested in them.

Responsibility for maintenance of proximity as quantified by the Hinde index is a commonly used measure of the nature of the mother-infant relationship [Hinde and Atkinson 1970], and is conceptually well-suited to assessing infant interest. However, it was not used here to assess infant interest (or interest in any other type of relationships between age/sex classes) because it did not lend itself well to being used across different types of dyadic relationships. Different types of dyads engaged in dramatically different rates of proximity changes, and as such, a Hinde index would not have characterized the interaction patterns of all types of dyads equally well. For example, while the average number of proximity changes per adult female-infant dyad per month was approximately 11, the average number of proximity changes per adult male-infant dyad per month was only 4.5. First of all, I considered 4.5 proximity changes to be an insufficient number to accurately characterize responsibility for proximity. Secondly, the disparity among the rates of proximity changes that characterized the different types of dyads meant that some types of dyadic relationships would be well-characterized because they had sufficient samples of proximity changes, while others would be prone to biased estimates as a result of small sample sizes, and I did not think comparisons of these types of variably well-characterized relationships would be meaningful.

SCENT MARKING

In this study, scent-marking behavioral events recorded were: anogenital marking, brachial marking, ante-brachial marking, anoint tail, tail wave, and tail play. Anogenital scent marking is performed by rubbing the anogenital scent glands [Palagi et al. 2002] on branches. Antebrachial marking involves depositing secretions from the antebrachial glands on a branch using a stereotyped sequence of motions; first the animal grasps a branch with the manus (which usually involves moving to an orthograde posture), then forcefully rotates the manus and forearm around the branch (clockwise when marking with the right forelimb, counterclockwise when marking with the left), gouging the substrate with a keratinous brachial spur and squeezing secretions from the brachial gland [Palagi et al. 2002]. Brachial marking sometimes immediately precedes antebrachial marking. It involves passing the antebrachial scent glands over the ipsilateral brachial scent glands, thereby mixing the secretions of the brachial and antebrachial scent glands prior to their deposition

[Palagi et al. 2002]. Anoint tail involves an individual drawing its tail repeatedly between the antebrachial scent glands, depositing olfactory secretions onto the tail, usually just prior to waving the tail over the back toward another individual in a "tail wave" [Kappeler 1998]. Tail play involves drawing the tail repeatedly through the forearms in the context of play [Pereira and Kappeler 1997] and is included here because it may serve as a precursor to or a developmental component of the scent marking behaviors of anoint tail and tail wave. The following analyses investigate adult sex differences in: hourly rates of anogenital marking, brachial marking and ante-brachial marking, anoint tail and tail wave, and tail play. Both sexes have anogenital scent glands and engage in anogenital scent marking [Palagi et al. 2002]. Typically, only males have antebrachial and brachial scent glands and antebrachial spurs [Palagi et al. 2002; Sauther and Cuozzo 2008], so brachial and antebrachial scent marking is largely limited to males, as is tail anointing, tail waving, and tail play [Pereira 2002].

Ano-genital marking (A-G mark)

The best fit random intercepts LMEM indicates no significant sex difference in rates of anogenital marking, while the best fit mean RP model indicates a trend toward a sex difference in rates of anogenital marking. Qualitatively, a means model does not appear to fit the male data particularly well, but neither the best fit linear nor quadratic RP models detect significant sex differences or any sex*time interactions (Table 4-56, Figure 4-69).

TABLE 4-56. Model parameter estimates of rates of ano-genital marking.

Variable	Model	Effect	est	SE	DF	t	p
A-G mark	random int. LMEM	INT	1.62	0.54	16	3.02	0.008*
		SEX	-0.76	0.73	103	-1.04	0.30
	mean RP	INT	0.45	0.17	16	2.61	0.02*
		SEX	0.42	0.24	16	1.75	0.10†

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

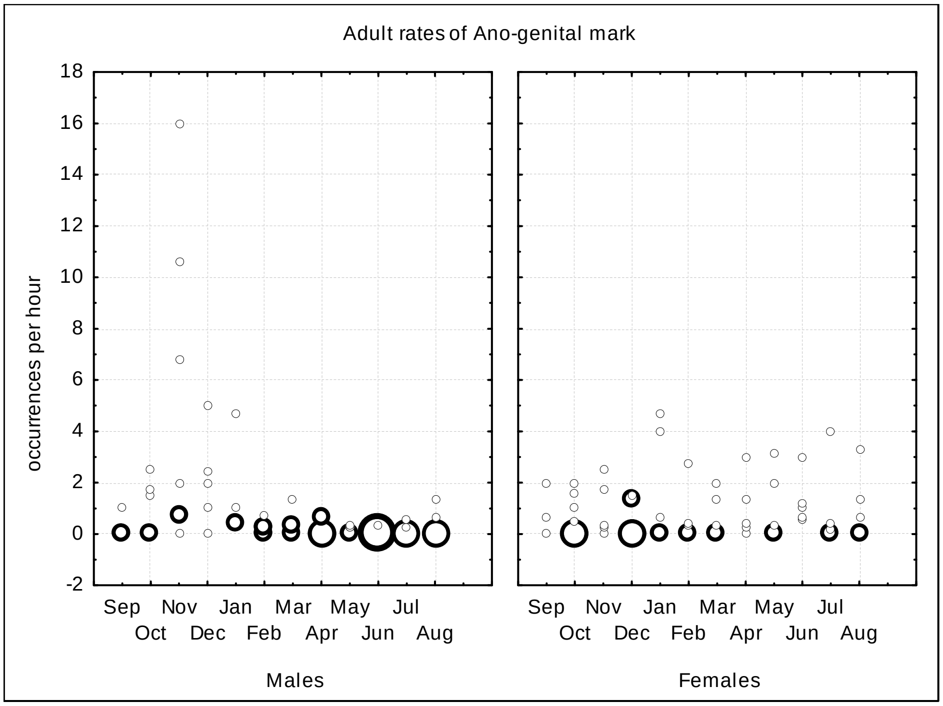


Fig. 4-69. Rates of ano-genital marking among adults.

Antebrachial and brachial marking

The best fit random intercepts LMEM indicates a significant sex difference in rates of antebrachial marking, with females wrist-marking significantly less often than males. A linear LMEM could not be fit, but the best fit RP model is a linear model that indicates a significant sex difference as well as a significant sex*time interaction, with adult females wrist-marking significantly less than adult males and with adult males wrist-marking less as the observation year progressed (Table 4-57).

Indeed, focal females were never observed to wrist-mark, and males wrist-marked more during the first quadrant of the observation year (September-December) and less throughout the rest of the year (Figure 4-70).

TABLE 4-57. Model parameter estimates of rates of antebrachial marking.

Variable	Model	Effect	est	SE	DF	t	p
Rate antebrachial mark	random int. LMEM	INT	14.19	4.12	16	3.44	0.003*
		SEX	-14.19	5.58	103	-2.54	0.01*
	linear RP	INT	3.69	0.73	16	5.03	0.0001*
		SEX	-3.69	1.06	16	-3.50	0.003*
		TIME	-0.33	0.07	101	-4.70	<.0001*
		SEX*TIME	0.33	0.10	101	3.26	0.002*

* $p \leq 0.05$

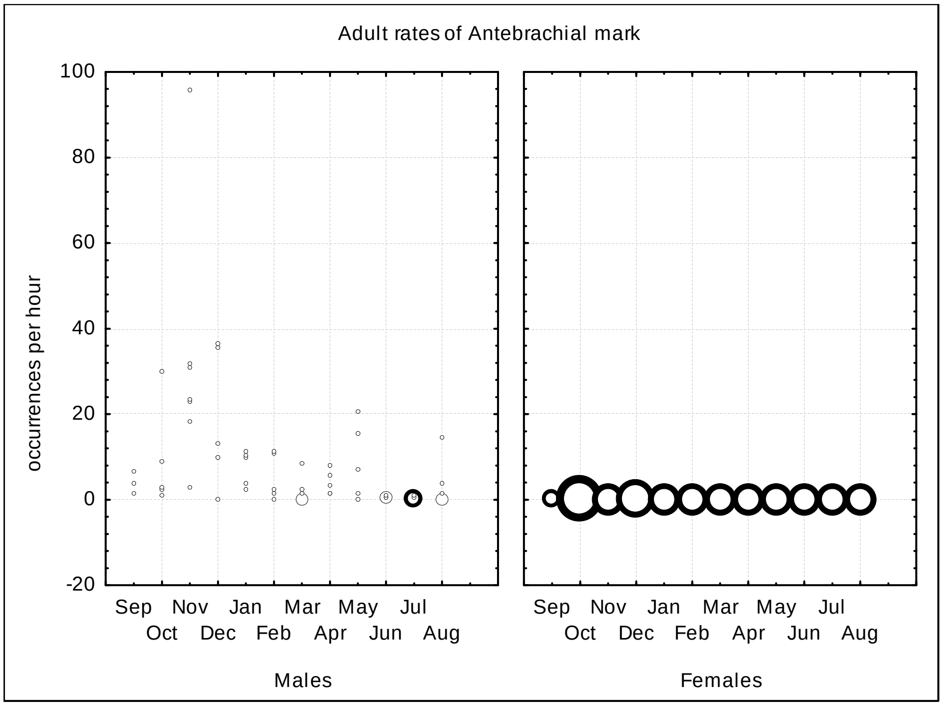


Fig. 4-70. Rates of antebrachial marking among adults.

The results for brachial marking are similar to but not exactly concordant with those for antebrachial marking. The best fit random intercepts LMEM indicates a significant sex difference in rates of antebrachial marking, with females marking less than males. In contrast, the best fit mean RP model does not find a significant sex difference in rates of brachial marking, even though females were never observed to brachial mark (Table 4-58). A qualitative examination of the scatterplot of brachial marking suggests that a linear or quadratic model may better fit the male data (Figure 4-71). More complex LMEMs could not be fit, but the best fit quadratic RP model indicates significant sex*time and sex*time^2 interactions, with males brachial marking less as time increases and slightly more as time^2 increases. Here, I conclude that these data do not fit any of these models well, but that adult males brachial-mark significantly more than females and significantly less as the observation year progresses.

TABLE 4-58. Model parameter estimates of rates of brachial marking.

Variable	Model	Effect	est	SE	DF	t	p
Rate brachial mark	random int. LMEM	INT	3.28	0.82	16	3.99	0.001*
		SEX	-3.28	1.12	103	-2.94	0.004*
	mean RP	INT	0.22	0.10	16	2.08	0.05*
		SEX	-0.22	0.15	16	-1.48	0.16
	quad RP	INT	-0.23	0.25	16	-0.93	0.37
		SEX	0.23	0.35	16	0.66	0.52
		TIME	0.57	0.16	99	3.54	0.0006*
		SEX*TIME	-0.57	0.23	99	-2.53	0.01*
		TIME$^{\wedge 2}$	-0.05	0.01	99	-3.61	0.0005*
		SEX*TIME$^{\wedge 2}$	0.05	0.02	99	2.58	0.01*

* $p \leq 0.05$

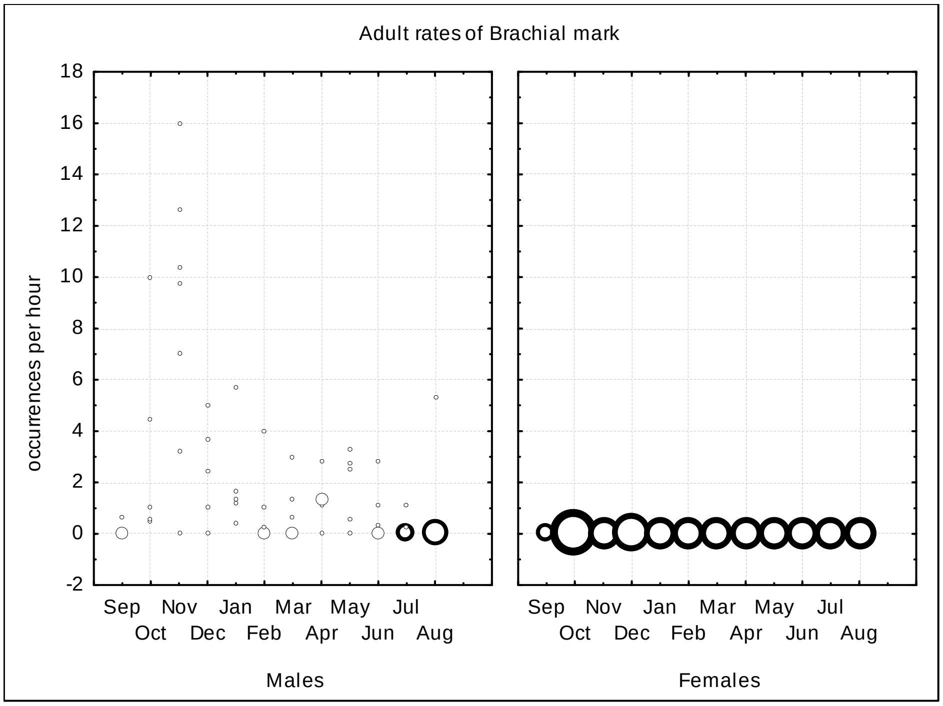


Fig. 4-71. Rates of brachial marking among adults.

Rates of Anoint Tail and Tail Wave

One focal female was observed to "anoint tail" on one occasion. According to the best fit random intercepts LMEM, males and females differ significantly in their rates of anoint tail, with females anointing less than males, but according to the best fit mean RP model, they do not (Table 4-59). As with brachial and antebrachial marking, a mean model does not appear to be a particularly good fit for the male data (Figure 4-72), but the best fit linear and quadratic RP models also do not find significant sex differences or sex*time interactions. Again, that these data do not fit any of these models well, but adult males anoint their tails significantly more than do adult females.

TABLE 4-59. Model parameter estimates of rates of anoint tail.

Variable	Model	Effect	est	SE	DF	t	p
Anoint tail	random int. LMEM	INT	1.14	0.25	16	4.49	0.0004*
		SEX	-1.13	0.35	103	-2.23	0.002*
	mean RP	INT	0.02	0.07	16	0.23	0.82
		SEX	-0.02	0.10	16	-0.17	0.86

* $p \leq 0.05$

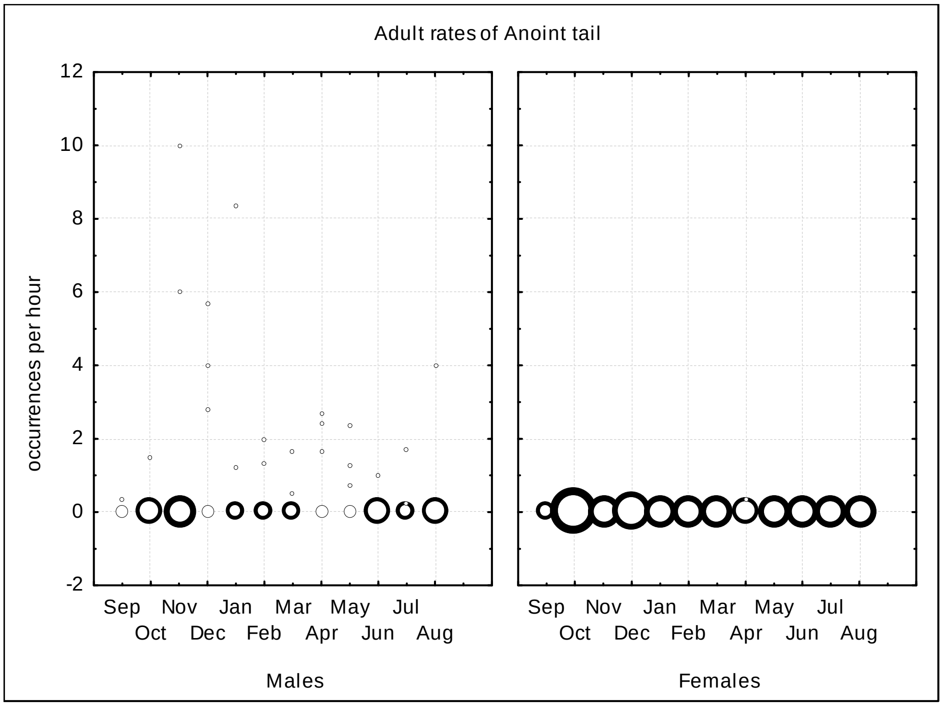


Fig. 4-72. Rates of anoint tail among adults.

Focal females were never observed to tail wave. An LMEM could not be fit, but the best fit RP model indicates a significant sex difference in rates of tail waving, with males tail waving more than females (Table 4-60, Figure 4-73).

TABLE 4-60. Model parameter estimates of rates of tail wave.

Variable	Model	Effect	est	SE	DF	t	p
Tail wave	mean RP	INT	0.39	0.05	16	7.18	<.0001*
		SEX	-0.39	0.08	16	-5.04	0.0001*

* $p \leq 0.05$

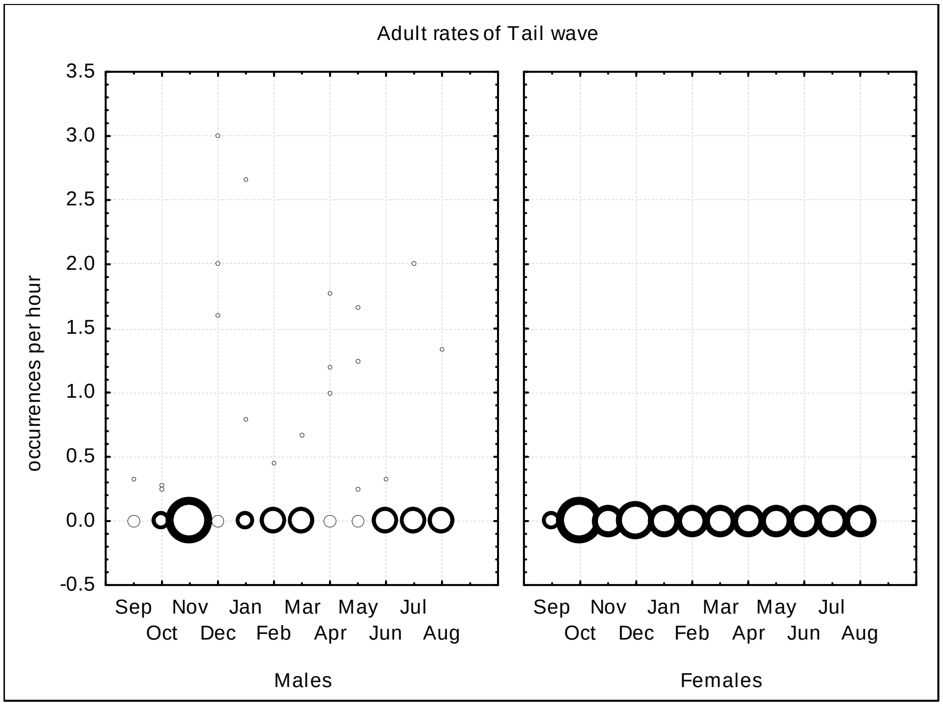


Fig. 4-73. Rates of tail wave among adults.

Rates of Tail Play

Adult males were never observed to anoint their tails in the context of play. One focal adult female was observed to "anoint" her tail during play on two occasions (Figure 4-74). This female was a member of the 2-3 year old cohort.

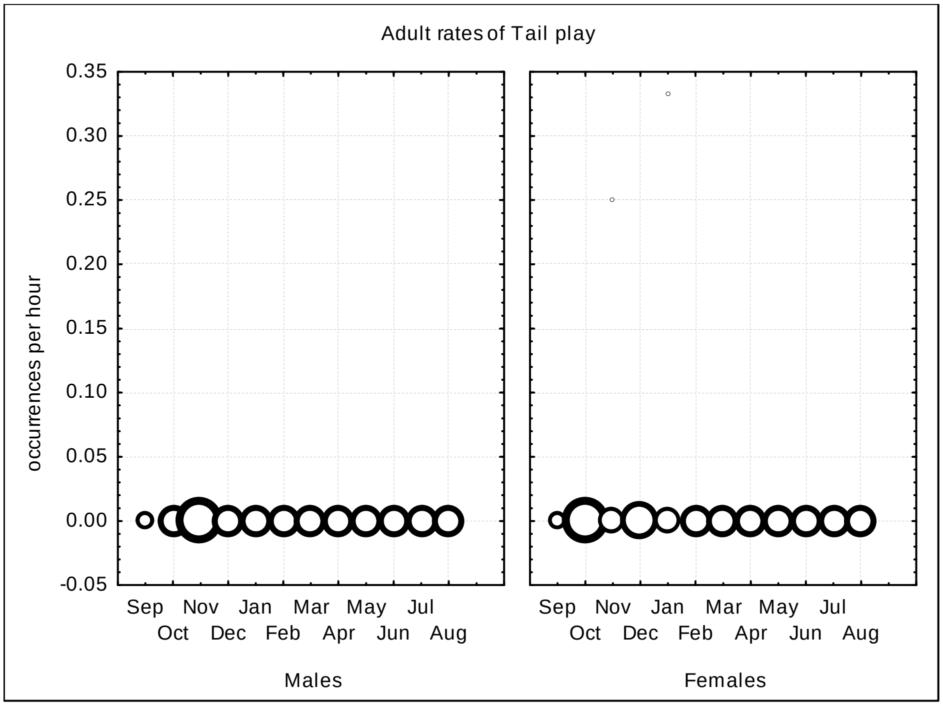


Fig. 4-74. Rates of tail play among adults.

Summary and Discussion – Scent marking

There are no sex differences in rates of ano-genital marking, but as expected, adult males antebrachial and brachial mark, anoint tail, and tail wave significantly more often than adult females (Table 4-61). Male brachial and antebrachial marking behavior is characterized by strong temporal patterns of high rates of marking just after infants are born, but no other clear peaks of scent marking activity. Even though there is no significant effect of time on ano-genital marking, male ano-genital marking appears to share the temporal patterning of brachial and antebrachial marking. In other words, male scent marking behavior "jumps" from baseline in October to December.

TABLE 4-61. Summary of results of tests for sex differences in scent marking behaviors.

Scent marking	Sex Difference	Time effects
Ano-genital	·	·
Antebrachial	♂ +	♂ –
Brachial	♂ +	♂ –
Anoint tail	♂ +	·
Tail wave	♂ +	·

Sex difference: + significantly greater
· no difference
Time effects: – decrease with time
· no effect

It could be argued that this male marking behavior serves to "defend" territories or core areas in the service of protection of infants and/or resources for use by lactating females. However, males are not typically involved in inter-group aggressive encounters in *Lemur catta* [Sauther et al. 1999], suggesting that they are not especially motivated to defend resources. On the other hand, this period of time coincided with a number of male emigrations. In fact, I lost two male focal individuals from one group during the month of November because three adult males emigrated from that group. I know their disappearance was not due to death, because after their emigration from my study group, I regularly found them together in the range of a neighboring group. They eventually immigrated into this group, but it took some months for them to do so. During the time leading up to that emigration, these males would make periodic forays so far away from their group that I terminated their focal observations if they were more than 50m away from the group for fear that I would lose the group for the rest of the day. Emigrations occurred in another group during this time, as well, and those males were also not predated because they rejoined the group many months later, and one of my group was shadowed regularly enough by an extra-group male during this time that I dye-marked him. He did not eventually join the group. Therefore, it seems that the peak in male scent marking during this time is probably related to male migration events.

However, this was not the only period of male emigration during the year. Each of my study groups gained two immigrant males in February and one gained an immigrant male in June. Yet, there is no spike in scent marking behavior during this time, nor during the mating season. Perhaps, then, elevations in male marking behavior are a function of particular males and their own impending moves. Given my sample sizes, it may not be possible to know, but it could be that males who are going to emigrate are responsible for the spike in marking behavior. Or, it could be that male migration events are more threatening when infants are young, and males are more inclined to "defend" their core areas against potential immigrants during this time.

SUMMARY – ADULT SEX DIFFERENCES

This chapter has investigated and quantified intrinsic adult behavioral sex differences in agonism, affiliation, proximity, infant interest, and scent marking. Twenty-three statistically significant behavioral sex differences were identified (Tables 4-62 and 4-63).

TABLE 4-62. Summary of sex differences in adult intrinsic behaviors.

Intrinsic behavior	Sex Difference	Time effects	
Aggression	♀ +	·	·
Supplant	♀ +	·	·
Total # neighbors in contact	♀ +	·	·
Total # neighbors in reach	♀ +	·	·
Total # neighbors in 3m	♀ +	·	·
Time in contact with others	♀ +	·	♂ +
Time in reach of others	♀ +	♀ –	·
Time in 3m of others	♀ +	♀ +	♂ +
Time in 5m of others	♀ +	♀ +	♂ +
Antebrachial mark	♂ +	♂ –	
Brachial mark	♂ +	♂ –	
Anoint tail	♂ +	·	
Tail wave	♂ +	·	

Sex difference: + significantly greater
Time effects: + increase with time
– decrease with time
· no effect

TABLE 4-63. Summary of sex differences in bias in intrinsic behaviors toward each partner age/sex class.

Intrinsic behavior	Partner type	Sex-typed bias		Time effect	
Supplant	AM	·	♂ +	·	·
Grooming	AM	♀ –	·	·	·
Grooming	INFs	♀ +	·	♀ –	·
Time in contact	AF	♀ +	·	·	·
Time in 3m	AF	♀ +	·	♀ –	·
Time in contact	AM	♀ –	♂ +	♀ +	♂ –
Time in 3m	AM	♀ —	♂ –	·	♂ –
Time in contact	JM	♀ —	♂ –	·	·
Time in 3m	JM	·	♂ +	♀ +	·
Time in contact	INFs	·	♂ –	·	·

Sex-typed bias: + significantly more than expected at random
– significantly less than expected at random
— significantly less than –
· no difference from expected at random
Time effects: + increase with time
– decrease with time
· no effect

For a female dominant species, there are surprisingly few quantifiable sex differences in agonistic behavior, but sex differences in patterns of proximity to others are quite marked. Adult females are generally more agonistic toward others than adult males, but are also more spatially cohesive than adult males. Whether higher rates of agonism partially result from greater cohesion is a question for future research. Greater cohesion does not result in higher rates of affiliative interaction (grooming) overall. Instead, adult females bias their grooming toward young infants and away from adult males. Adult males are either constrained to or motivated to focus most of their supplanting behavior on other adult males. The following chapter will investigate which of these adult sex-typed behaviors become sexually differentiated in the subadult period and are therefore reasonable candidates for behaviors that might rely on the social environment for their development.

CHAPTER 5: INTRINSIC SUBADULT SEX DIFFERENCES

This chapter will investigate the development of adult sex-typed behaviors documented in the previous chapter. By limiting my investigation of juvenile sex differences to behaviors known to differ by sex in adults, it may seem that I assume that juvenile sex differences function only in preparation for adult behavioral roles. This is not the case. I recognize that some juvenile behaviors may function as preparatory for adult roles while other juvenile behaviors may serve to promote behavioral competence specific to life as a juvenile, and that the latter may also be sex-typed. I limit my investigation here to the investigation of the developmental components of adult sex-typed behaviors because I am interested, ultimately, in understanding how adult sex-typed behaviors develop and how selection acts on the developmental processes that produce adult sex-typed behavior.

AGONISM

As in the adult analyses, LMEMs are presented alone when they are the best fitting model according to AICc. When LMEMs are not the best-fitting model, their results are presented in conjunction with the best fit RP model. If an LMEM could not be fit, only the best fit RP model is presented.

Aggression

Rates of Aggression toward others

While adult females exhibit higher rates of overtly aggressive behavior than do adult males, there is no evidence of such a sex difference in either infants or juveniles (Table 5-1). Infants were only overtly aggressive on six occasions. While six aggressive events were directed by infant females at other infants (Figure 5-1), closer examination reveals that a single infant—08F(154)—was responsible for five of them. Qualitatively, three infants were noted to be generally more aggressive to their single infant groupmates and all of these were female, but they were also all of mothers of higher rank than the groupmate to which they were aggressive. The high rates of infant mortality in this sample, and the fact that infants only direct aggression toward other infants combined to create a low rate of occurrence of infant aggression from which no real conclusions about sex differences can be drawn. Juveniles also show no sex difference in rates of overt aggression (Table 5-1, Figure 5-2), and this is not an artifact of poor sampling.

TABLE 5-1. Model parameter estimates of overall rates of aggression directed by subadults.

Age	Variable	Model	Effect	est	SE	DF	t	p
INF	Aggression	random int LMEM	INT	0.00	0.02	26	0.00	1.00
			SEX	0.02	0.02	78	1.22	0.23
JUV	Aggression	mean RP	INT	0.14	0.05	7	3.13	0.02*
			SEX	0.12	0.07	7	1.78	0.12

INF = infant cohort; JUV = juvenile cohort; * $p \leq 0.05$. All tables follow these conventions.

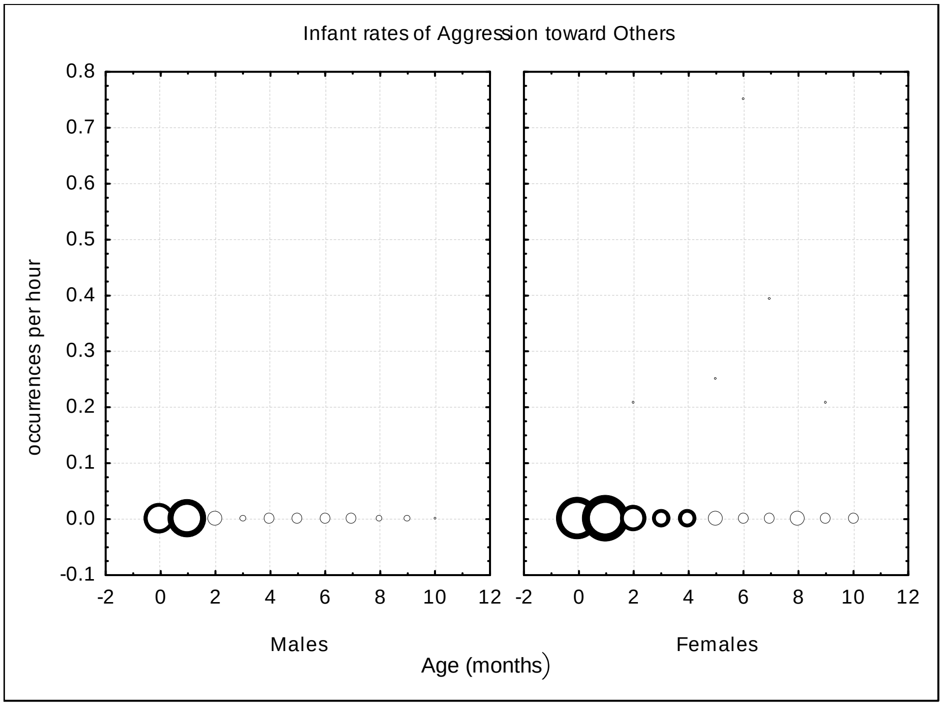


Fig. 5-1. Overall rates of aggression directed by infants toward others.

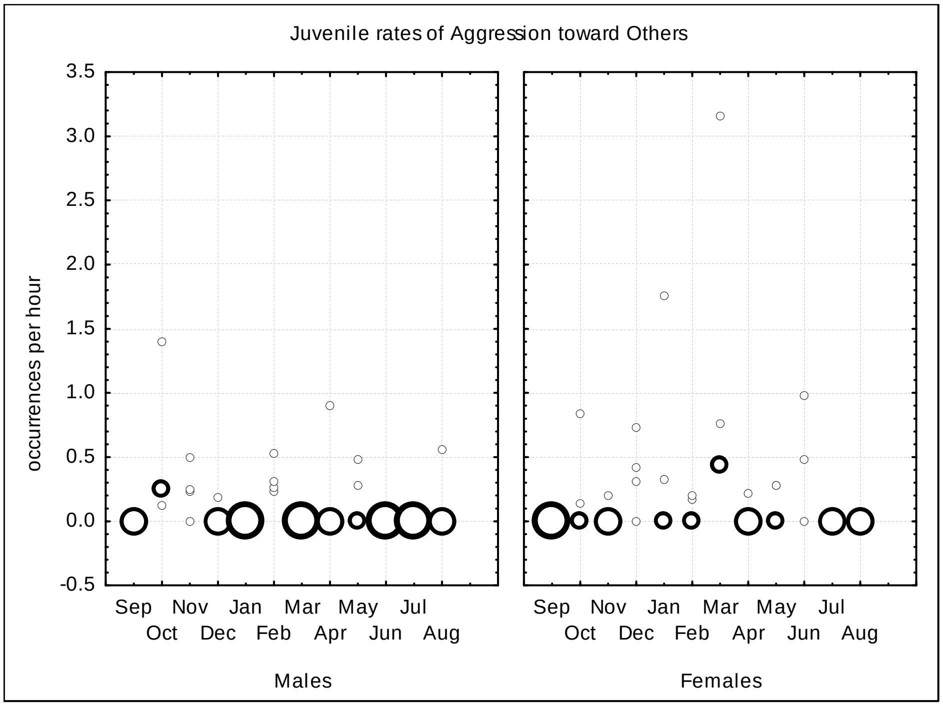


Fig. 5-2. Overall rates of aggression directed by juveniles toward others.

Non-aggressive dominance

Rates of supplanting others

While adult females supplant others more often than adult males do, neither infants nor juveniles exhibit this sex difference (Table 5-2, Figure 5-3, Figure 5-4). As with overt aggression, all seven instances of supplanting others were exhibited by female infants. In contrast to overt aggression, four different female infants supplanted others. Unfortunately, the pattern of surviving infants across groups left male infants in the sample with fewer age-mates than the female infants in the sample. Therefore, given that infants only supplant infants, a comparison of male and female infants may not be a fair one in this case. The juvenile analysis is not confounded by these sampling problems, but juveniles show no sex difference in rates of supplanting others (Table 5-2, Figure 5-4).

TABLE 5-2. Model parameter estimates of rates of supplanting others by subadults.

Age	Variable	Model	Effect	est	SE	DF	t	p
INF	Supplant	mean RP	INT	0.00	0.02	26	0.00	1.00
			SEX	0.04	0.02	26	1.62	0.12
JUV	Supplant	random int LMEM	INT	0.08	0.03	7	2.75	0.03*
			SEX	0.03	0.04	83	0.78	0.44

* $p \leq 0.05$

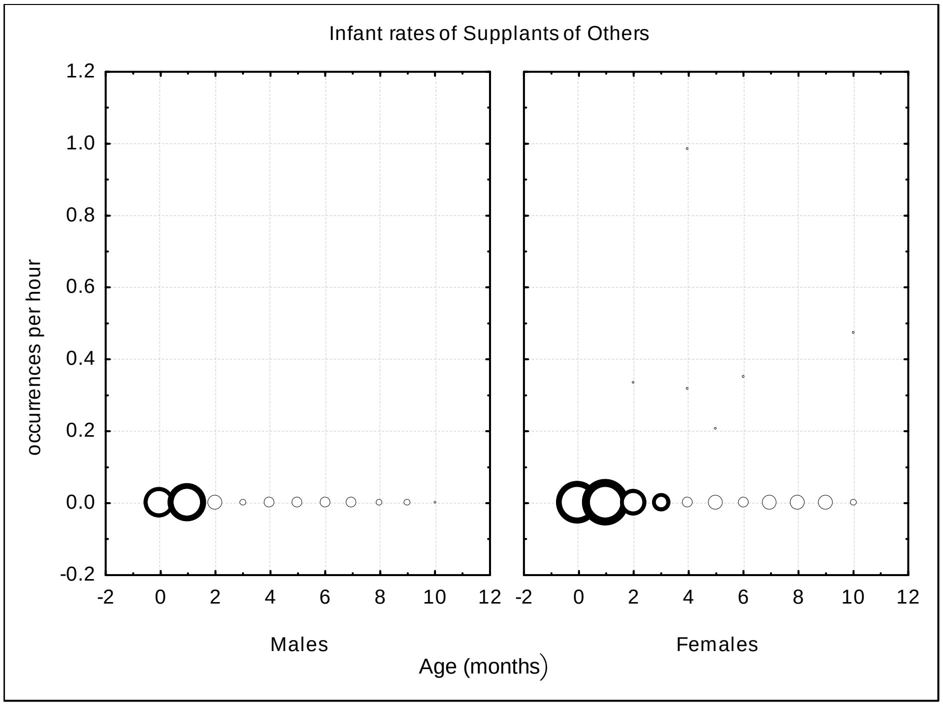


Fig. 5-3. Overall rates of supplants of others by infants.

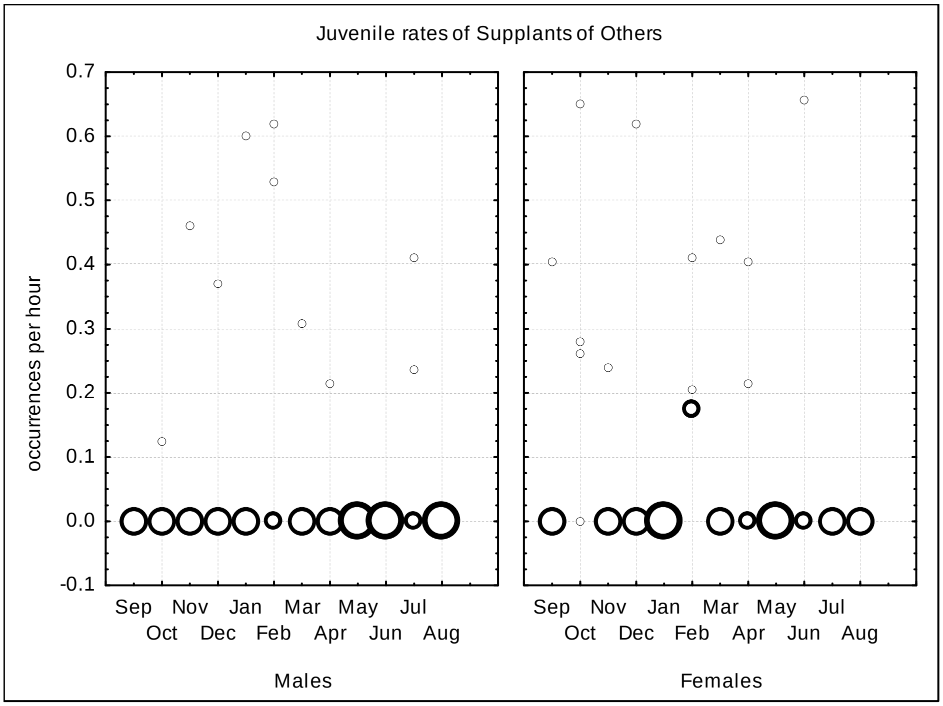


Fig. 5-4. Overall rates of supplants of others by juveniles.

Deviations from rates of supplanting juvenile females expected at random

While adult males supplant same-sex agemates more often than expected and adult females supplant opposite-sex agemates less often than expected, there is no evidence of subadult bias in distribution of supplanting behavior. However, these results are strongly constrained by the lack of choice in objects of subadult supplanting behavior. For infants, the particular distribution of surviving infants across groups resulted in their having no opportunity to choose the sex of the infant they supplanted, so analyses by sex were not performed. Juvenile females were in groups that offered them a choice between male and female age-mates, but juvenile males had no choice in the sex of juveniles available to them for supplanting (or any other behavioral interactions)—two males had only female peers available to them and the other two had only male peers. Given that juveniles do not supplant adults, choices of social partners available as targets of supplanting behavior were limited for juvenile males. In other words, the exhibition of a sex-bias on the part of juvenile males is constrained—the only way for juvenile males to exhibit a bias toward or away from supplanting peers would have been for them to bias their supplants away from or toward infants—to exhibit a cross age-group bias rather than just a within age-group sex bias. Nevertheless, juvenile females were not constrained thusly, and juveniles exhibited no sex differences the rates at which they biased their supplanting of juvenile females, juvenile males, or infants (Table 5-3).

TABLE 5-3. Model parameter estimates of deviations from expected juvenile rates of supplanting juveniles and infants.

Age	Variable	Model	Effect	est	SE	DF	t	p
JUV	Dev Supplant JF	random int LMEM	INT	0.02	0.02	7	0.85	0.42
			SEX	0.02	0.03	83	0.69	0.49
JUV	Dev Supplant JM	random int LMEM	INT	0.01	0.01	7	1.01	0.35
			SEX	0.01	0.02	83	0.31	0.76
JUV	Dev Supplant INFs	random int LMEM	INT	0.03	0.02	7	1.64	0.15
			SEX	0.00	0.02	83	-0.09	0.93

SUMMARY – AGONISM

There are no sex differences in intrinsic agonism before 24 months of age (Tables 5-4 and 5-5.). There are hints that female infants might be more agonistic toward other infants than infant males—a pattern very similar to that found by Gould [1990] at Berenty—but at present, the most reasonable conclusion is that these patterns are artifacts of small sample sizes of agonistic behaviors and are due more to individual differences than to sex differences. Juveniles exhibit no sex differences in agonism (Tables 5-4 and 5-5). In short, adult sex-differential patterns of agonism do not appear to have a subadult developmental component.

TABLE 5-4. Summary of sex differences in overall rates of agonism in subadults.

Age	Intrinsic Agonism	Sex Difference	Time effects	
INF	Aggression	·	·	·
INF	Supplant	·	·	·
JUV	Aggression	·	·	·
JUV	Supplant	·	·	·

Sex Difference: · no significant difference
Time effects: · no effect

TABLE 5-5. Summary of sex differences in bias of agonism toward each partner age/sex class in subadults.

Age	Intrinsic Agonism bias	Partner type	Sex-typed bias	Time effect
INF	Supplant bias	JF	n/a	
INF	Supplant bias	JM	n/a	
INF	Supplant bias	INFs	n/a	
JUV	Supplant bias	JF	· ·	· ·
JUV	Supplant bias	JM	· ·	· ·
JUV	Supplant bias	INFs	· ·	· ·

For Sex-typed bias: · no significant difference from that expected at random
For Time effects: · no effect

AFFILIATION

Grooming

Adult females bias their grooming time away from adult males. Since it is unclear whether a similar pattern in subadults would involve adult males or male peers, both were investigated.

Subadult deviations from time spent grooming adult males expected at random

Infants do not bias their grooming away from adult males, although the best fit linear RP model indicates that there is a time*sex interaction, with infant females spending less of their grooming time on adult males as the observation year progresses (Table 5-6, Figure 5-5). However, by the end of the observation year, there was only one surviving infant male (Figures 5-3 and 5-4), so sex differences that are related to the timing of behavior throughout the year in this cohort are unreliable and should not be seriously considered.

Juveniles, on the other hand, show a clear sex difference in the distribution of their grooming time of adult males, with both fit models indicating that juvenile females bias their grooming away from adult males significantly more than juvenile males do (Table 5-6, Figure 5-6).

This sex difference justifies investigating juvenile patterns of grooming adult males by sex. Results from LMEM and RP models for each sex are not in complete agreement (Table 5-6). The random intercept LMEMs indicate that juvenile females groom adult males significantly less than expected at random but that juvenile males groom adult males at expected rates. In contrast, mean RP models suggest that juvenile females only tend to groom adult males less than expected at random, but that juvenile males groom adult males significantly less than expected random (Table 5-6). As usual with conflicting results between the LMEM and RP models, I preferentially accept the LMEM results, because these analyses account for inter-individual variation. Furthermore, a visual examination of the individual OLS regressions (Figure 5-7) supports the interpretation that, on average, juvenile females spend less time than expected grooming adult males but that juvenile males groom adult males as expected at random.

TABLE 5-6. Model parameter estimates of deviations from expected time spent grooming adult males by subadults.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	Dev Groom AM	linear RP	INT	-0.02	0.01	28	-1.69	0.10†
			TIME	0.00	0.01	77	0.33	0.74
			SEX	0.01	0.02	28	0.77	0.45
			TIME*SEX	-0.05	0.01	77	-5.39	<.0001*
JUV	Dev Groom AM	random int LMEM	INT	-0.05	0.08	7	-0.64	0.54
			SEX	-0.40	0.12	83	-3.41	0.001*
		mean RP	INT	-0.17	0.04	7	-3.94	0.006*
			SEX	-0.25	0.06	7	-4.05	0.005*
	JF Dev Groom AM	random int. LMEM	INT	-0.45	0.09	3	-5.27	0.01*
		mean RP	INT	-0.09	0.03	3	-2.78	0.07†
	JM Dev Groom AM	random int. LMEM	INT	-0.05	0.08	4	-0.61	0.57
		mean RP	INT	-0.10	0.02	4	-5.12	0.007*

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

Fig. 5-5. Deviations from expected time spent grooming adult males by infants.

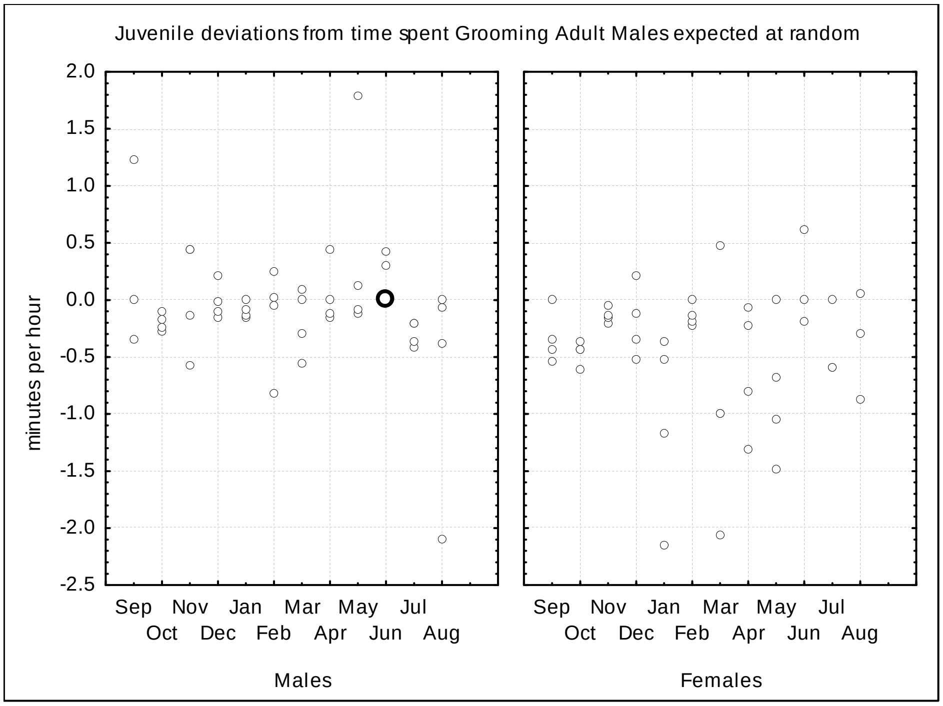


Fig. 5-6. Deviations from expected time spent grooming adult males by juveniles.

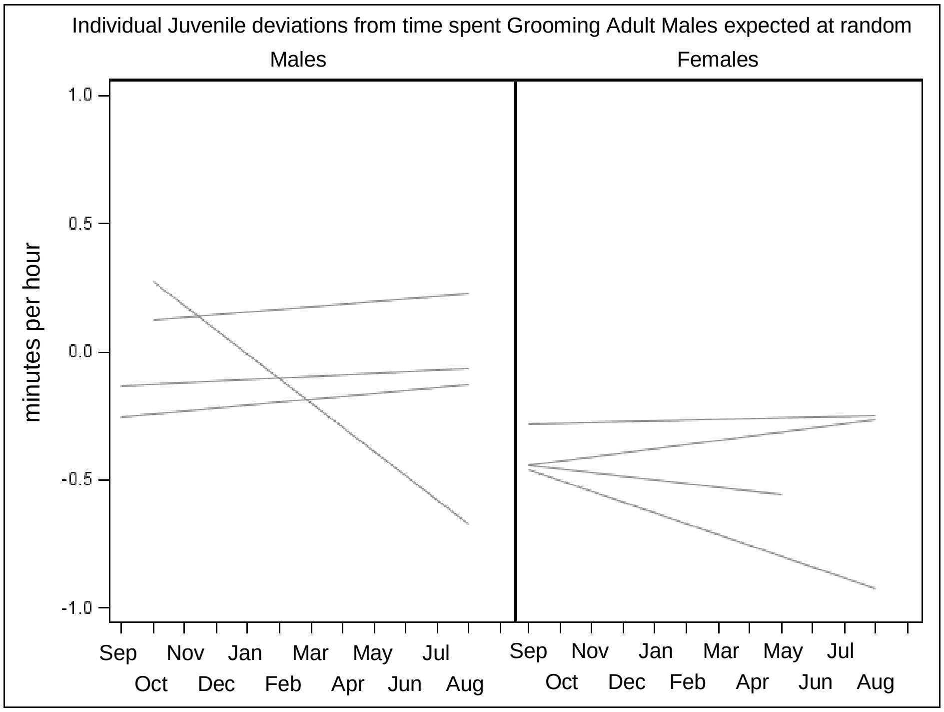


Fig. 5-7. Individual ordinary least squares regressions of deviations from expected time spent grooming adult males by juveniles.

Subadult deviations from time spent grooming juvenile females expected at random

Infants do not bias their grooming toward or away from juvenile females (Table 5-7, Figure 5-8), but juvenile females bias their grooming away from other juveniles females significantly more than juvenile males do (Table 5-7, Figure 5-9). This sex difference justifies investigating patterns of grooming juvenile females by sex. According to analyses by sex, juvenile females bias their grooming significantly away from juvenile females while juvenile males tend to bias their grooming away from juvenile females at the beginning of the observation year but tend to do less so as the observation year progresses (Table 5-7). It is important to note that although these analyses find statistically significant sex difference for this variable, the amount of bias found here is very, very small compared to the degree of negative grooming bias juvenile females exhibit toward adult males. In fact, they are comparable to the deviations from expected found in the following analysis of grooming juvenile males (Table 5-8), in which no significant differences were found.

TABLE 5-7. Model parameter estimates of deviations from expected time spent grooming juvenile females by subadults.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	Dev Groom JF	random int. LMEM	INT	-0.01	0.03	28	-0.50	0.62
			SEX	0.04	0.04	79	1.20	0.24
INF	Dev Groom JF	mean RP	INT	0.00	0.00	28	-0.49	0.63
			SEX	0.00	0.00	28	0.18	0.86
JUV	Dev Groom JF	mean RP	INT	-0.02	0.01	7	-2.07	0.08†
			SEX	-0.03	0.01	7	-3.22	0.01*
	JF Dev Groom JF	mean RP	INT	-0.02	0.00	3	-3.35	0.04*
	JM Dev Groom JF	linear LMEM	INT	-0.06	0.02	4	-2.46	0.07†
			TIME	0.01	0.00	41	1.71	0.09†

$*\ p \leq 0.05$; † $0.05 < p \leq 0.10$

Fig. 5-8. Deviations from expected time spent grooming juvenile females by infants.

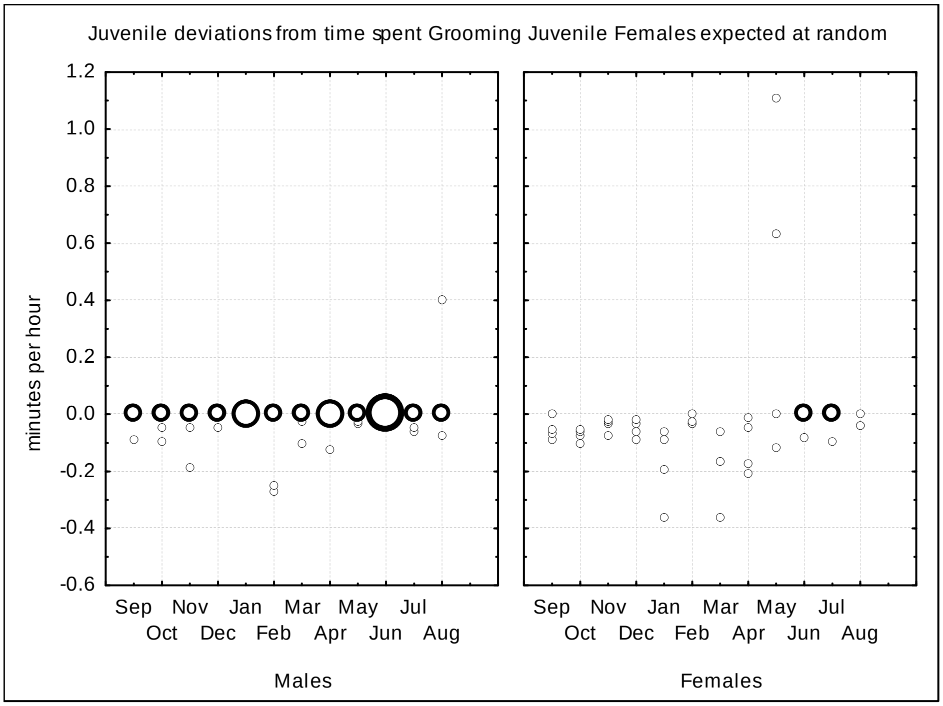


Fig. 5-9. Deviations from expected time spent grooming juvenile females by other juveniles.

Subadult deviations from time spent grooming juvenile males expected at random

Infants show no significant sex difference in their bias in grooming juvenile males (Table 5-8, Figure 5-10). According to the best fit random intercept model, juveniles also show no significant sex difference in their bias in grooming juvenile males, but according to the best fit mean RP model, juvenile females more strongly bias their grooming away from juvenile males than juvenile males do (Table 5-8, Figure 5-11). As with most instances of disagreement between the LMEM and RP models, I preferentially accept the results of the LMEM because it partially accounts for inter-individual variation. An investigation of the individual OLS regressions for this variable (Figure 5-12) also does not support an interpretation that juvenile females, as a group, bias their grooming away from juvenile males more strongly than do juvenile males.

TABLE 5-8. Model parameter estimates of deviations from expected time spent grooming juvenile males by subadults.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	Dev Groom JM	mean RP	INT	0.00	0.00	28	-2.23	0.03*
			SEX	0.00	0.00	28	1.70	0.10†
JUV	Dev Groom JM	random int. LMEM	INT	-0.04	0.03	7	-1.27	0.24
			SEX	0.01	0.04	83	0.26	0.80
		mean RP	INT	0.00	0.01	7	-0.36	0.73
			SEX	-0.02	0.01	7	-3.40	0.01*

* $p \leq 0.05$

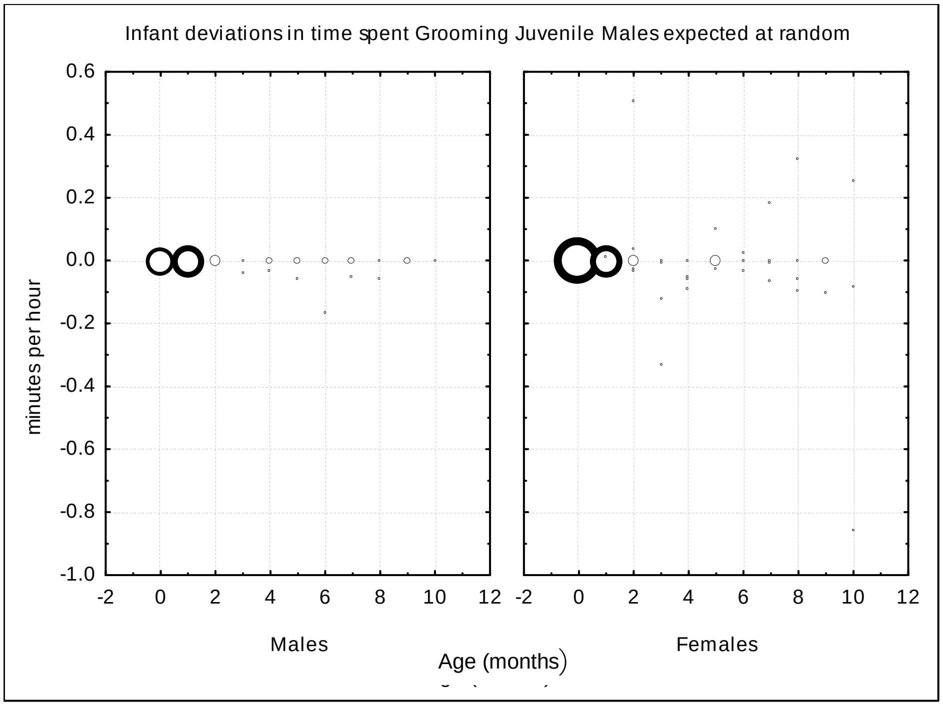


Fig. 5-10. Deviations from expected time spent grooming juvenile males by infants.

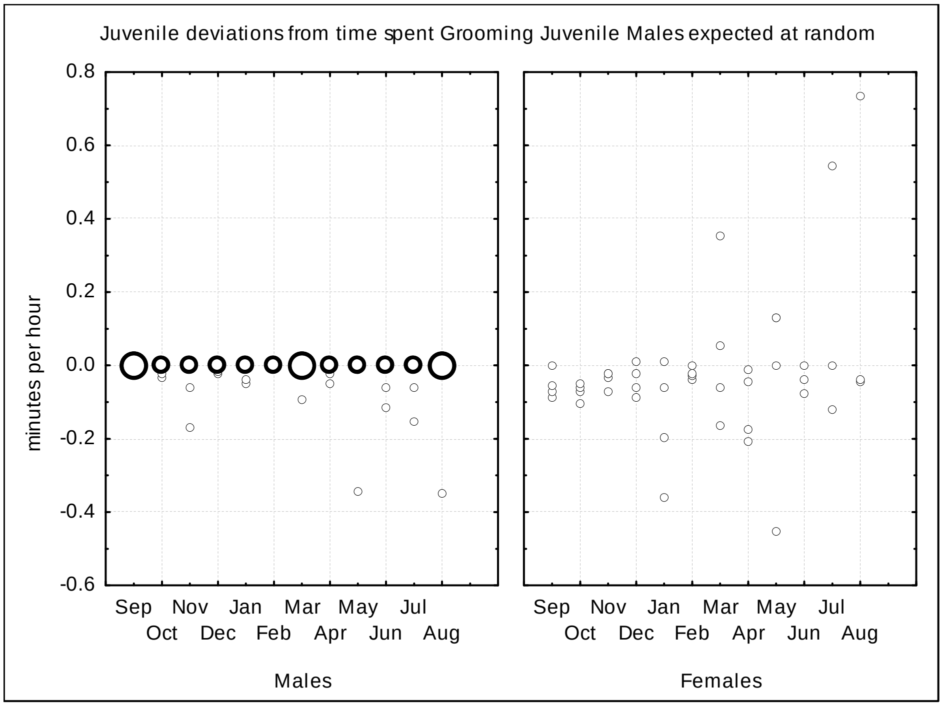


Fig. 5-11. Deviations from expected time spent grooming juvenile males by other juveniles.

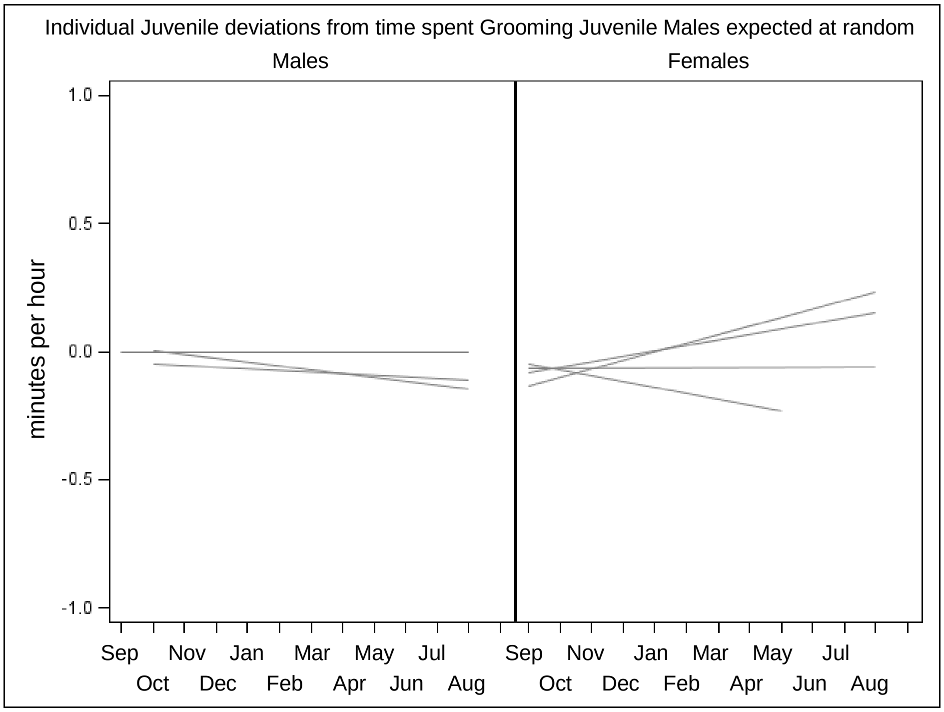


Fig. 5-12. Individual ordinary least squares regressions of deviations from expected time spent grooming juvenile males by other juveniles.

Subadult deviations from time spent grooming infants expected at random

Adult females bias their grooming toward infants of young ages while adult males show no such bias. Infants show no clear sex difference in biasing their grooming toward or away from infants (Table 5-9, Figure 5-13). Juveniles exhibit a sex difference similar to the adult sex difference, with juvenile females biasing their grooming much more strongly toward infants than juvenile males do (Table 5-9, Figure 5-14). Analyses by sex indicate that juvenile females bias their grooming significantly toward infants while juvenile males bias their grooming time significantly away from infants (Table 5-9).

TABLE 5-9. Model parameter estimates of deviations from expected time spent grooming infants by subadults.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	Dev Groom INFs	mean RP	INT	0.00	0.00	28	0.28	0.78
			SEX	-0.01	0.00	28	-1.64	0.11
JUV	Dev Groom INFs	mean RP	INT	-0.05	0.03	7	-1.69	0.14
			SEX	0.10	0.04	7	2.50	0.04*
	JF Dev Groom INFs	mean RP	INT	0.22	0.03	3	7.01	0.006*
	JM Dev Groom INFs	mean RP	INT	-0.04	0.01	4	-2.78	0.05*

* p ≤ 0.05

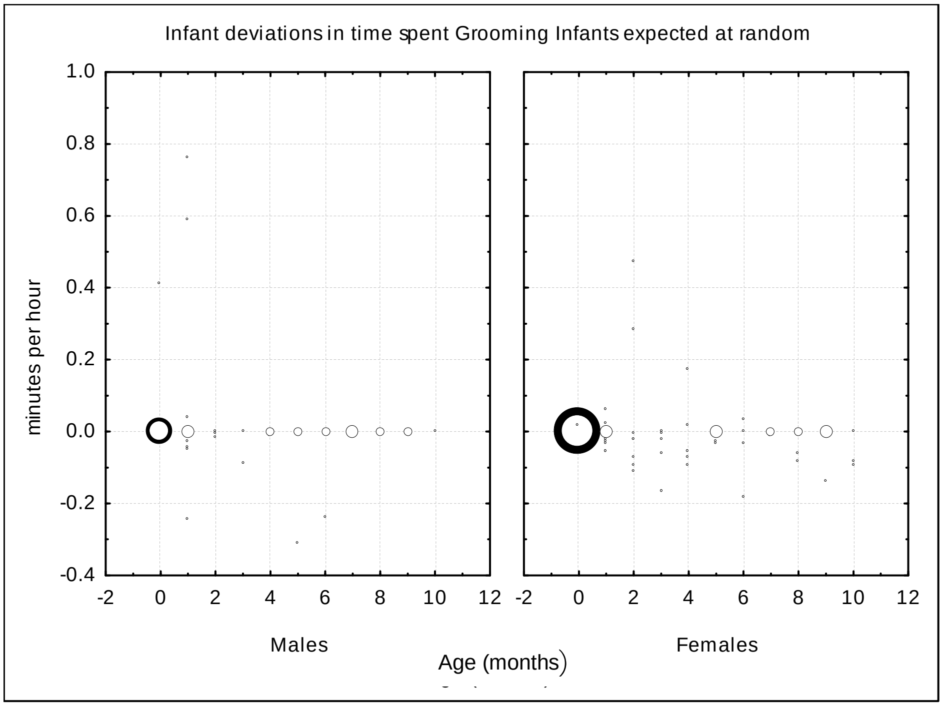


Fig. 5-13. Deviations from expected time spent grooming infants by other infants.

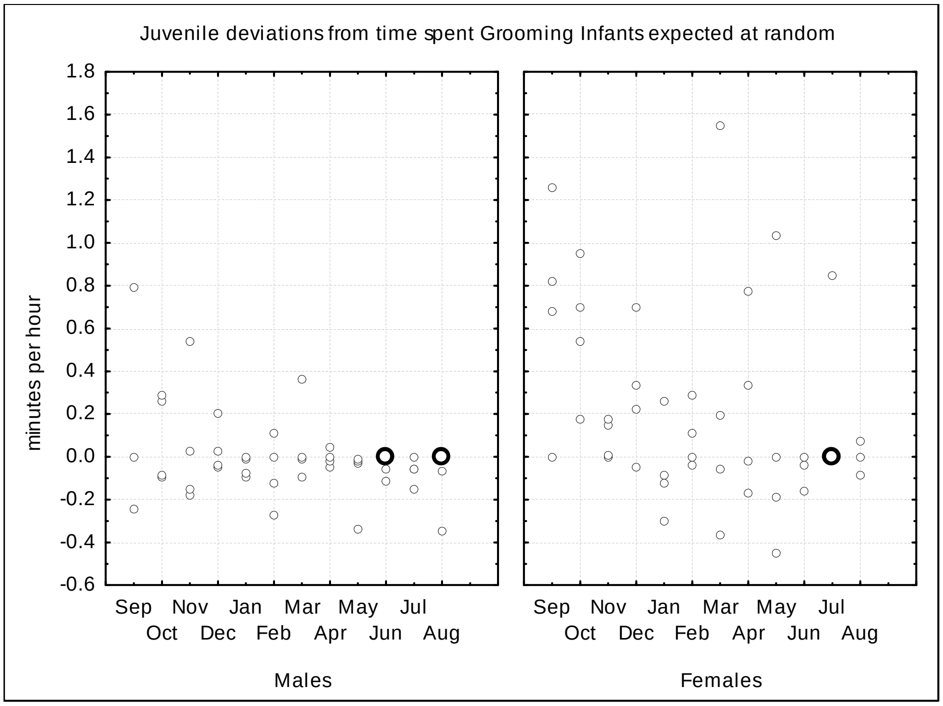


Fig. 5-14. Deviations from expected time spent grooming infants by juveniles.

Summary – Affiliation

Infants do not exhibit any clear sex differences in the rates at which they groom others (Tables 5-10, 5-11). It is important to recall that, due to exceptionally high mortality in the infant cohort, these results are effectively derived primarily from a robust cross-sectional sample of infants from ages 0-2 months and a small longitudinal sample of infants from 3-11 months, of which only 3 were male. One of these males was unusual because his mother was very ill, she had weaned him completely by 3 months of age, and, at times, she tended not even to maintain contact with him or to allow him to maintain contact with her. As a result, these data cannot be relied upon to accurately characterize the sex-typed behavior of infants at later ages. Therefore, any significant sex*time interactions in the infant cohort are not considered.

Juveniles, on the other hand, exhibit clear sex differences in grooming behavior that echo those seen in adults. Like adult females, juvenile females spend less time than expected at random grooming adult males and more time than expected grooming infants, with no other strong or clear biases in grooming behavior toward or away from other age/sex classes (Tables 5-10, 5-11). Also as in adults, whether or not juveniles exhibit a sex difference in overall time spent grooming is unclear (Table 5-12, Figure 5-15), but any sex difference in total time spent grooming is probably driven largely by the sex difference in time spent grooming infants.

TABLE 5-10. Summary of sex differences in overall rates of affiliation in subadults.

Age	Intrinsic affiliative behavior	Sex Difference	Time effects	
INF	Grooming overall	·	·	·
JUV	Grooming overall	♀ + ?	·	·

Sex difference: + significantly greater
? equivocal result
· no difference
Time effects: · no effect

TABLE 5-11. Summary of sex differences in bias of affiliation toward each partner age/sex class in subadults.

Intrinsic affiliative bias	Age	Partner type	Sex-typed bias		Time effect	
Grooming	INF	AM	·	·	♀ –	?
		JF	·	·	·	·
		JM	·	·	·	·
		INFs	·	·	·	·
	JUV	AM	♀ –	·	·	·
		INFs	♀ +	♂ –	·	·

Sex-typed bias: + significantly more than expected at random
– significantly less than expected at random
· no difference from expected at random
Time effects: – decrease with time
? equivocal result
· no effect

TABLE 5-12. Model parameter estimates of total time spent grooming by juveniles.

Age	Variable	Model	Effect	est.	SE	DF	t	p
JUV	Groom	random int. LMEM	INT	0.96	0.23	7	4.12	0.004*
			SEX	0.56	0.33	83	1.67	0.10†
		mean RP	INT	0.42	0.13	7	3.29	0.01*
			SEX	0.42	0.18	7	2.35	0.05*

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

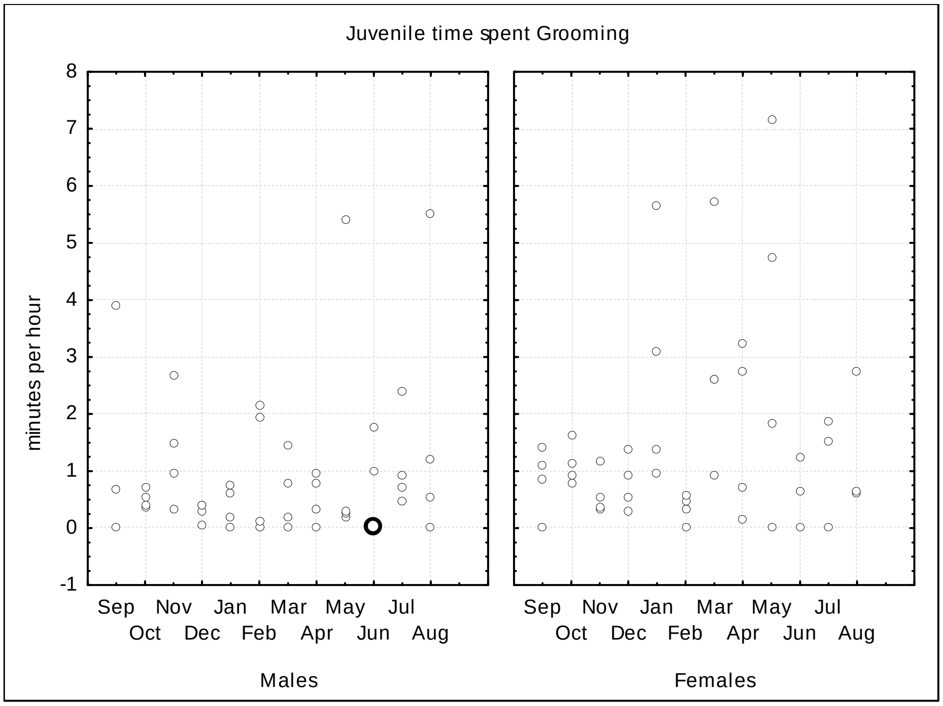


Fig. 5-15. Overall time spent grooming by juveniles.

PROXIMITY

Average number of neighbors in proximity – contact, within reach, and within 3m

Adult females have more neighbors in proximity per scan at all distances than adult males do. Additionally, adult females spent less time in contact with and within reach of others and more time within 3m of others throughout the observation year. In contrast, no pattern of overall sex-differential space use is found in subadults.

There are no significant sex differences or significant sex*time interactions in overall proximity patterns for infants or juveniles, and only a tendency for juvenile females to have more individuals within reach than juvenile males (Table 5-13, Figures 5-16 - 5-22). As in other analyses, time*sex interactions for infants are not considered, because the infant male sample is so small after the first quadrant of the observation year.

Infant proximity patterns are strongly marked by temporal trends related to maturation in which infants have fewer neighbors in contact and within reach (but not within 3m) as time progresses, but slightly more, again, in contact toward the end of the observation year. In other words, infants become less cohesive through time overall, as one would expect, and resembling the temporal pattern of reduced cohesion exhibited by adult females throughout the observation year.

Juvenile contact patterns are also marked by temporal trends in which juveniles seem to have more neighbors in contact at the beginning of the observation year, fewer in the middle, and more at the end of the observation year, but there are no significant temporal trends in the number of neighbors at other proximities (Table 5-13).

TABLE 5-13. Model parameter estimates of number of neighbors in proximity to subadults.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	# neighbors in contact	random int. LMEM	INT	0.71	0.09	25	8.34	<.0001*
			SEX	-0.10	0.12	78	-0.87	0.39
		quadratic RP	INT	1.08	0.07	25	15.20	<.0001*
			SEX	-0.12	0.09	25	-1.27	0.21
			TIME	-0.30	0.05	74	-6.32	<.0001*
			TIME^2	0.03	0.01	74	4.83	<.0001*
			SEX*TIME	0.07	0.06	74	1.17	0.24
			SEX*TIME^2	-0.01	0.01	74	-1.47	0.15
JUV	# neighbors in contact	quadratic LMEM	INT	0.36	0.08	7	4.77	0.002*
			SEX	0.13	0.11	73	1.25	0.22
			TIME	-0.09	0.03	6	-3.57	0.01*
			TIME^2	0.01	0.00	73	3.46	0.0009*
			SEX*TIME	-0.02	0.04	73	-0.50	0.62
			SEX*TIME^2	0.00	0.00	73	0.63	0.53
		mean RP	INT	0.06	0.03	7	2.09	0.08†
			SEX	-0.02	0.04	7	-0.45	0.66
INF	# neighbors in reach	random int. LMEM	INT	0.61	0.08	25	7.73	<.0001*
			SEX	-0.15	0.11	78	-1.38	0.17
		linear RP	INT	0.62	0.09	25	7.23	<.0001*
			TIME	-0.06	0.01	76	-4.69	<.0001*
			SEX	-0.15	0.11	25	-1.36	0.19
			TIME*SEX	0.03	0.02	76	1.70	0.09†
JUV	# neighbors in reach	random int. LMEM	INT	0.21	0.04	7	5.78	0.0007*
			SEX	0.09	0.05	83	1.78	0.08†
		mean RP	INT	0.06	0.02	7	2.59	0.04*
			SEX	0.05	0.03	7	1.71	0.13
INF	# neighbors in 3m	mean RP	INT	2.76	0.18	25	15.48	<.0001*
			SEX	-0.03	0.23	25	-0.14	0.89
JUV	# neighbors in 3m	random int. LMEM	INT	2.49	0.17	7	14.32	<.0001*
			SEX	0.13	0.25	83	0.54	0.59
		mean RP	INT	1.28	0.26	7	4.86	0.002*
			SEX	-0.11	0.38	7	-0.29	0.78

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

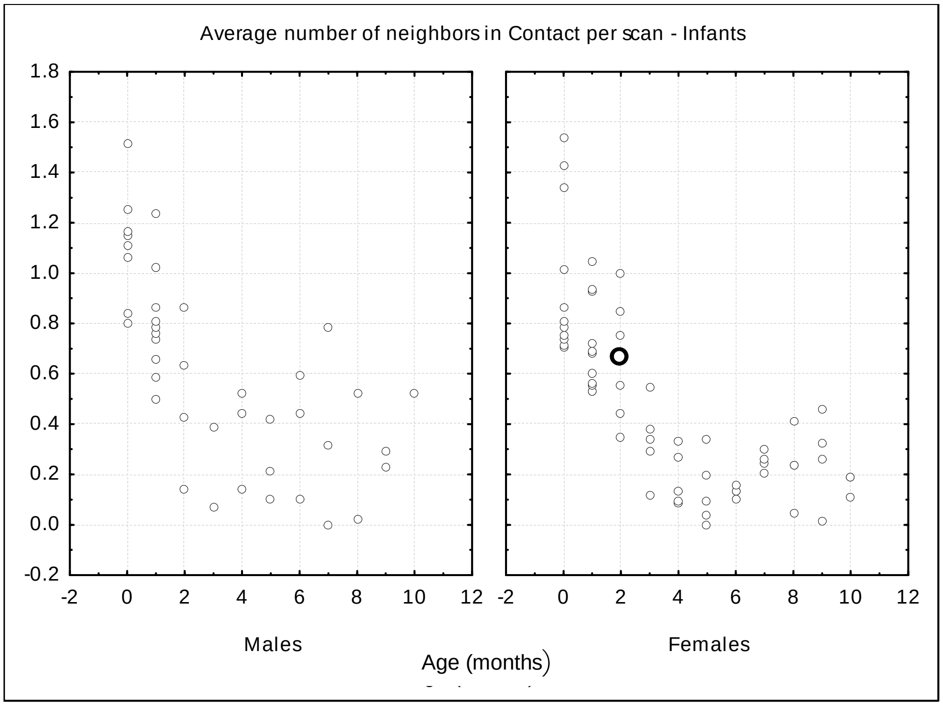


Fig. 5-16. Average number of neighbors in contact with infants per scan.

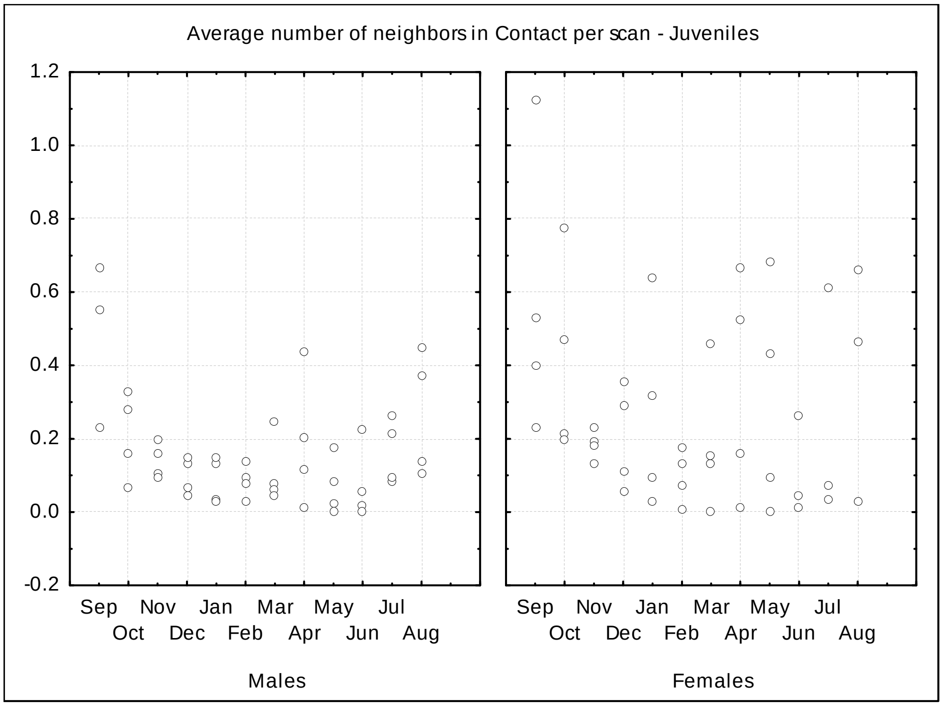


Fig. 5-17. Average number of neighbors in contact with juveniles per scan.

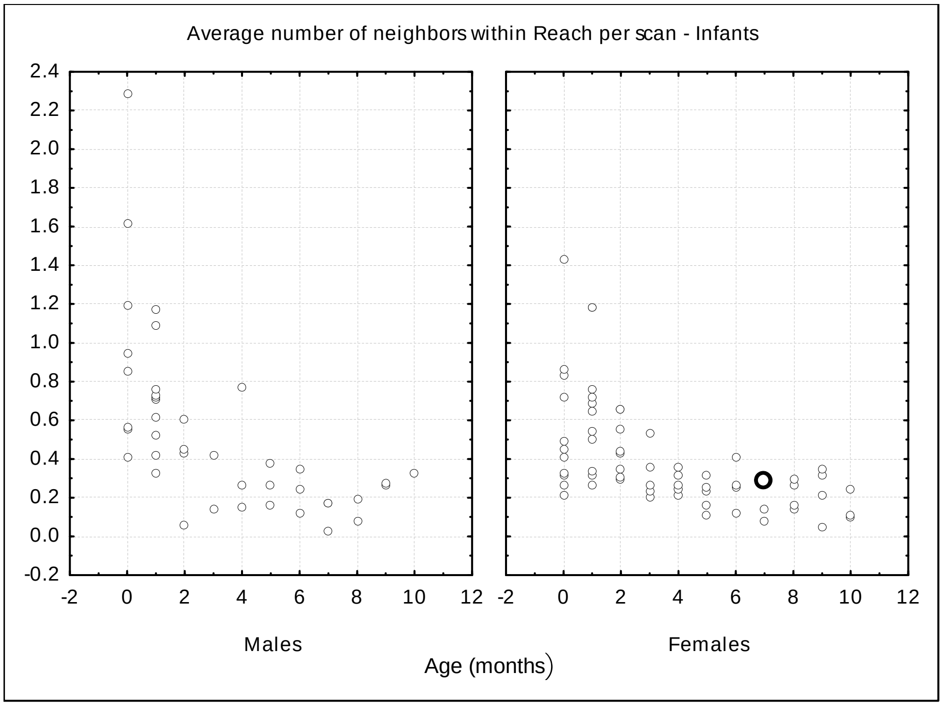


Fig. 5-18. Average number of neighbors within reach of infants per scan.

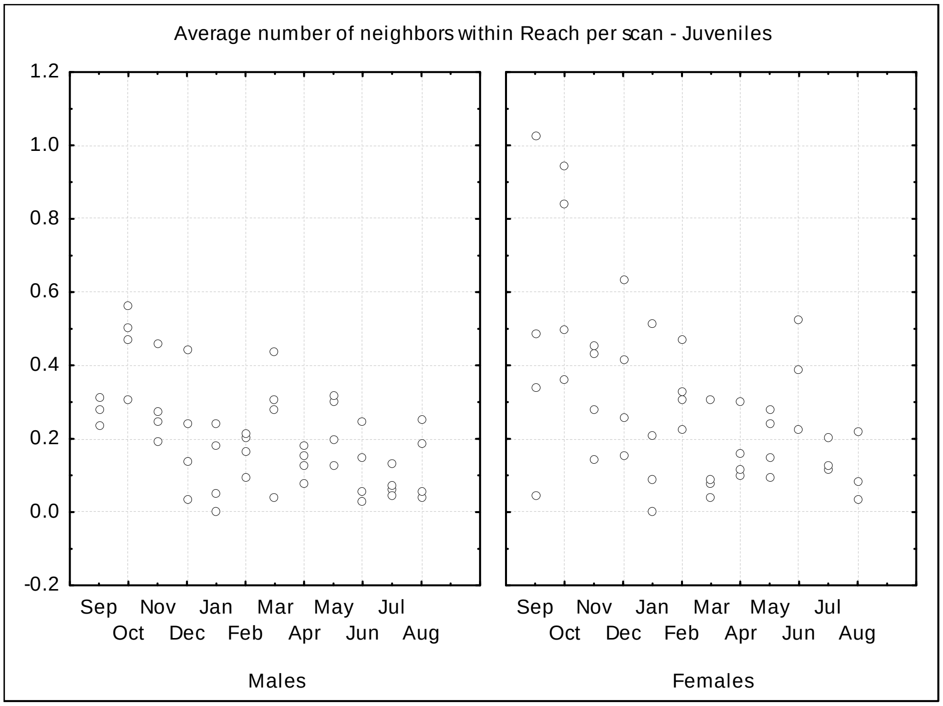


Fig. 5-19. Average number of neighbors within reach of juveniles per scan.

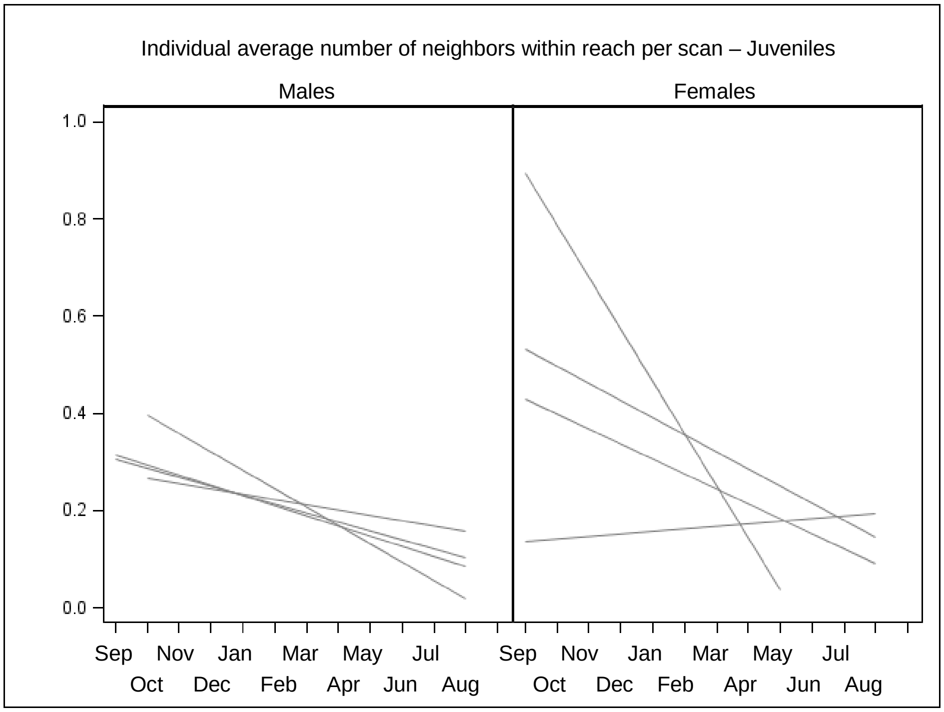


Fig. 5-20. Individual ordinary least squares regressions of number of individuals within reach of juveniles per scan.

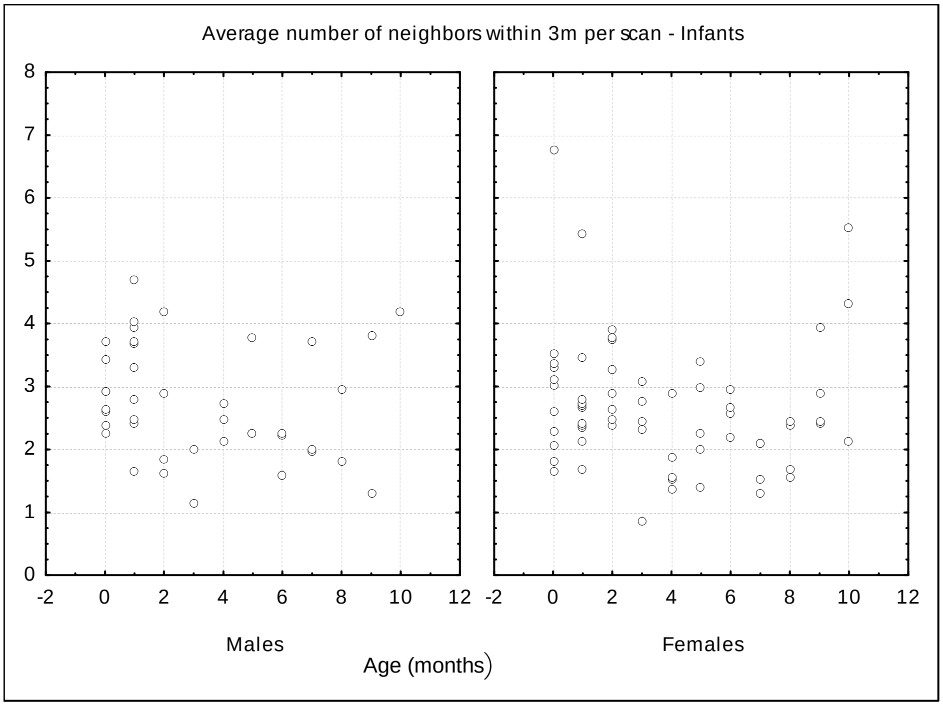


Fig. 5-21. Average number of neighbors within 3 meters of infants per scan.

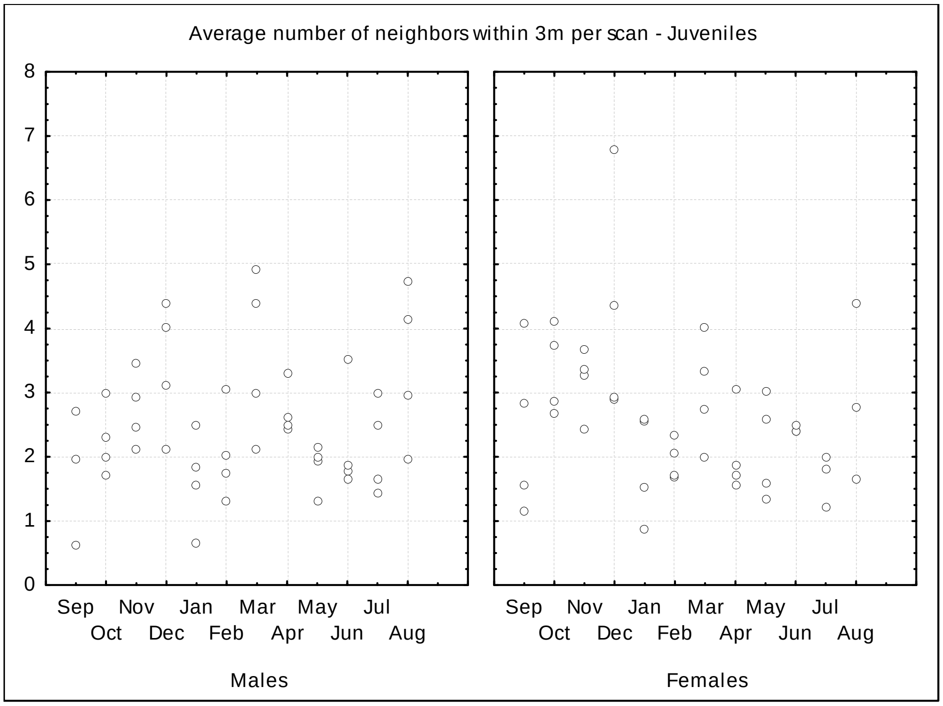


Fig. 5-22. Average number of neighbors within 3 meters of juveniles per scan.

Average number of scans per hour in proximity – contact, within reach, within 3m, within 5m

Adult females spend more time in proximity to other individuals than adult males at all distances. In addition, adult females spend more time in contact with and within reach to other individuals early in the year and less as the year progresses, while males increase their contact time throughout the year and remain fairly constant in their time within reach of others.

In contrast, there are no sex differences in the number of scans spent in contact with others, within reach of others, within 3m of others, or within 5m of others for infants or juveniles (Table 5-14; Figures 5-23 through 5-30). There is only a tendency for juvenile females to spend more time in contact with others than juvenile males. As with other analyses, infant time*sex interactions are not considered due to problems with sample sizes after the first quarter of the observation year. As with the number of neighbors at different proximity levels, above, there are significant temporal trends in the amount of time spent in proximity to others. As the observation year progresses, infants spend significantly less time in proximity to others at all distances, and juveniles spend significantly less time in contact with, within reach of, and within 3m of others. These patterns in infants and juveniles resemble adult female temporal proximity patterns and not those of adult males.

TABLE 5-14. Model parameter estimates of time in proximity to others for subadults.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	Time in contact	random int. LMEM	INT	12.79	1.58	25	8.11	<.0001*
			SEX	-0.76	2.15	78	-0.35	0.72
		quadratic RP	INT	19.05	0.41	25	46.41	<.0001*
			SEX	0.54	0.54	25	0.99	0.33
			TIME	-4.71	0.41	74	-11.59	<.0001*
			$TIME^2$	0.34	0.04	74	8.37	<.0001*
			SEX*TIME	-0.50	0.52	74	-0.95	0.34
			$SEX*TIME^2$	0.02	0.05	74	0.38	0.70
JUV	Time in contact	random int. LMEM	INT	2.84	0.51	7	5.54	0.0009*
			SEX	1.35	0.73	83	1.84	0.07†
		quadratic RP	INT	5.81	0.99	7	5.88	0.0006*
			SEX	1.55	1.38	7	1.12	0.30
			TIME	-1.46	0.36	79	-4.01	0.0001*
			$TIME^2$	0.12	0.03	79	3.88	0.0002*
			SEX*TIME	-0.02	0.50	79	-0.03	0.97
			$SEX*TIME^2$	0.00	0.04	79	-0.06	0.96
INF	Time in reach	quadratic LMEM	INT	8.87	0.76	25	11.74	<.0001*
			SEX	-0.87	1.02	58	-0.86	0.39
			TIME	-1.91	0.38	16	-4.97	0.0001*
			$TIME^2$	0.13	0.04	58	3.21	0.002*
			SEX*TIME	0.91	0.47	58	1.95	0.06†
			$SEX*TIME^2$	-0.08	0.05	58	-1.57	0.12
		linear RP	INT	8.07	0.72	25	11.26	<.0001*
			TIME	-0.73	0.18	76	-4.07	0.0001*
			SEX	-0.58	0.97	25	-0.60	0.56
			TIME*SEX	0.25	0.23	76	1.09	0.28
JUV	Time in reach	linear RP	INT	4.77	0.51	7	9.40	<.0001*
			TIME	-0.32	0.06	81	-5.13	<.0001*
			SEX	0.84	0.72	7	1.17	0.28
			TIME*SEX	0.02	0.09	81	0.28	0.78

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

TABLE 5-14. Continued.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	Time in 3m	random int. LMEM	INT	15.35	0.32	25	48.28	<.0001*
			SEX	0.78	0.41	78	1.92	0.06†
		mean RP	INT	15.36	0.40	25	37.94	<.0001*
			SEX	0.83	0.53	25	1.56	0.13
JUV	Time in 3m	linear RP	INT	15.73	0.40	7	39.02	<.0001*
			SEX	0.48	0.58	7	0.84	0.43
INF	Time in 5m	random int. LMEM	INT	19.63	0.16	25	120.80	<.0001*
			SEX	0.04	0.22	78	0.19	0.85
		linear RP	INT	19.98	0.18	25	114.06	<.0001*
			TIME	-0.15	0.04	76	-3.55	0.0007*
			SEX	-0.01	0.23	25	-0.06	0.95
			TIME*SEX	0.05	0.05	76	0.91	0.37
JUV	Time in 5m	random int. LMEM	INT	18.52	0.22	7	83.03	<.0001*
			SEX	0.28	0.32	83	0.87	0.39
		linear RP	INT	18.96	0.18	7	105.82	<.0001*
			SEX	0.04	0.26	7	0.15	0.88

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

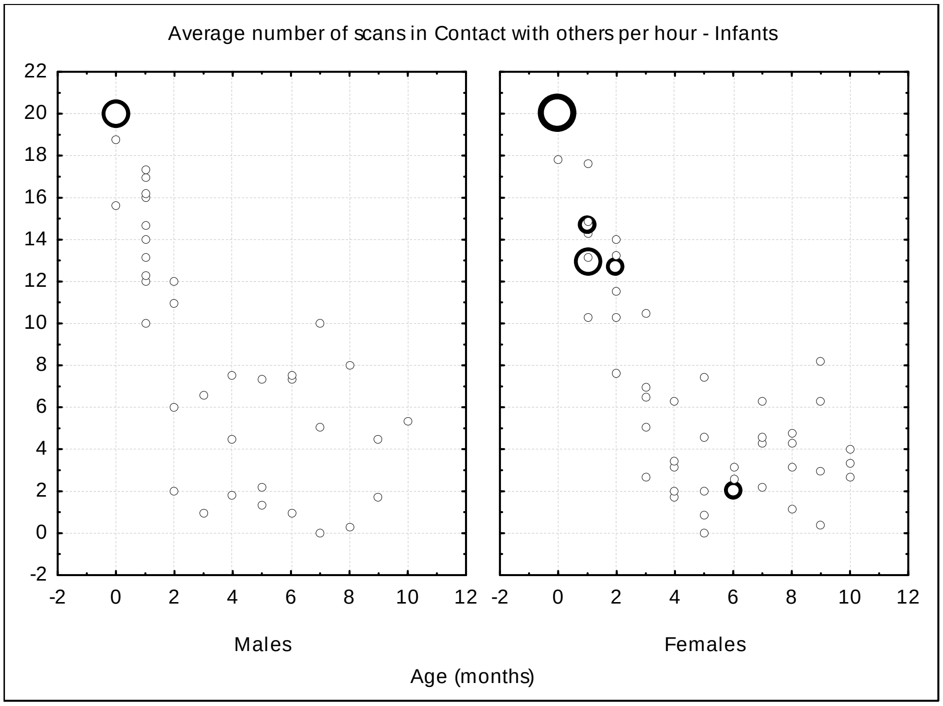


Fig. 5-23. Average infant time in contact with others.

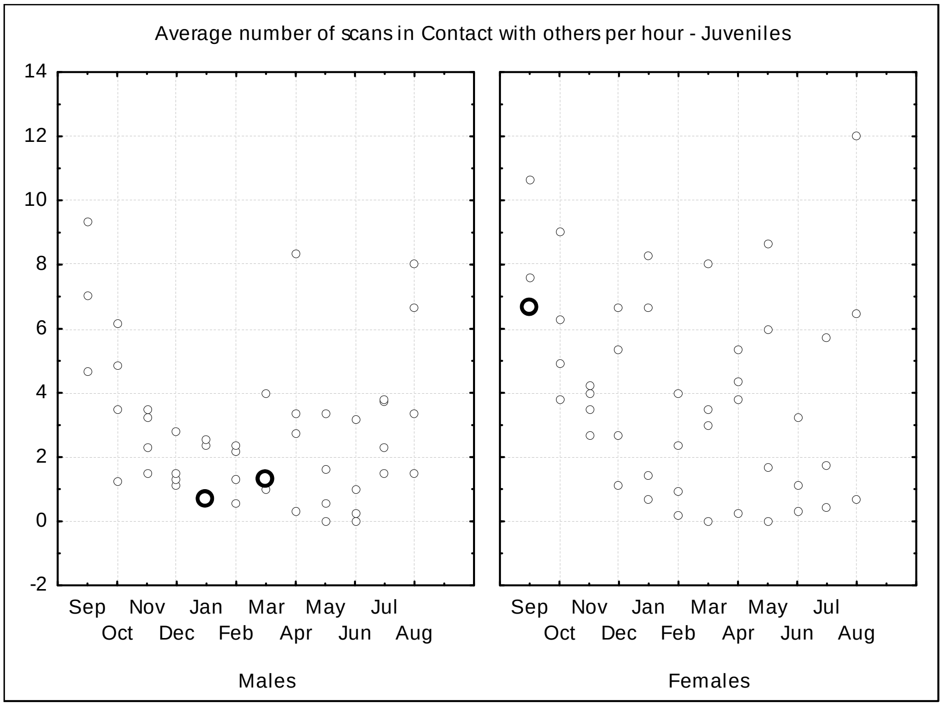


Fig. 5-24. Average juvenile time in contact with others.

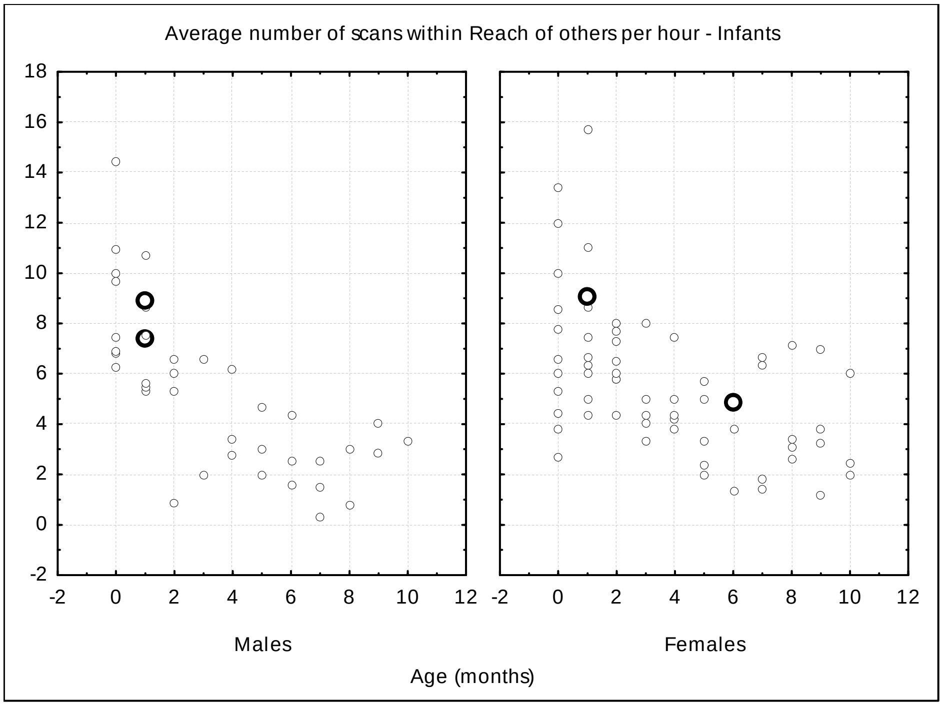


Fig. 5-25. Average infant time within reach of others.

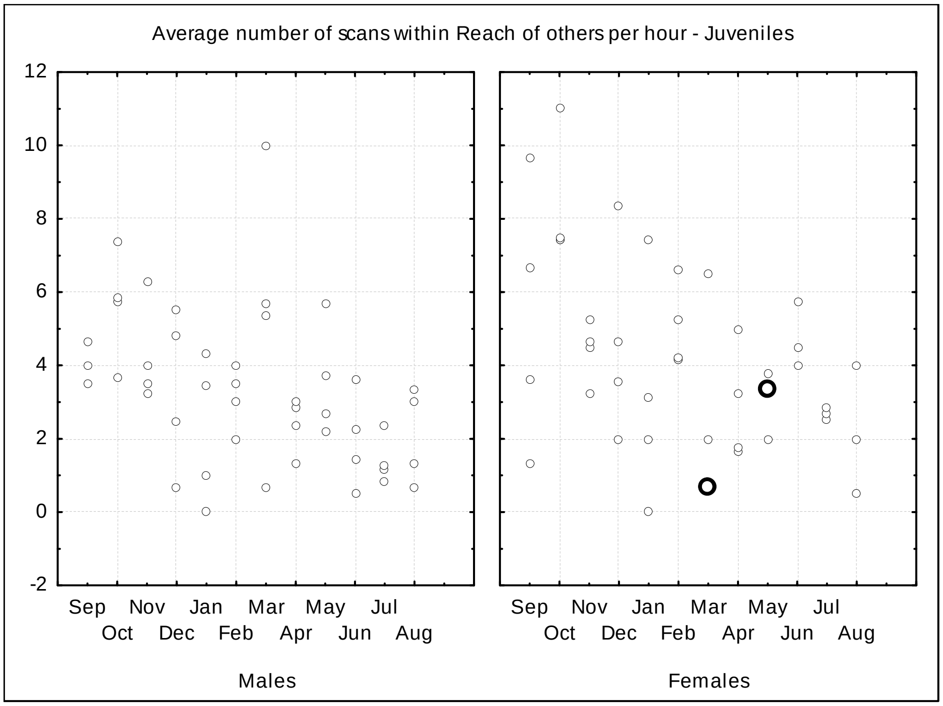


Fig. 5-26. Average juvenile time within reach of others.

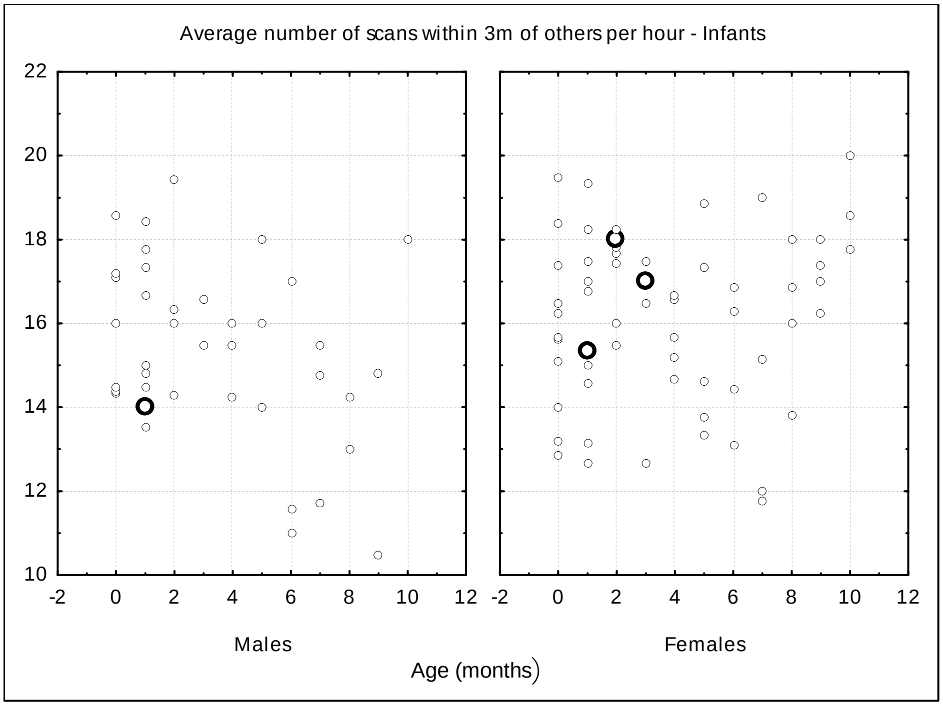


Fig. 5-27. Average infant time within 3m of others.

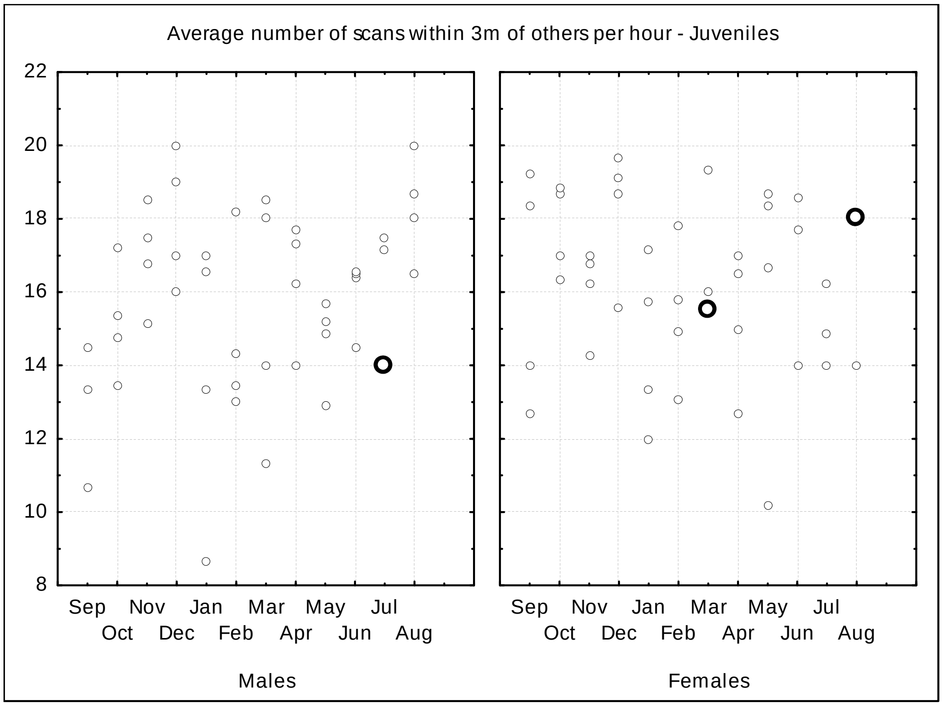


Fig. 5-28. Average juvenile time within 3m of others.

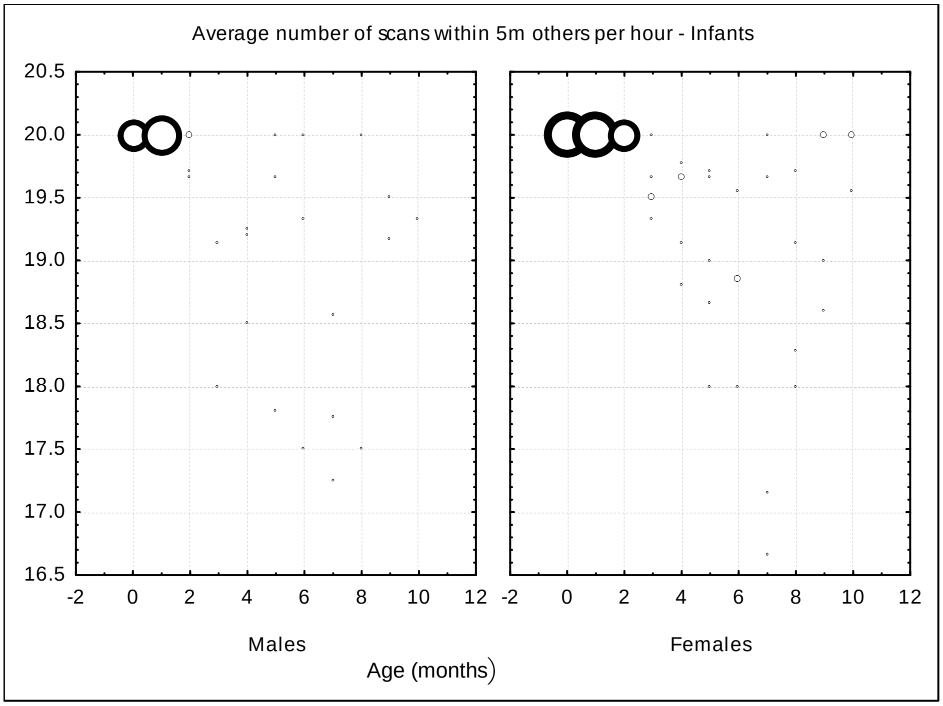


Fig. 5-29. Average infant time within 5m of others.

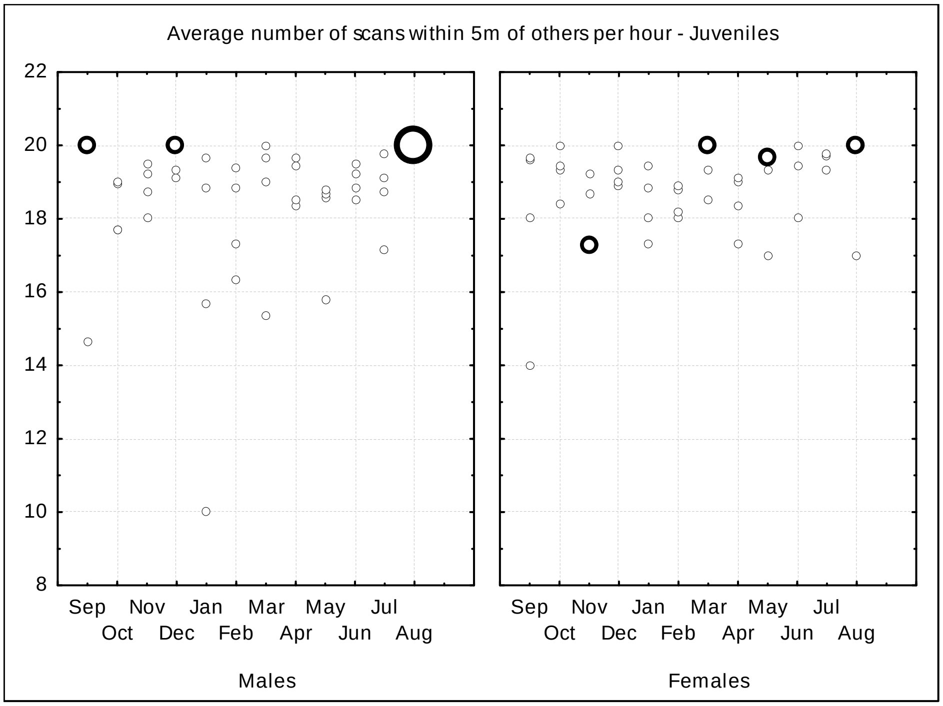


Fig. 5-30. Average juvenile time within 5m of others.

Subadult deviations from time spent in proximity to other age/sex classes expected at random

In general, where adults show sex differences in biases of time spent in proximity to peers, they show a bias toward proximity with same-sex peers at the beginning of the observation year and less bias toward same-sex peers as the year progresses. With regard to juveniles and infants, adult females bias their contact time more strongly away from juvenile males than adult males do, and adult males spend more time within 3m of juvenile males than expected at random throughout the year, while adult females show a temporal trend of increasing allocation of their time within 3m of others to juvenile males as time progresses. Adult males also significantly bias their contact time strongly away from infants while adult females do not.

Among infants, there are very few sex differences in proximity biases. The best fit RP model suggests that infant females spend less of their contact time with adult females than infants males do (Table 5-15), and this is supported by a qualitative examination of the scatterplot of the infant data at early ages (Figure 5-31). However, the best fit random intercepts LMEM does not find a significant sex difference (Table 5-15), perhaps because, at later ages, infant females appear to spend more of their contact time with adult females than infant males do (Fig. 5-31). Infant females may also tend to spend more of their time within 3m of others with adult females than infant males do (Table 5-15, Figure 5-32), and individual OLS regressions indicate that this effect is not only due to the one unusual male infant (Fig. 5-33). Infants exhibit no sex difference in the amount of their time in proximity to others spent with any other age/sex class at any distance (Tables 5-16 through 5-19).

It is worth noting that infants are less in control of their own proximity at early ages as they are at later ones. Infants do not begin feeding on their own until at least 6 weeks of age. Given the sampling issues in this cohort and the changes this cohort undergoes in controlling its use of space, it may be more appropriate, in future, to analyze 0-2 month old infants and 3-11 month old infants separately. In general, though, there is almost no evidence for infant sex differences in proximity to other age/sex classes, and all potential sex differences are limited to proximity to adult females.

TABLE 5-15. Model parameter estimates of deviations from expected time spent in proximity to adult females by infants.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	Dev Time in contact AF	random int. LMEM	INT	-2.84	0.45	25	-6.37	<.0001*
			SEX	-0.42	0.60	78	-0.69	0.49
		quadratic RP	INT	-4.20	0.35	25	-12.15	<.0001*
			SEX	-1.16	0.46	25	-2.54	0.02*
			TIME	1.16	0.23	74	5.05	<.0001*
			TIME^2	-0.10	0.03	74	-3.70	0.0004*
			SEX*TIME	0.10	0.29	74	0.35	0.73
			SEX*TIME^2	0.02	0.03	74	0.53	0.60
INF	Dev Time in reach AF	random int. LMEM	INT	0.52	0.36	25	1.44	0.16
			SEX	-0.33	0.49	78	-0.68	0.50
		linear RP	INT	1.14	0.43	25	2.64	0.01*
			TIME	-0.26	0.11	76	-2.41	0.02*
			SEX	-0.78	0.58	25	-1.33	0.20
			TIME*SEX	0.24	0.14	76	1.75	0.08†
INF	Dev Time in 3m AF	random int. LMEM	INT	4.40	0.55	25	8.06	<.0001*
			SEX	1.36	0.70	78	1.94	0.06†
		linear RP	INT	5.77	0.86	25	6.74	<.0001*
			TIME	-0.41	0.20	76	-2.05	0.04*
			SEX	-0.19	1.13	25	-0.17	0.87
			TIME*SEX	0.46	0.25	76	1.85	0.07†

* $p \le 0.05$; † $0.05 < p \le 0.10$

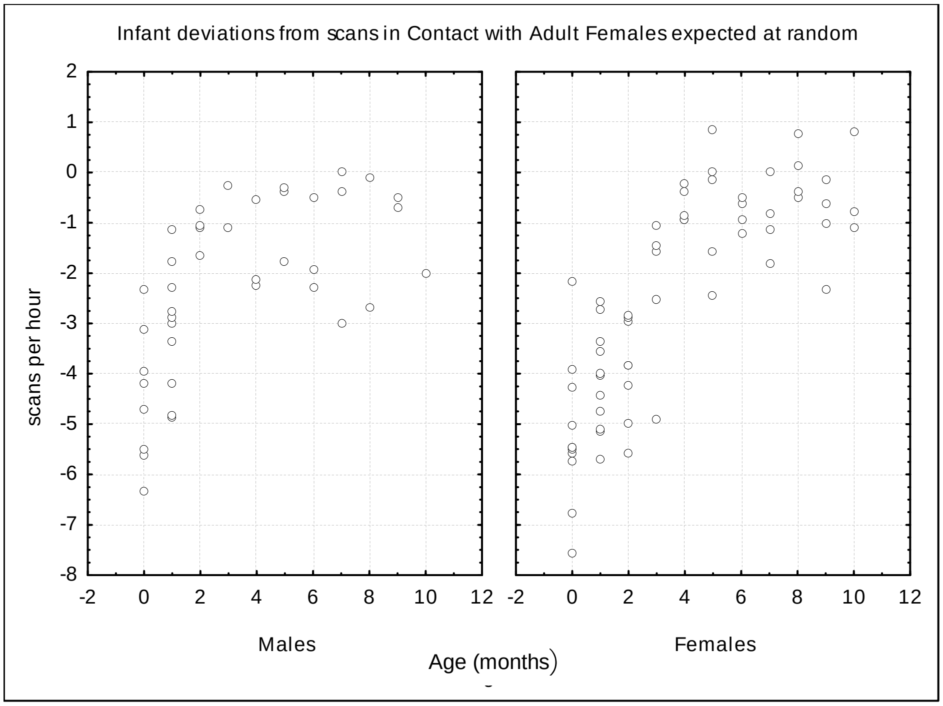


Fig. 5-31. Deviations from expected time in contact with adult females by infants.

Fig. 5-32. Deviations from expected time in 3m of adult females by infants.

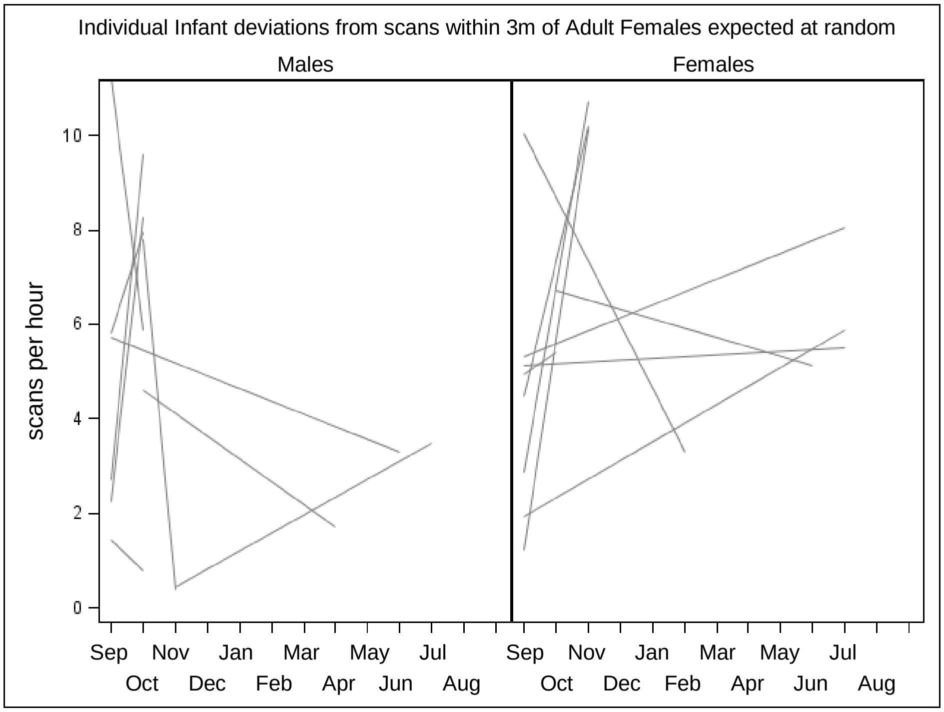


Fig. 5-33. Individual OLS regressions of deviations from expected time in 3m of adult females by infants.

TABLE 5-16. Model parameter estimates of deviations from expected time in proximity to adult males by infants.

Age	Var.	Model	Effect	est.	SE	DF	t	p
INF	Dev Time in contact AM	quad. LMEM	INT	-7.33	0.47	25	-15.58	<.0001*
			SEX	-0.29	0.63	58	-0.46	0.64
			TIME	2.15	0.25	16	8.62	<.0001*
			TIME^2	-0.18	0.03	58	-6.18	<.0001*
			SEX*TIME	-0.09	0.31	58	-0.31	0.76
			SEX*TIME^2	0.03	0.03	58	0.89	0.37
INF	Dev Time in reach AM	random int. LMEM	INT	-3.59	0.72	25	-4.96	<.0001*
			SEX	0.49	0.99	78	0.49	0.62
		linear RP	INT	-2.52	0.51	25	-4.96	<.0001*
			TIME	0.36	0.07	76	4.93	<.0001*
			SEX	0.67	0.64	25	1.05	0.30
			TIME*SEX	-0.28	0.09	76	-3.10	0.003*
INF	Dev Time in 3m AM	random int. LMEM	INT	-9.36	1.23	25	-7.60	<.0001*
			SEX	0.00	1.67	78	0.00	1.00
		linear RP	INT	-10.29	1.35	25	-7.64	<.0001*
			TIME	0.45	0.29	76	1.57	0.12
			SEX	2.11	1.81	25	1.17	0.25
			TIME*SEX	-0.90	0.35	76	-2.61	0.01*

* $p \leq 0.05$

TABLE 5-17. Model parameter estimates of deviations from expected time spent in proximity to juvenile females by infants.

Age	Var	Model	Effect	est.	SE	DF	t	p
INF	Dev Time in contact JF	quad. LMEM	INT	-0.64	0.24	25	-2.65	0.01*
			SEX	-0.09	0.33	58	-0.28	0.78
			TIME	0.17	0.10	16	1.62	0.13
			TIME^2	-0.01	0.01	58	-1.00	0.32
			SEX*TIME	0.10	0.13	58	0.80	0.43
			SEX*TIME^2	-0.01	0.01	58	-0.70	0.49
INF	Dev Time in reach JF	random int. LMEM	INT	0.46	0.22	25	2.08	0.05*
			SEX	-0.24	0.30	78	-0.80	0.43
		mean RP	INT	0.14	0.11	25	1.18	0.25
			SEX	-0.14	0.15	25	-0.95	0.35
INF	Dev Time in 3m JF	random int. LMEM	INT	0.98	0.48	25	2.05	0.05*
			SEX	-0.28	0.65	78	-0.44	0.66
		mean RP	INT	0.69	0.42	25	1.65	0.11
			SEX	-0.63	0.56	25	-1.12	0.27

* $p \leq 0.05$

TABLE 5-18. Model parameter estimates of deviations from expected time spent in proximity to juvenile males by infants.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	Dev Time in contact JM	random int. LMEM	INT	-0.42	0.15	25	-2.73	0.01*
			SEX	-0.07	0.21	78	-0.32	0.75
		linear RP	INT	-0.60	0.19	25	-3.21	0.004*
			TIME	0.07	0.05	76	1.60	0.11
			SEX	-0.19	0.26	25	-0.72	0.48
			TIME*SEX	0.03	0.06	76	0.48	0.63
INF	Dev Time in reach JM	random int. LMEM	INT	-0.19	0.08	25	-2.37	0.03*
			SEX	0.08	0.11	78	0.72	0.47
		mean RP	INT	-0.10	0.06	25	-1.71	0.10†
			SEX	0.02	0.07	25	0.30	0.77
INF	Dev Time in 3m JM	mean RP	INT	0.32	0.32	25	0.99	0.33
			SEX	0.35	0.41	25	0.85	0.41

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

TABLE 5-19. Model parameter estimates of deviations from expected time spent in proximity to infants by infants.

Age	Var.	Model	Effect	est.	SE	DF	t	p
INF	Dev Time in contact Infants	random int. LMEM	INT	-1.96	0.39	25	-5.01	<.0001*
			SEX	0.82	0.53	78	1.53	0.13
		mean RP	INT	-0.04	0.05	25	-0.71	0.49
			SEX	-0.01	0.07	25	-0.16	0.88
INF	Dev Time in reach Infants	random int. LMEM	INT	2.19	0.77	25	2.86	0.009*
			SEX	0.09	1.06	78	0.08	0.93
		mean RP	INT	0.00	0.04	25	0.05	0.96
			SEX	0.06	0.05	25	1.13	0.27
INF	Dev Time in 3m Infants	quad. LMEM	INT	4.84	1.13	25	4.28	0.0002*
			SEX	-0.83	1.55	58	-0.53	0.60
			TIME	-0.62	0.39	16	-1.59	0.13
			TIME^2	0.02	0.04	58	0.38	0.70
			SEX*TIME	-0.21	0.47	58	-0.44	0.66
			SEX*TIME^2	0.04	0.05	58	0.83	0.41
		quad. RP	INT	4.38	0.90	25	4.89	<.0001*
			SEX	-1.50	1.19	25	-1.26	0.22
			TIME	-1.17	0.31	74	-3.75	0.0004*
			TIME^2	0.08	0.03	74	2.72	0.008*
			SEX*TIME	0.34	0.39	74	0.86	0.39
			SEX*TIME^2	-0.02	0.04	74	-0.60	0.55

* $p \leq 0.05$

In contrast, juveniles exhibit a number of sex differences in how they allocate their time in proximity to others. Juvenile females tend to spend more of their time within 3m of others with adult females than do juvenile males (Table 5-20). Analyses by sex indicate that both sexes significantly bias their time spent within 3m of others toward adult females, but that juvenile females simply allocate more of their time within 3m of others to adult females than juvenile males do (Table 5-20). Additionally, according to the best fit models by sex, juvenile females spend significantly less of their time within 3m of others toward adult females as the observation year progresses (or at the very least, they tend to) while juvenile males show no change through time (Table 5-20, Figure 5-34).

TABLE 5-20. Model parameter estimates of deviations from expected time spent in proximity to adult females by juveniles.

Age	Variable	Model	Effect	est.	SE	DF	t	p
JUV	Dev Time in contact AF	random int. LMEM	INT	-0.48	0.20	7	-2.42	0.05*
			SEX	0.11	0.28	83	0.38	0.70
		mean RP	INT	-0.43	0.15	7	-2.94	0.02*
			SEX	0.11	0.21	7	0.50	0.63
JUV	Dev Time in reach AF	mean RP	INT	-0.29	0.12	7	-2.39	0.05*
			SEX	0.14	0.17	7	0.84	0.43
JUV	Dev Time in 3m AF	random int. LMEM	INT	3.20	0.79	7	4.03	0.005*
			SEX	2.07	1.14	83	1.81	0.07†
		linear RP	INT	3.32	1.26	7	2.64	0.03*
			TIME	0.00	0.19	81	-0.01	0.99
			SEX	3.74	1.78	7	2.10	0.07†
			TIME*SEX	-0.36	0.27	81	-1.30	0.20
	JF Dev Time in 3m AF	linear LMEM	INT	7.33	1.24	3	5.91	0.01*
			TIME	-0.40	0.14	40	-2.81	0.008*
		linear RP	INT	6.93	1.47	3	4.70	0.02*
			TIME	-0.33	0.23	40	-1.45	0.15
	JM Dev Time in 3m AF	random int. LMEM	INT	3.25	0.51	4	6.42	0.003*
		mean RP	INT	3.29	0.57	4	5.73	0.005*

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

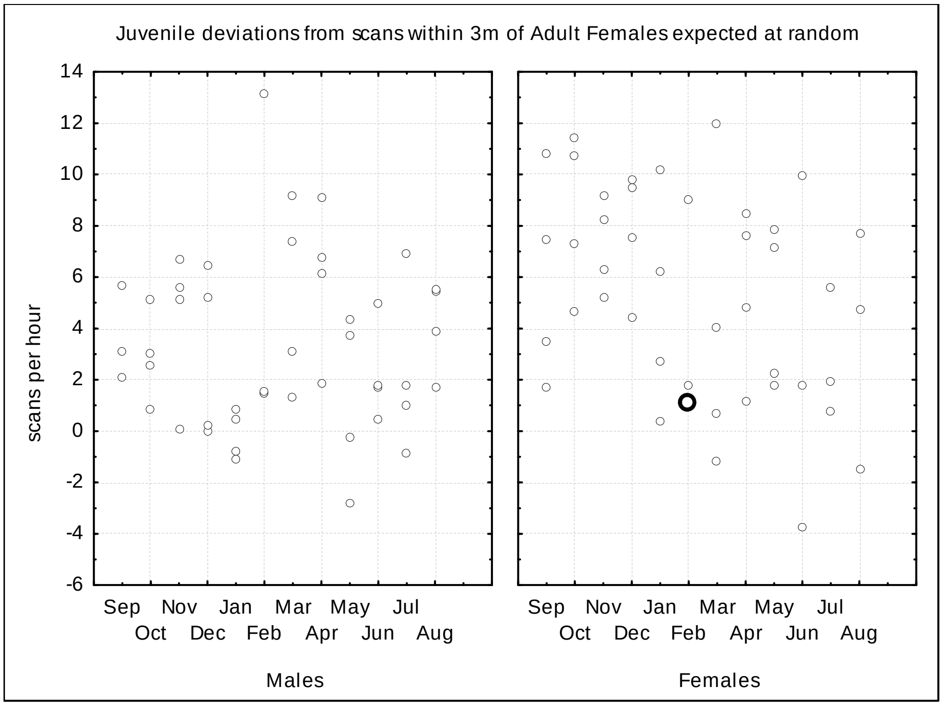


Fig. 5-34. Deviations from time expected within 3m of adult females for juveniles

Furthermore, juveniles exhibit consistent sex differences in the amount of their proximity time spent with adult males. Juvenile females spend less of their time in proximity to others with adult males than juvenile males do at all distances (Table 5-21, Figures 5-35 through 5-37). Analyses by sex indicate that juvenile females bias their contact time away from adult males while juvenile males probably do not—the best fit random intercept LMEM finds no difference from time expected in contact with adult males than expected at random, while the best fit mean RP model finds that juvenile males bias their contact time slightly away from adult males (Table 5-21). Both sexes bias their time spent in reach of others away from adult males (but juvenile females show a stronger negative bias), and both allot more of their time in reach of others to adult males as the observation year progresses (Table 5-21). Both sexes also bias their time spent within 3m of others away from adult males, and females, but not males, allot more of their time within 3m of others to adult males as the observation year progresses (Table 5-21).

TABLE 5-21. Model parameter estimates of deviations from expected time spent in proximity to adult males by juveniles.

Age	Var.	Model	Effect	est.	SE	DF	t	p
JUV	Dev Time in contact AM	random int. LMEM	INT	-0.23	0.34	7	-0.69	0.51
			SEX	-1.29	0.48	83	-2.68	0.009*
		mean RP	INT	-0.53	0.24	7	-2.27	0.06†
			SEX	-0.09	0.33	7	-0.27	0.80
	JF Dev Time in contact AM	random int. LMEM	INT	-1.52	0.40	3	-3.78	0.03*
		mean RP	INT	-1.53	0.47	3	-3.26	0.05*
	JM Dev Time in contact AM	random int. LMEM	INT	-0.23	0.27	4	-0.85	0.45
		mean RP	INT	-0.53	0.09	4	-5.60	0.005*
JUV	Dev Time in reach AM	random int. LMEM	INT	-0.39	0.29	7	-1.35	0.22
			SEX	-1.14	0.41	83	-2.77	0.007*
		linear RP	INT	-0.59	0.43	7	-1.36	0.22
			TIME	0.05	0.05	81	1.03	0.30
			SEX	-1.72	0.61	7	-2.79	0.03*
			TIME*SEX	0.11	0.07	81	1.53	0.13
	JF Dev Time in reach AM	random int. LMEM	INT	-2.68	0.47	3	-5.70	0.01*
			TIME	0.23	0.07	40	3.29	0.002*
		linear RP	INT	-0.41	0.19	4	-2.15	0.10†
	JM Dev Time in reach AM	random int. LMEM	INT	-0.86	0.30	4	-2.84	0.05*
			TIME	0.09	0.04	41	2.02	0.05*
		linear RP	INT	-2.69	0.58	3	-4.64	0.02*
			TIME	0.24	0.09	40	2.60	0.01*

TABLE 5-21. Continued

JUV	Dev Time in 3m AM	random int. LMEM	INT	-6.62	1.05	7	-6.32	0.0004*
			SEX	-4.16	1.50	83	-2.77	0.007*
		linear RP	INT	-5.30	1.63	7	-3.26	0.01*
			TIME	-0.23	0.21	81	-1.13	0.26
			SEX	-7.46	2.31	7	-3.22	0.01*
			TIME*SEX	0.62	0.30	81	2.07	0.04*
	JF Dev Time in 3M AM	random int. LMEM	INT	-12.75	1.82	3	-7.02	0.006*
			TIME	0.38	0.22	40	1.70	0.10†
		linear RP	INT	-12.75	1.99	3	-6.40	0.008*
			TIME	0.38	0.23	40	1.66	0.10†
	JM Dev Time in 3M AM	linear RP	INT	-5.24	1.47	4	-3.58	0.02*
			TIME	-0.25	0.22	41	-1.12	0.27

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

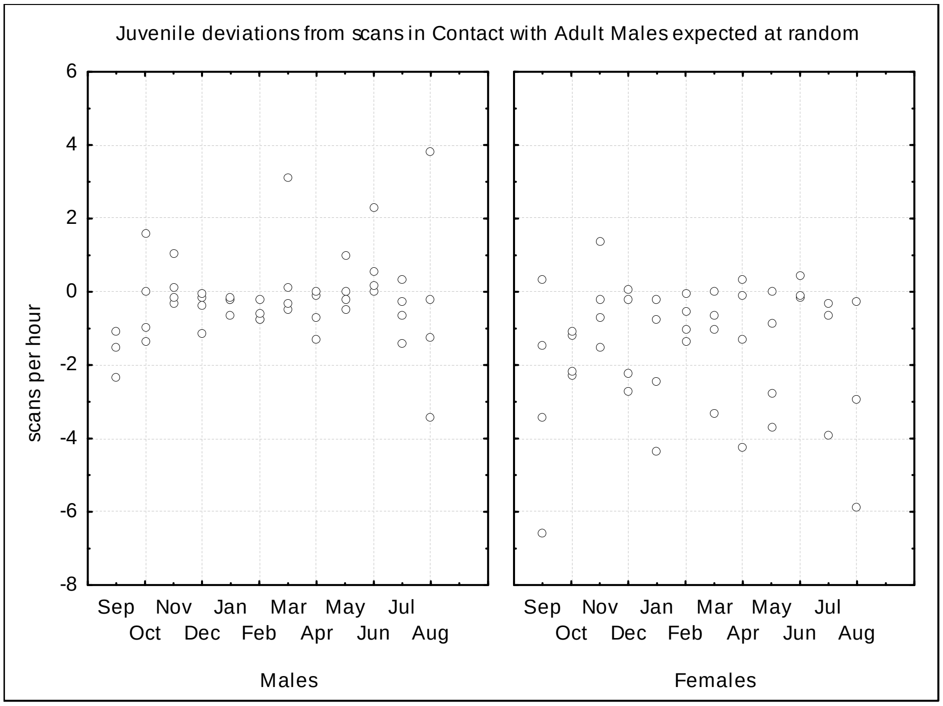


Fig. 5-35. Deviations from expected time in contact with adult males for juveniles.

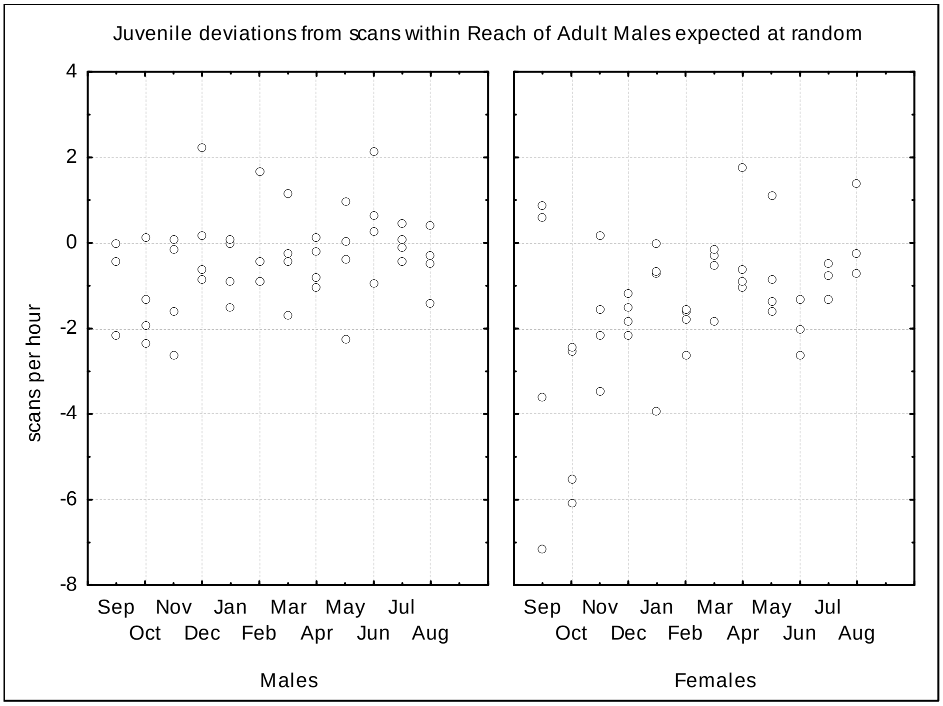


Fig. 5-36. Deviations from expected time within reach of adult males for juveniles.

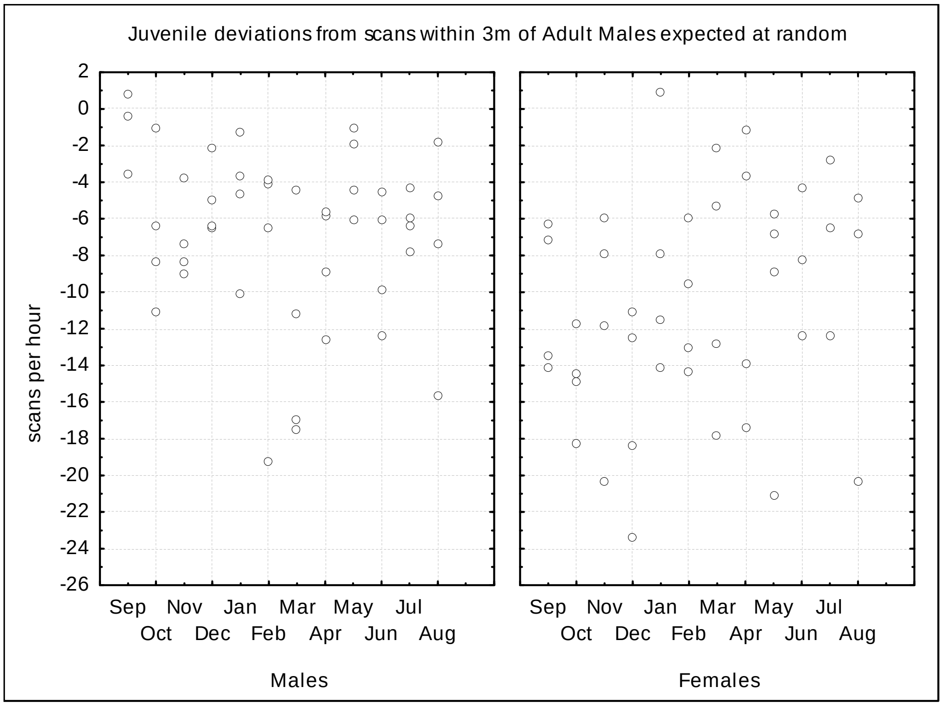


Fig. 5-37. Deviations from expected time within 3m of adult males for juveniles.

There are no sex differences in how much of their contact time or time within 3m juveniles spend with infants, but the best fit random intercepts LMEM suggests that juvenile females bias the time they spend within reach of others more strongly toward infants than do juvenile males (Table 5-22, Figure 5-38). In contrast, the best fit mean RP model finds no sex difference (Table 5-22). A qualitative examination of the individual OLS regressions suggests that, on average, juvenile females do spend more of their time within reach of others with infants than juvenile males do (Fig. 5-39). Analyses by sex find that juvenile males spend time within reach of infants expected at random (Table 5-22). The best fit linear LMEM finds that juvenile females spend more time than expected at random in reach of infants at the beginning of the year, but less as the year progresses, but the best fit mean RP model finds no difference from random expectation (Table 5-22). Therefore, I conclude that if juvenile females bias their time in proximity to others toward infants, it is limited to the distance of being within reach.

TABLE 5-22. Model parameter estimates of deviations from expected time spent in proximity to infants by juveniles.

Age	Variable	Model	Effect	est.	SE	DF	t	p
JUV	Dev Time in contact Infants	random int. LMEM	INT	-0.12	0.22	7	-0.54	0.61
			SEX	0.33	0.32	83	1.03	0.31
		mean RP	INT	-0.06	0.07	7	-0.86	0.42
			SEX	-0.10	0.11	7	-0.92	0.39
JUV	Dev Time in reach Infants	random int. LMEM	INT	0.17	0.30	7	0.56	0.59
			SEX	1.03	0.43	83	2.43	0.02*
		mean RP	INT	-0.11	0.06	7	-1.87	0.10†
			SEX	0.08	0.09	7	0.83	0.44
	JF Dev Time in reach Infants	linear LMEM	INT	2.01	0.47	3	4.32	0.02*
			TIME	-0.16	0.06	40	-2.47	0.02*
		mean RP	INT	-0.14	0.08	3	-1.78	0.17
	JM Dev Time in reach Infants	random int. LMEM	INT	0.16	0.21	4	0.77	0.49
		mean RP	INT	0.15	0.23	4	0.65	0.55
JUV	Dev Time in 3m Infants	random int. LMEM	INT	1.48	0.46	7	3.19	0.02*
			SEX	0.82	0.67	83	1.23	0.22
		mean RP	INT	1.54	0.40	7	3.85	0.006*
			SEX	0.03	0.58	7	0.04	0.97

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

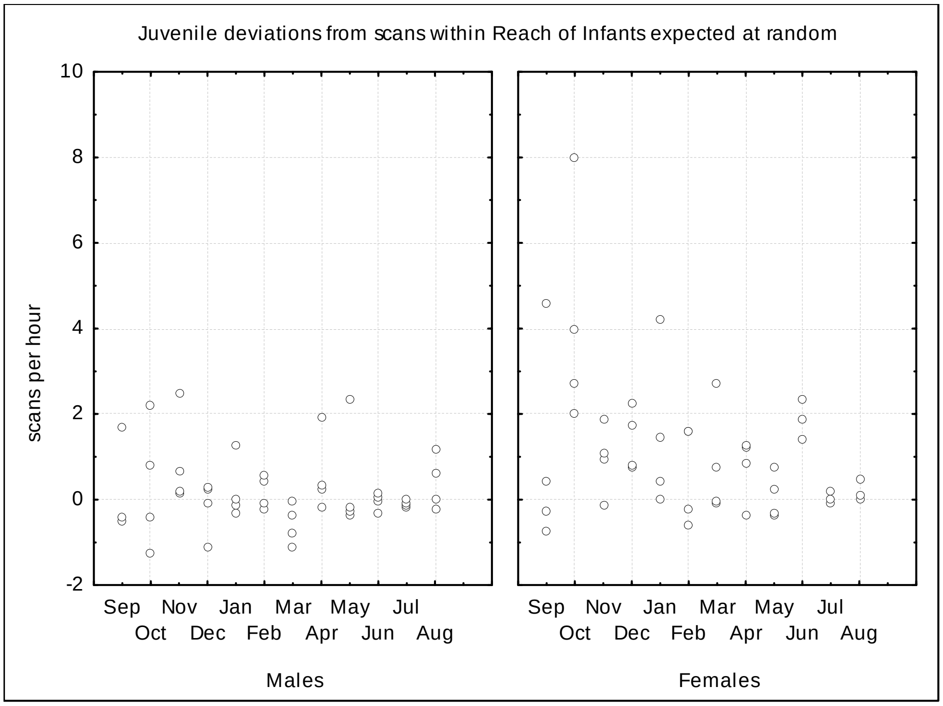


Fig. 5-38. Deviations from expected time within reach of infants for juveniles.

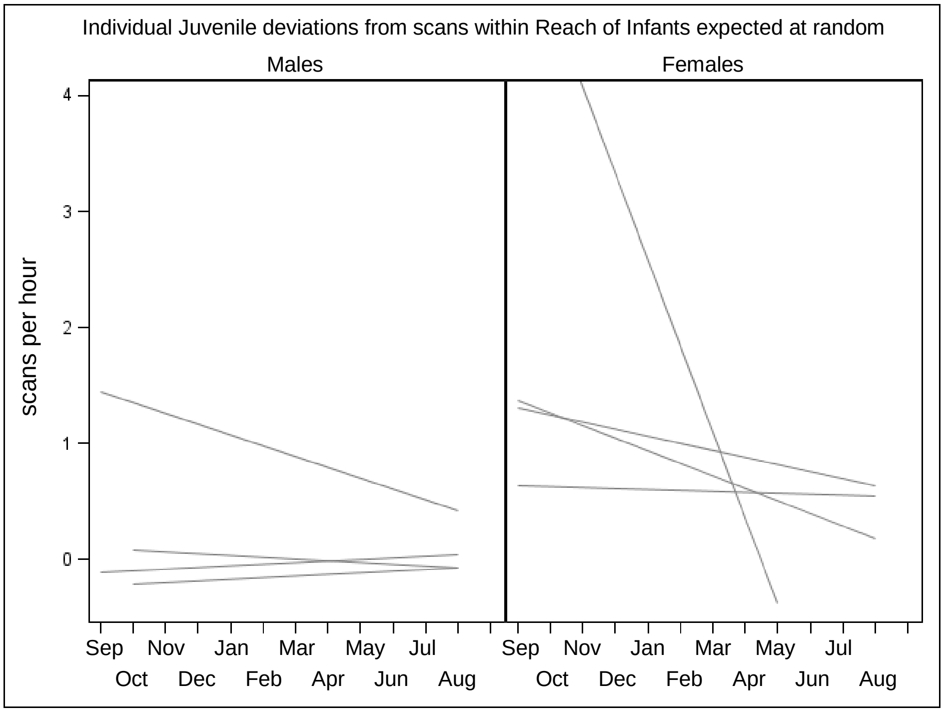


Fig. 5-39. Individuals OLS regressions of deviations from expected time within reach of infants for juveniles.

With respect to juvenile peers, the picture is even less clear, due to sampling issues. Due to the particular distribution of juveniles across study groups, only two juvenile males had access to juvenile females as social partners. Furthermore, in the fourth quarter of the observation year, only two juvenile females had access to another juvenile female. Similarly, only two juvenile males had access to another juvenile male throughout the year. As a result, any trends and significant differences in time spent in proximity to other juveniles are based on extremely small samples.

That said, with respect to time spent in proximity to juvenile females, the best fit quadratic LMEM suggests that there may be sex-differential tendencies in time spent in proximity to juvenile females in which juvenile females spend less of their contact time with juvenile females than juvenile males do, but more of it as time progresses (Table 5-23, Figure 5-40). However, the best fit mean RP model finds no overall difference across the year. With respect to time spent in proximity to juvenile males, the best fit LMEMs (which, in these cases, were the best fitting models overall) suggest that juvenile females bias their contact time away from juvenile males more than juvenile males do (Table 5-23, Figure 5-41) and but bias their time within 3m of others toward juvenile males than juvenile males do (Table 5-23, Figure 5-42). Notably, the effect sizes for these findings of trends and significant sex differences are smaller than those for measures of proximity to both infants and adults (Tables 5-22 through 5-21), and much smaller than measures of proximity to adults (Tables 5-20 and 5-21). Therefore, because the apparent sex differences are slight and are based on very small samples, I conclude that there is no strong evidence for sex-differential patterns of proximity to juveniles among other juveniles. There are no unequivocal temporal patterns in the allocation of time in proximity to other juveniles throughout the observation year.

TABLE 5-23. Model parameter estimates of deviations from expected time spent in proximity to juveniles by juveniles.

Age	Variable	Model	Effect	est.	SE	DF	t	p
JUV	Dev Time in contact JF	quadratic LMEM	INT	0.59	0.29	7	2.06	0.08†
			SEX	-0.80	0.41	73	-1.94	0.06†
			TIME	-0.25	0.10	6	-2.61	0.04*
			TIME^2	0.02	0.01	73	2.77	0.007*
			SEX*TIME	0.22	0.13	73	1.66	0.10†
			SEX*TIME^2	-0.01	0.01	73	-1.15	0.26
		mean RP	INT	-0.02	0.05	7	-0.33	0.75
			SEX	0.01	0.08	7	0.12	0.91
JUV	Dev Time in reach JF	mean RP	INT	-0.04	0.03	7	-1.36	0.22
			SEX	-0.09	0.05	7	-1.82	0.11
JUV	Dev Time in 3m JF	random int. LMEM	INT	0.65	0.31	7	2.08	0.08†
			SEX	0.46	0.45	83	1.03	0.31
		mean RP	INT	0.64	0.36	7	1.79	0.12
			SEX	0.47	0.51	7	0.93	0.38
JUV	Dev Time in contact JM	quadratic LMEM	INT	0.09	0.16	7	0.58	0.58
			SEX	-0.46	0.22	73	-2.07	0.04*
			TIME	0.00	0.05	6	0.03	0.98
			TIME^2	0.00	0.00	73	-0.65	0.52
			SEX*TIME	0.10	0.07	73	1.38	0.17
			SEX*TIME^2	-0.01	0.01	73	-1.05	0.30
JUV	Dev Time in reach JM	random int. LMEM	INT	0.09	0.08	7	1.06	0.32
			SEX	-0.18	0.12	83	-1.55	0.13
		mean RP	INT	-0.02	0.04	7	-0.35	0.74
			SEX	-0.09	0.06	7	-1.43	0.20
JUV	Dev Time in 3m JM	random int. LMEM	INT	0.48	0.27	7	1.77	0.12
			SEX	0.82	0.39	83	2.09	0.04*
			INT	0.29	0.22	7	1.32	0.23
			SEX	0.25	0.31	7	0.79	0.46

$* \ p \leq 0.05$; † $0.05 < p \leq 0.10$

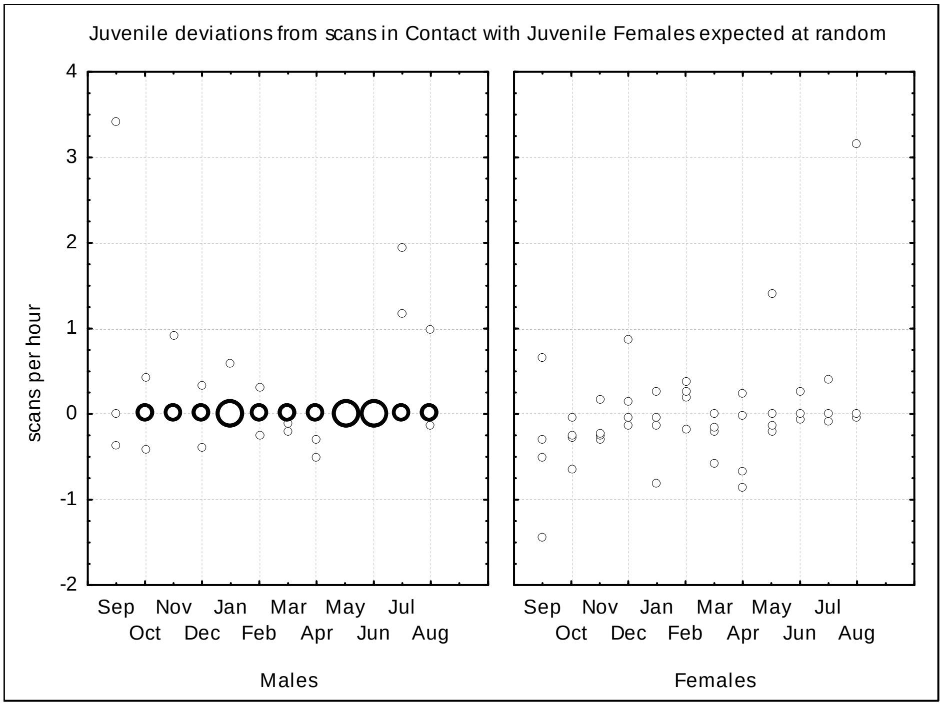


Fig. 5-40. Deviations from expected time in contact with juvenile females for juveniles.

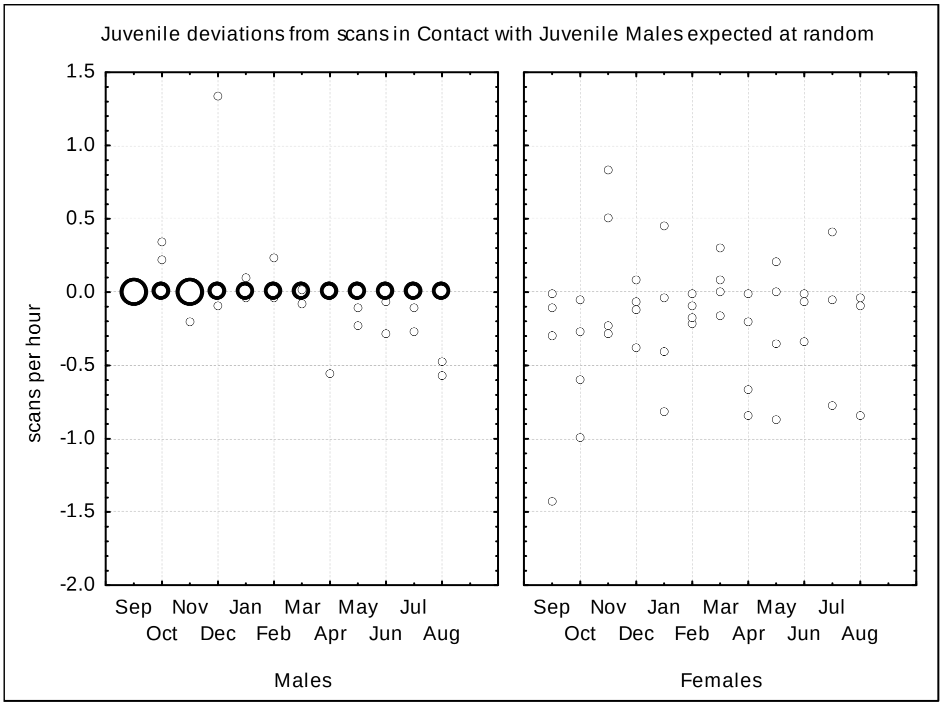


Fig. 5-41. Deviations from expected time in contact with juvenile males for juveniles.

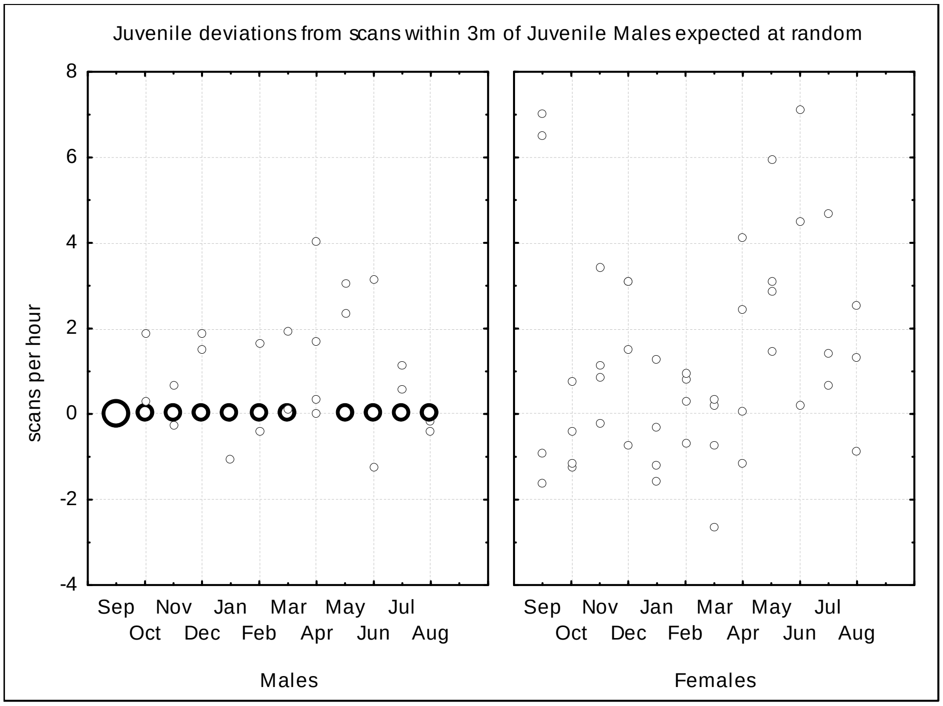


Figure 5-42. Deviations from expected time in contact with juvenile males for juveniles.

Summary – Proximity Patterns

Subadults do not exhibit sex differences in any global measures of proximity (Table 5-24).

TABLE 5-24. Summary of sex differences in global proximity measures in subadults.

Age	Intrinsic affiliation	Sex Difference	Time effects	
fINF	Total # neighbors in contact	·	♀ ⍰	♂ ⍰
	Total # neighbors in reach	·	♀ –	♂ –
	Total # neighbors in 3m	·	·	·
	Time in contact with others	·	♀ ⍰	♂ ⍰
	Time in reach of others	·	♀ ⍰	♂ ⍰
	Time in 3m of others	·	·	·
	Time in 5m of others	·	♀ –	♂ –
JUV	Total # neighbors in contact	·	♀ ⍰	♂ ⍰
	Total # neighbors in reach	·	·	·
	Total # neighbors in 3m	·	·	·
	Time in contact with others	·	♀ ⍰	♂ ⍰
	Time in reach of others	·	♀ –	♂ –
	Time in 3m of others	·	·	·
	Time in 5m of others	·	·	·

Sex difference: · no difference
Time effects: – decrease with time
⍰ quadratic effect (decrease with time, increase with time^2)
· no effect

Infants exhibit no convincing sex differences in their proximity patterns to particular age/sex classes at these sample sizes (Table 5-25). In contrast, some sex differences in proximity patterns to particular age/sex classes are well-established by the ages of 12-13 months (Table 5-25).

Juvenile sex differences are largely limited to patterns of proximity to adults in which each sex biases its time in proximity to others more strongly toward same-sex adults than the other. Both sexes of juveniles bias their time within 3m of others toward adult females, but juvenile females tend to do so more strongly (Table 5-25).

Furthermore, the pattern of bias toward adult females is attenuated through time for juvenile females but remains constant for juvenile males. This is similar to the adult sex-differential pattern in which adult females bias their time within 3m of others toward adult females at the beginning of the observation year, but less so as the year progresses while adult males show no temporal change. It is dissimilar to the adult pattern in that juveniles of both sexes bias their time within 3m of others more heavily toward adult females than do adults (Fig. 5-43), such that even though juvenile males spend less of their time within 3m of adult females than juvenile females do, they still spend more of it with adult females than expected at random, while adult males spend time within 3m of adult females as expected at random.

The juvenile pattern is also dissimilar to the adult pattern in that juvenile females do not spend more of their time in contact to adult females than do juvenile males. The matrilineal relationships of adults older than four years of age in this sample are not well-known. As such, it is possible that adult females who were spending more time in contact with other adult females were actually spending time in contact with their own mothers, and that this pattern might be present in analyses of juvenile time in proximity to their mothers. However, no clear sex differences in juvenile proximity to their mothers were found (Table 5-26).

TABLE 5-25. Summary of sex differences in bias of proximity to each partner age/sex class in subadults.

Age	Partner type	Proximity level	Sex-typed bias		Time effect	
INF	AF	contact	♀ — ?	♂ – ?	♀ ∩	♂ ∩
		reach	·	·	♀ –	♂ –
		3m	·	·	♀ –	♂ –
	AM	contact	·	·	♀ ∩	♂ ∩
		reach	·	·	♀ +	♂ +
		3m	·	·	·	·
	JF	contact	·	·	·	·
		reach	·	·	·	·
		3m	·	·	·	·
	JM	contact	·	·	·	·
		reach	·	·	·	·
		3m	·	·	·	·
	INFs	contact	·	·	·	·
		reach	·	·	·	·
		3m	·	·	·	·
JUV	AF	contact	·	·	·	·
		reach	·	·	·	·
		3m	♀ ++	♂ +	·	·
	AM	contact	♀ –	·	·	·
		reach	♀ —	♂ –	♀ ++	♂ +
		3m	♀ —	♂ –		
	JF	contact	·	·	·	·
		reach	·	·	·	·
		3m	·	·	·	·
	JM	contact	·	·	·	·
		reach	·	·	·	·
		3m	·	·	·	·
	INFs	contact	·	·	·	·
		reach	♀ + ?	·	♀ – ?	·
		3m	·	·	·	·

TABLE 5-25. Continued.

Sex-typed bias: + significantly more than expected at random
++ significantly more than +;
– significantly less than expected at random;
— significantly less than –;
? equivocal result
· no difference from expected at random
Time effects: + increase with time
– decrease with time
⍰ quadratic effect (– with time, + with time^2);
⍰ quadratic effect (+ with time, – with time^2);
? equivocal result
· no effect

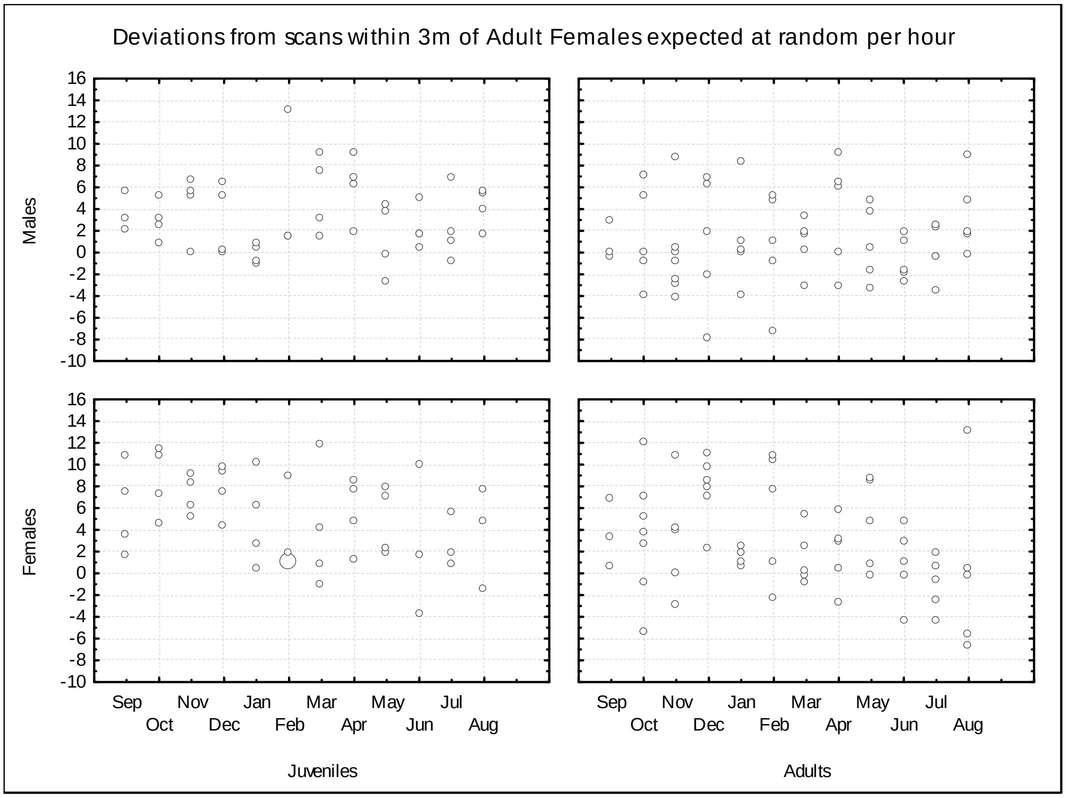


Figure 5-43. Deviations from expected time in within 3m of adult females for adults and juveniles.

TABLE 5-26. Model parameter estimates of deviations from expected time in contact with mother by juveniles.

Age	Variable	Model	Effect	est.	SE	DF	t	p
JUV	Dev Time in contact MOM	random int. LMEM	INT	0.76	0.47	7	1.61	0.15
			SEX	1.19	0.68	83	1.75	0.08†
		mean RP	INT	-0.08	0.14	7	-0.60	0.57
			SEX	0.32	0.19	7	1.63	0.15
JUV	Dev Time in reach MOM	mean RP	INT	0.51	0.12	7	4.26	0.004*
			SEX	-0.07	0.17	7	-0.38	0.72
JUV	Dev Time in 3m MOM	random int. LMEM	INT	0.81	0.45	7	1.79	0.12
			SEX	0.00	0.65	83	0.00	1.00
		mean RP	INT	0.80	0.51	7	1.57	0.16
			SEX	0.00	0.73	7	0.00	1.00

MOM = the focal individual's mother; * $p \leq 0.05$; † $0.05 < p \leq 0.10$. All tables follow these conventions.

The most marked sex difference in proximity patterns among juveniles are in proximity to adult males. Juvenile females bias their time in proximity to others away from adult males at all distances, and more strongly than juvenile males do at all distances (Table 5-25). This is similar to the adult pattern in which adult females bias their time in contact with and within 3m of others more strongly away from adult males than adult males do. It is different from the adult pattern in that adult females exhibit significantly less bias away from proximity to males as the observation year progresses, while juvenile females exhibit no temporal change in contact bias, but do tend to be less biased against spending time within reach and within 3m of adult males as the observation year progresses.

The juvenile male pattern also does not match the adult male pattern of proximity to adult males. Adult males spend less of their contact time and time within 3m of others on adult males as time progresses, while juvenile males exhibit no temporal change in the amount of contact time or time within 3m of others they spend with adult males, and increase the amount of time within reach of others they spend with adult males (Table 5-25). For juveniles, there is no strong evidence of sex differences in proximity bias toward other juveniles and infants.

INFANT INTEREST

In terms of behaviors that can be interpreted as measures of infant interest, adult females bias their grooming toward infants while males do not, and adult females spend more time in contact with infants than males do (although less time than expected at random). Like adults, juvenile females bias their grooming time toward infants (Table 5-11), while juvenile males bias them slightly away from infants (Table 5-11). But unlike adults, there is no sex difference in bias toward time spent in contact with infants (Table 5-25), and instead juvenile females may exhibit a bias toward spending more of their time within reach of others with infants when infants are young (Table 5-25), while adult females show no such bias. The lack of a sex-difference in contact time bias with respect to infants does not lie with juvenile females, but with juvenile males. Unlike adult males, who spend significantly less time in contact with infants than expected at random, juvenile males do not bias their contact time toward or away from infants (Table 5-25), just like juvenile and adult females do not.

The juvenile female bias in time within reach of others toward infants when infants are young could indicate a stronger desire on the part of juvenile females to be near infants than adult females, or it could be a sampling artifact of juvenile proximity maintenance to their mothers, who tended to have dependent infants. The juvenile bias toward proximity within 3m of infants is probably due simply to their spending more time in proximity to their mothers and/or adult females than juvenile males do.

SCENT MARKING

In adults, males antebrachial and brachial mark, anoint tail, and tail wave significantly more often than adult females, but there is no sex difference in rates of anogenital marking, and adults were almost never observed to tail play.

Infants

Infants were never observed to anogenital mark, anoint tail, or tail wave. One infant male was observed to brachial “mark” on one occasion and to antebrachial “mark” on two occasions. The same infant was observed to tail play on three occasions.

Juveniles

Juveniles were never observed to anogenital mark, anoint tail, or tail wave. Juveniles of both sexes were observed to tail play, but juvenile males exhibited significantly higher rates of tail play than juvenile females (Table 5-27, Figure 5-44). Juvenile males also exhibited significantly higher rates of brachial and antebrachial marking (Table 5-27, Figures 5-45 and 5-46); like adult females, juvenile females were never observed to engage in these behaviors. It seems that juvenile males are developing sex-typed scent marking behavior, and exhibit tail play in place of anointing their tails (which involves the identical motor pattern) and tail waving.

TABLE 5-27. Model parameter estimates for rates of scent-marking related behavior by juveniles.

Age	Variable	Model	Effect	est.	SE	DF	t	p
JUV	Rates of tail play	mean RP	INT	0.67	0.15	7	4.36	0.003*
			SEX	-0.62	0.22	7	-2.82	0.03*
	Rates of antebrachial mark	mean RP	INT	0.63	0.13	7	4.67	0.002*
			SEX	-0.63	0.19	7	-3.26	0.01*
	Rates of brachial mark	mean RP	INT	0.13	0.03	7	5.09	0.001*
			SEX	-0.13	0.04	7	-3.56	0.01*

* $p \leq 0.05$

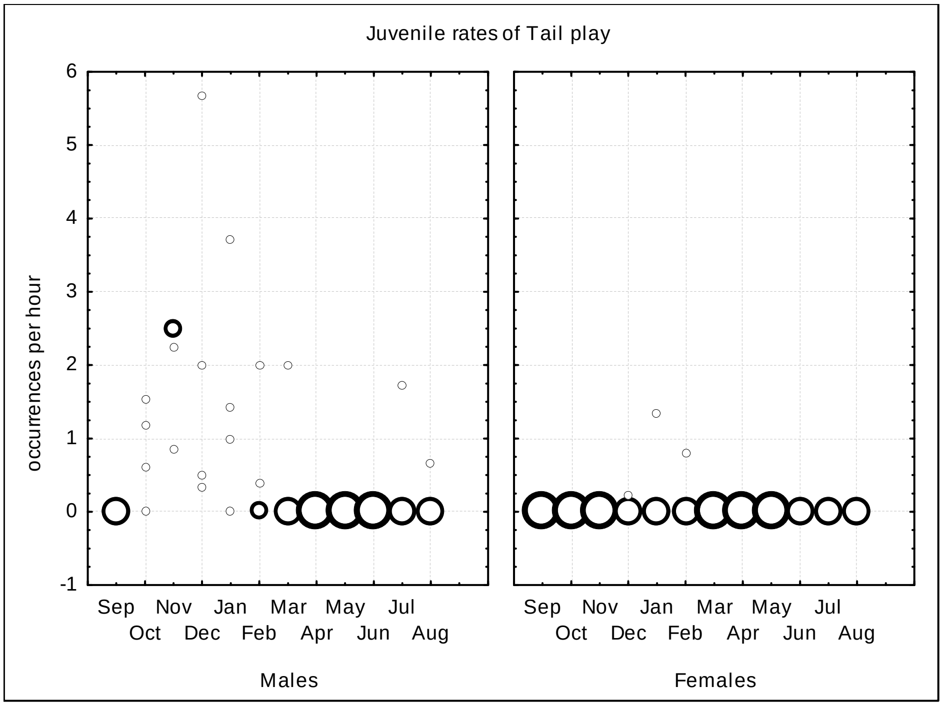


Fig. 5-44. Juvenile rates of tail play.

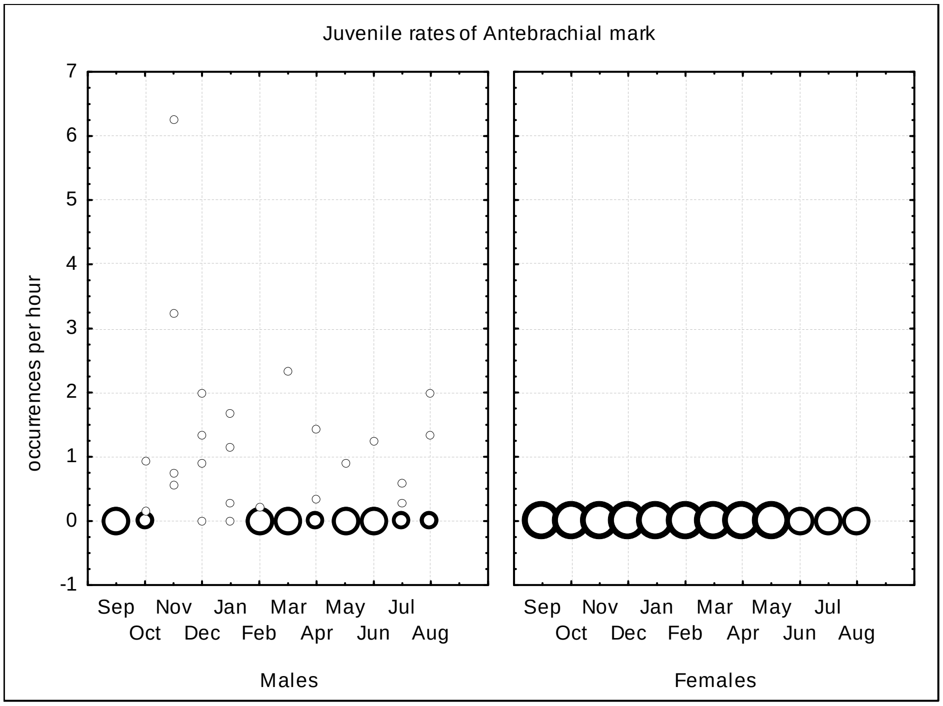


Fig. 5-45. Juvenile rates of antebrachial mark.

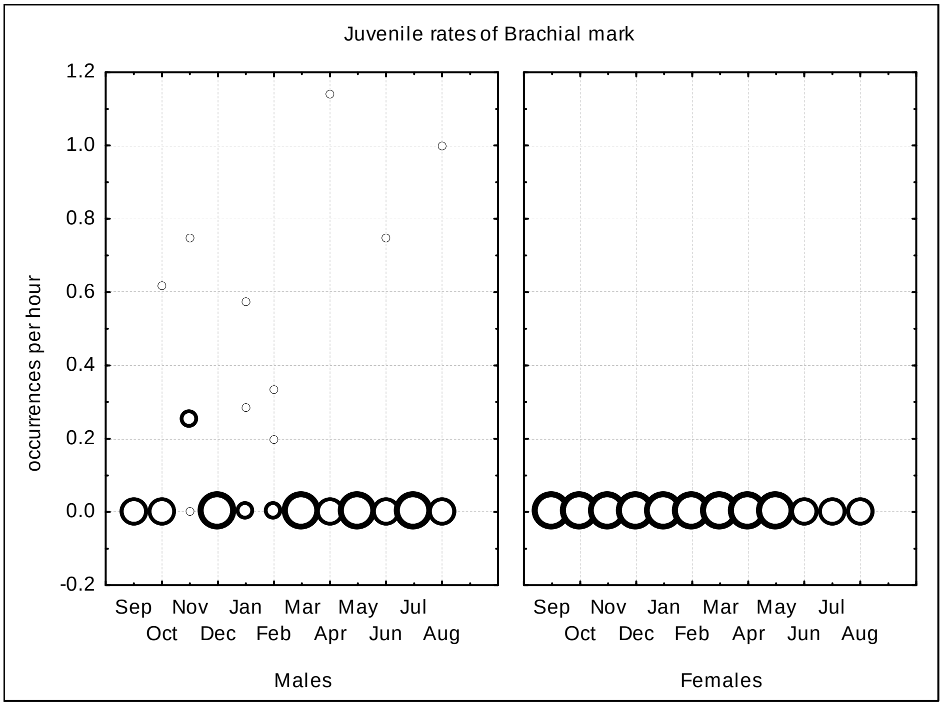


Fig. 5-46. Juvenile rates of brachial mark.

SUMMARY – SUBADULT DEVELOPMENT OF ADULT SEX-TYPED BEHAVIORS

Adult sex-typed patterns of agonism do not have a subadult developmental component. Higher rates of overall aggression and supplanting by adult females are not mirrored by the subadult cohorts (Table 5-28). Nor to subadults exhibit any agonistic bias toward any particular age/sex class as is found in adults (Table 5-29), even when adjustments are made to consider age-mates rather than adult partners. Global adult sex-typed proximity patterns are also not found in subadults; females subadults are not more cohesive than males (or males less so) as in adults (Table 5-28).

However, juveniles do show some similarities to adults in terms of their affiliation with and proximity to particular age/sex classes. Juvenile females bias their grooming away from adult males and toward infants, just as adult females do (Table 5-29). Additionally, adult sex-typed patterns of proximity bias with respect to adult males and females are partially exhibited by juveniles—juvenile females bias their contact time away from adult males and more strongly toward adult females than their male peers (Table 5-29).

Juvenile males also exhibit behavioral patterns that resemble those of same-sex adults. Juvenile males exhibit significantly more brachial and antebrachial marking than do females, even if they do not exhibit the temporal patterns in their marking behavior found in adult males (Table 5-30).

TABLE 5-28. Summary of sex differences in adult sex-typed global agonism and proximity measures across age classes.

Intrinsic behavior	Age	Sex Difference	Time effects	
Aggression	AD	♀ +	·	·
	JUV	·	·	·
	INF	·	·	·
Supplant	AD	♀ +	·	·
	JUV	·	·	·
	INF	·	·	·
Total # neighbors in contact	AD	♀ +	·	·
	JUV	·	♀ ⍰	♂ ⍰
	INF	·	♀ ⍰	♂ ⍰
Total # neighbors in reach	AD	♀ +	·	·
	JUV	·	·	·
	INF	·	♀ –	♂ –
Total # neighbors in 3m	AD	♀ +	·	·
	JUV	·	·	·
	INF	·	·	·
Time in contact with others	AD	♀ +	·	♂ +
	JUV	·	♀ ⍰	♂ ⍰
	INF	·	♀ ⍰	♂ ⍰
Time in reach of others	AD	♀ +	♀ –	·
	JUV	·	♀ –	♂ –
	INF	·	♀ ⍰	♂ ⍰
Time in 3m of others	AD	♀ +	♀ +	♂ +
	JUV	·	·	·
	INF	·	·	·
Time in 5m of others	AD	♀ +	♀ +	♂ +
	JUV	·	·	·
	INF	·	♀ –	♂ –

Sex difference: + significantly greater
· no difference
Time effects: + increase with time
– decrease with time
⍰ quadratic effect (– with time, + with time^2)
· no effect

TABLE 5-29. Summary of sex differences in adult sex-typed agonism to, grooming of, and proximity to each partner age/sex class in subadults.

Intrinsic behavior	Partner type	Age	Sex-typed bias		Time effect	
Supplant	AM	AD	·	♂ +	·	·
		JUV	n/a			
		INF	n/a			
	JM	JUV	·	·	·	·
		INF	n/a			
Grooming	AM	AD	♀ –	·	·	·
		JUV	♀ –	·	·	·
		INF	·	·	♀ –	?
	INFs	AD	♀ +	·	♀ –	·
		JUV	♀ +	♂ –	·	·
		INF	·	·	·	·
Time in contact	AF	AD	♀ +	·	·	·
		JUV	·	·	·	·
		INF	♀ —	♂ –	♀ ∩	♂ ∩
Time in 3m	AF	AD	♀ +	·	♀ –	·
		JUV	♀ ++	♂ +	·	·
		INF	·	·	♀ –	♂ –
Time in contact	AM	AD	♀ –	♂ +	♀ +	♂ –
		JUV	♀ –	·	·	·
		INF	·	·	♀ ∩	♂ ∩
Time in 3m	AM	AD	♀ —	♂ –	·	♂ –
		JUV	♀ —	♂ –	·	·
		INF	·	·	·	·
Time in contact	JM	AD	♀ —	♂ –	·	·
		JUV	·	·	·	·
		INF	·	·	·	·
Time in 3m	JM	AD	·	♂ +	♀ +	·
		JUV	·	·	·	·
		INF	·	·	·	·
Time in contact	INFs	AD	·	♂ –	·	·
		JUV	·	·	·	·
		INF	·	·	·	·

TABLE 5-29. Continued.

Sex-typed bias: + significantly more than expected at random
++ significantly more than +;
– significantly less than expected at random;
— significantly less than –;
· no difference from expected at random
Time effects: + increase with time
– decrease with time
⍰ quadratic effect (+ with time, – with time^2);
· no effect

TABLE 5-30. Summary of sex differences in adult sex-typed scent marking across all age classes.

Intrinsic behavior	Age	Sex Difference	Time effects	
Antebrachial mark	AD	♂ +	♂ –	·
	JUV	♂ +	·	·
	INF	n/a	·	·
Brachial mark	AD	♂ +	♂ –	
	JUV	♂ +	·	·
	INF	n/a	·	·
Anoint tail	AD	♂ +	·	
	JUV	n/a	·	·
	INF	n/a	·	·
Tail wave	AD	♂ +		
	JUV	n/a	·	·
	INF	n/a	·	·

Sex difference: + significantly greater
Time effect: – decrease with time
· no effect

Infants do not exhibit any sex differences in any adult sex-typed behaviors (Tables 5-28 through 5-30); adult-like behavioral sex differences are only found in juveniles. Due to the sampling issues in the infant cohort, I cannot exclude the possibility that juvenile sex-differences begin to develop before one year of age, but I can clearly conclude that some adult sex-differences develop during the subadult period, between 12 and 23 months at the latest.

Additionally, these juvenile sex differences almost certainly develop before gonadal maturation. These juveniles were captured during the months of June and July, and they were still smaller in body size than adults, with no indication of the development of secondary sexual characteristics (personal obs.). Furthermore, the juvenile cohort was never seen to anogenital mark, a behavior which is thought to be a behavioral marker of sexual maturation.

The behavioral sex differences exhibited by juveniles are not always entirely concordant with those seen in adults. However, this does not indicate that the juvenile sex differences found do not represent subadult developmental developmental trajectories of eventual adult sex-typed patterns. Developmental components of adult sex-typed behaviors are not expected to exactly match the fully developed adult manifestations of those behaviors. Furthermore, generalized or baseline sex-typed behavioral tendencies will be overlain and influenced by factors that will differ by age class. Baseline proximity patterns, for example, will be further shaped by the adult need to mate during the mating season, which will not influence juvenile proximity patterns, and by the juvenile tendency to maintain proximity to their mothers, which will not constrain the association patterns of non-natal adult males.

The adult sex-typed behaviors that appear to have a subadult developmental component that, therefore, might be influenced by subadult social interactions are: sex-typed patterns of grooming of adult males and infants, sex-typed patterns of proximity bias with respect to adult females and adult males, sex-typed patterns of infant interest (represented by grooming and proximity bias), and sex-typed patterns of scent marking (Table 5-31).

TABLE 5-31. Summary of adult sex-typed behaviors possessing a subadult developmental component.

Intrinsic behavior	Partner type	Age	Sex difference
Grooming	Adult ♂	AD	♀ –
		JUV	♀ –
	Infants	AD	♀ +
		JUV	♀ +
Time in 3m	Adult ♀	AD	♀ +
		JUV	♀ +
Time in contact	Adult ♂	AD	♀ –
		JUV	♀ –
Time in 3m	Adult ♂	AD	♀ –
		JUV	♀ –
Time in close proximity	Infants	AD	♀ +
		JUV	♀ +
Antebrachial mark	n/a	AD	♂ +
		JUV	♂ +
Brachial mark	n/a	AD	♂ +
		JUV	♂ +

Sex difference: + significantly greater
– significantly less

As discussed in Chapter 4, expression of adult social behavior (sexually differentiated and otherwise) appears to be strongly driven by seasonal variation—in particular, by the birth season and the mating season. This is to be expected, as most adult females will be directly involved in the social activities and pressures unique to the birth season as a result of caring for a dependent infant, most males will be involved in the social activities and pressures unique to one of dispersal "seasons" that loosely corresponds with the birth season, and adults of both sexes will be directly involved in the social activities and pressures unique to the mating season. It is less obvious whether or how patterns of subadult social behavior will be affected by these seasonal variations, but given that adult social patterns are changing, subadult social patterns may undergo concomitant change, even if only due to constraint resulting from changes in adult interaction patterns.

CHAPTER 6: POTENTIAL EXTRINSIC MOTIVATORS OF INTRINSIC SEXUAL DIFFERENTIATION

The adult sex-typed behaviors that appear to have a subadult developmental component are: sex-typed patterns of grooming of adult males and infants, sex-typed patterns of proximity bias with respect to adult females and adult males, sex-typed patterns of infant interest, and sex-typed patterns of scent marking. Because these behaviors have a developmental component that appears before gonadal maturation, they must be dependent on pre-maturational inputs for their development—either prenatal processes, and/or postnatal but prematurational hormonal and/or social processes or ecological constraints. Unfortunately, the effects of prenatal processes on subadult behavior are beyond the scope of this study and will not be considered further. Postnatal, prematurational hormone effects will be investigated in future work. The present study will be limited only to a consideration of social and gross ecological processes that may shape the development of subadult behavioral sex differences. There are two main types of behavioral interactions that might shape the development of behavioral sex differences—other individuals may be either differentially agonistic or affiliative toward subadults of each sex. Due to the particular distributions of juveniles and infants across groups in this sample, it is difficult to characterize the sex-typed interactions of juveniles with other juveniles and impossible to characterize those of infants with other infants. Therefore, only the behavior of older age cohorts toward infants and juveniles will be considered here.

AFFILIATION (GROOMING) FROM OTHERS

Infants

Although there were no clear intrinsic behavioral sex differences among infants, a number of intrinsic behavioral sex differences were found among juveniles. While the presence of sex-differential treatment by others toward infants apparently did not motivate the immediate development of sex-differential behavior in those individuals, sex-differential treatment of infants could be important for shaping later behavioral sex differences. Therefore, despite the lack of intrinsic behavioral sex differentiation in infants found in this sample, sex-differential treatment of infants by older cohorts was still investigated.

There is no clear evidence of sex-differential receipt of grooming in total, or from particular age/sex classes except from adult males (Table 6-1). The best fit linear RP model suggests that infant females tend to receive less overall grooming than infant males (Fig. 6-1), but that this difference tends to decrease over time. Still, neither effect on overall grooming rates received reaches statistical significance. There are also no significant sex differences in the amount of grooming received from mothers, non-maternal adult females, juvenile females, or juvenile males (Table 6-1).

In contrast, the best fit mean RP model indicates that infant females receive significantly less grooming from adult males than infant males do (Table 6-1). Analyses of grooming received by adult males for each sex indicate that infant males receive slightly more grooming from adult males than infant females do and there is no temporal change in receipt of grooming for infant males, but that infant females receive less grooming from adult males through time (Table 6-1, Fig. 6-2).

Qualitative examination of individual OLS regressions (Fig. 6-3) illustrates that this result is due to an unusual pattern of grooming received by only one infant male (08M234), in which his grooming by adult males increased through time. This particular infant male had an ill mother who weaned him early and who, after that time, groomed him little. He may have been seeking out grooming from whence he was most likely to receive it and least likely to receive aggression. This pattern also mirrors the trends seen in overall rates of receipt of grooming, begging the question of whether this one infant male's receipt of grooming is driving the sex differential trends in overall rates of grooming received, but an examination of individual infant OLS regressions of time groomed per hour (Fig. 6-4) shows that this infant's grooming patterns do not account for those trends. Considering these results all together, I conclude that there is no good evidence that infants experience sex-differential grooming by adult males or that they experience sex-differential rates of grooming overall, although the latter may merit further research.

TABLE 6-1. Model parameter estimates for time groomed by others for infants.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	Groomed total	linear RP	INT	2.91	0.35	27	8.23	<.0001*
			TIME	-0.33	0.06	77	-5.65	<.0001*
			SEX	-0.80	0.46	27	-1.73	0.09†
			TIME*SEX	0.14	0.08	77	1.81	0.07†
INF	Groomed by MOM	random int. LMEM	INT	0.84	0.17	27	4.89	<.0001*
			SEX	0.00	0.24	79	0.00	1.00
		linear RP	INT	0.71	0.16	27	4.34	0.0002*
			TIME	-0.09	0.02	77	-3.66	0.0005*
			SEX	0.06	0.21	27	0.28	0.78
			TIME*SEX	0.02	0.03	77	0.71	0.48
INF	Groomed by AF	quad. LMEM	INT	1.58	0.29	27	5.36	<.0001*
			SEX	-0.38	0.40	58	-0.95	0.34
			TIME	-0.50	0.18	17	-2.83	0.01*
			TIME^2	0.04	0.02	58	2.04	0.05*
			SEX*TIME	0.03	0.22	58	0.14	0.89
			SEX*TIME^2	0.01	0.02	58	0.35	0.73
		mean RP	INT	0.05	0.09	27	0.53	0.60
			SEX	0.13	0.11	27	1.20	0.24
INF	Groomed by AM	mean RP	INT	0.40	0.07	27	5.45	<.0001*
			SEX	-0.23	0.10	27	-2.36	0.03*
	Male groomed by AM	mean RP	INT	0.40	0.09	13	4.33	0.0008*
	Female groomed by AM	linear RP	INT	0.34	0.06	14	5.57	<.0001*
			TIME	-0.04	0.01	49	-3.33	0.002*
INF	Groomed by JF	random int. LMEM	INT	0.12	0.05	27	2.48	0.02*
			SEX	-0.06	0.06	79	-0.92	0.36
INF	Groomed by JM	mean RP	INT	0.01	0.02	27	0.73	0.47
			SEX	0.03	0.02	27	1.15	0.26

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

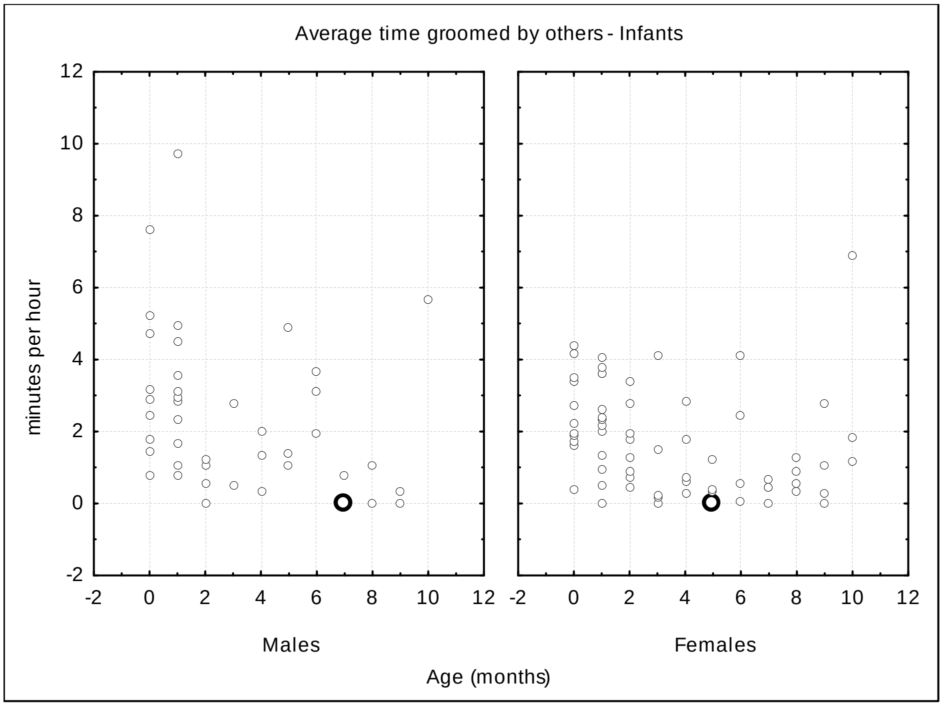


Fig. 6-1. Average time groomed by others for infants.

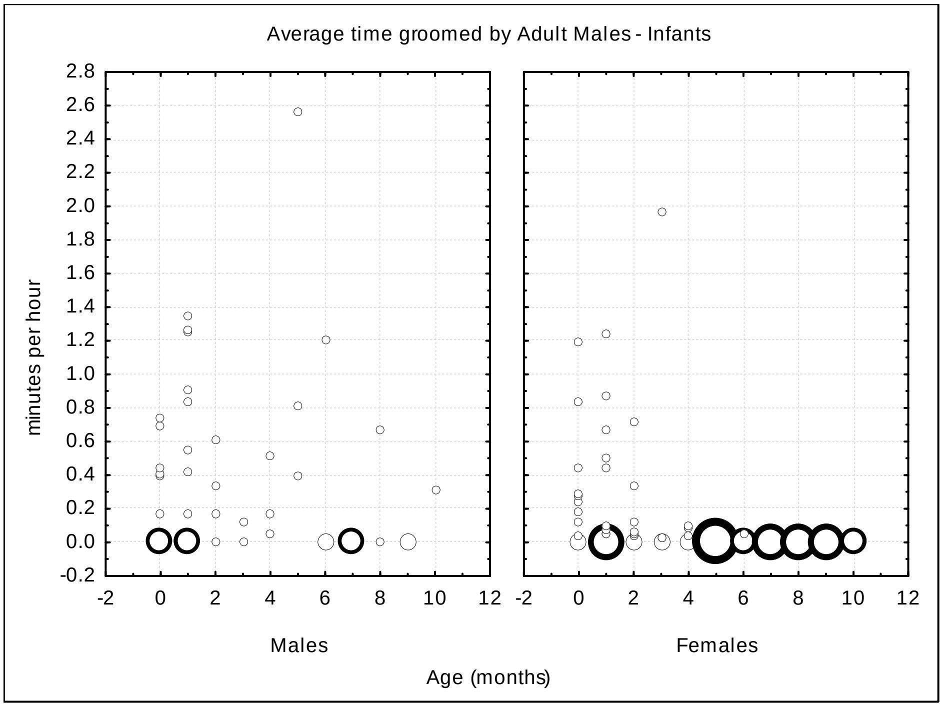


Fig. 6-2. Average time groomed by adult males for infants.

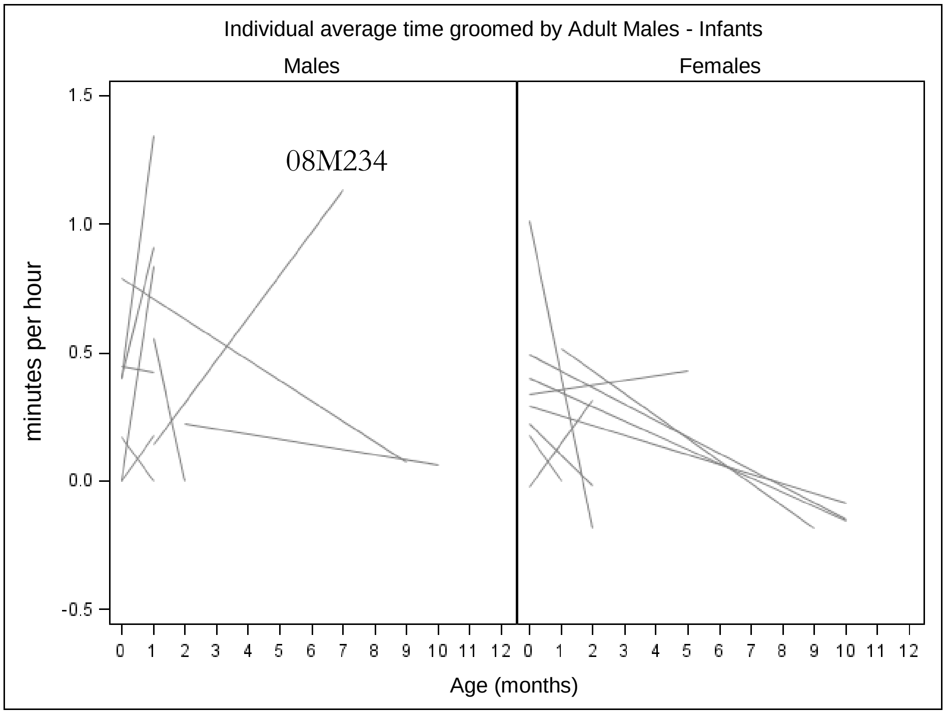


Fig. 6-3. Individual OLS regressions for average time groomed by adult males for infants.

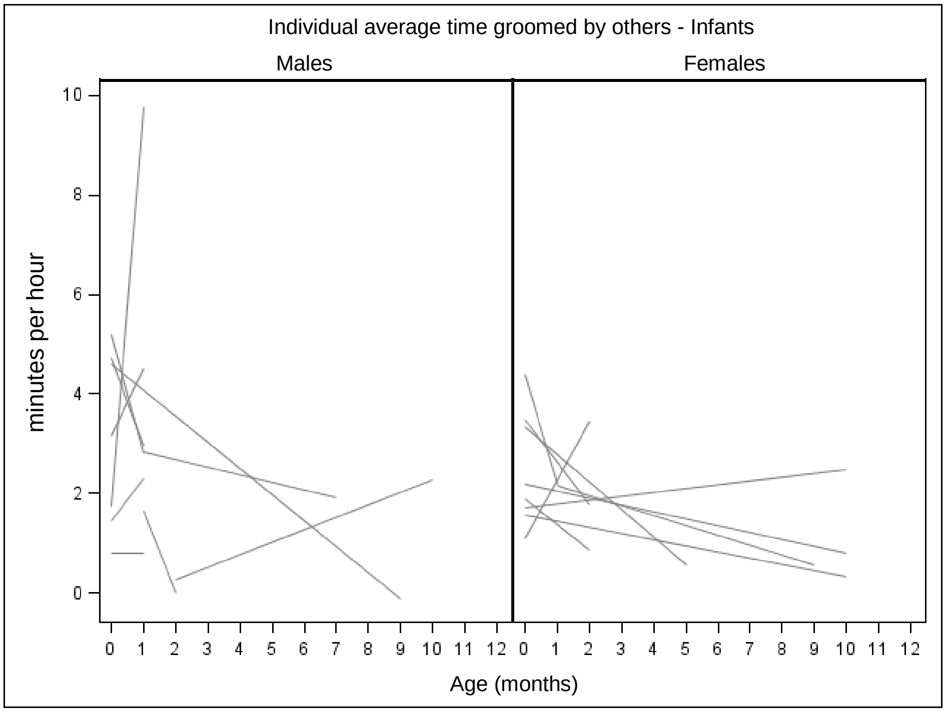


Fig. 6-4. Individual OLS regressions for average time groomed by others for infants.

Juveniles

There is no evidence that juveniles differ by sex in the rates at which they receive grooming—either overall, or from particular age/sex classes (Table 6-2).

TABLE 6-2. Model parameter estimates for time groomed by others for juveniles.

Age	Variable	Model	Effect	est.	SE	DF	t	p
JUV	Groomed TOT	random int. LMEM	INT	0.84	0.22	7	3.87	0.006*
			SEX	0.17	0.31	83	0.55	0.58
		mean RP	INT	0.18	0.06	7	2.81	0.03*
			SEX	-0.06	0.09	7	-0.62	0.56
JUV	Groomed by MOM	random int. LMEM	INT	0.16	0.13	7	1.28	0.24
			SEX	0.24	0.18	83	1.34	0.18
		mean RP	INT	0.00	0.03	7	0.02	0.99
			SEX	0.01	0.04	7	0.38	0.71
JUV	Groomed by AF	mean RP	INT	0.03	0.03	7	0.78	0.46
			SEX	0.01	0.04	7	0.21	0.84
JUV	Groomed by AM	random int. LMEM	INT	0.57	0.24	7	2.34	0.05*
			SEX	-0.48	0.36	83	-1.34	0.18
		mean RP	INT	0.01	0.01	7	0.92	0.39
			SEX	-0.01	0.01	7	-1.08	0.32

TOT = total; * $p \leq 0.05$. All tables follow these conventions.

AGGRESSION AND SUPPLANTS RECEIVED FROM OTHERS

Infants

There is no evidence that infants received sex-differential expressions of overt aggression—either overall, or from particular age/sex classes (Table 6-3).

TABLE 6-3. Model parameter estimates for rates of aggression received from others for infants.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	TOT Aggression received	random int. LMEM	INT	0.74	0.18	27	4.15	0.0003*
			SEX	-0.10	0.24	79	-0.44	0.66
		mean RP	INT	0.30	0.12	27	2.57	0.02*
			SEX	-0.15	0.15	27	-0.96	0.34
INF	Aggression from MOM	random int. LMEM	INT	0.14	0.08	27	1.67	0.11
			SEX	0.07	0.11	79	0.67	0.51
		mean RP	INT	0.14	0.08	27	1.61	0.12
			SEX	0.07	0.11	27	0.66	0.51
INF	Aggression from AF	mean RP	INT	0.1635	0.06	27	2.65	0.01*
			SEX	-0.066	0.08	27	-0.83	0.42
INF	Aggression from AM	mean RP	INT	0.06	0.02	27	3.38	0.002*
			SEX	-0.03	0.02	27	-1.49	0.15
INF	Aggression from JF	random int. LMEM	INT	0.02	0.02	27	0.92	0.37
			SEX	0.00	0.03	79	0.11	0.91
INF	Aggression from JM	random int. LMEM	INT	0.0074	0.04	27	0.18	0.85
			SEX	0.0628	0.05	79	1.17	0.25
		mean RP	INT	0.01	0.04	27	0.17	0.87
			SEX	0.06	0.06	27	1.04	0.31

* $p \leq 0.05$

Infants do not experience sex differences in overall rates of being supplanted, or in being supplanted by any age/sex class except for in being supplanted by adult females (Table 6-4). Infant females are supplanted by adult females significantly more often than infant males are (Fig. 6-5). However, infants were never supplanted until the age of 2 months, and there were only three infant males in the sample older than 2 months of age, such that this result should be regarded cautiously. I think that this result accurately describes what happened in this sample and results from real differences in how often the males and females in this particular infant sample were supplanted. Qualitatively, my impression is that males of the infant cohort kept themselves out of situations in which they would be supplanted and that they were largely ignored by adults compared to females of the infant cohort. However, I feel less certain as to whether the few male infants in this sample accurately represent male infants more broadly.

TABLE 6-4. Model parameter estimates for rates of supplants received from others by infants.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	TOT Supplants received	random int. LMEM	INT SEX	0.13 0.04	0.07 0.09	27 79	1.89 0.46	0.07† 0.65
INF	Supplants from MOM	random int. LMEM	INT SEX	0.03 -0.03	0.02 0.02	27 79	1.90 -1.18	0.07† 0.24
INF	Supplants from AF	mean RP	INT SEX	0.02 0.06	0.02 0.02	27 27	0.88 2.59	0.39 0.02*
INF	Supplants from AM	random int. LMEM	INT SEX	0.03 -0.01	0.02 0.02	27 79	1.74 -0.44	0.09† 0.66
INF	Supplants from JF	N/A	BEHAVIOR NOT SEEN					
INF	Supplants from JM	random int. LMEM	INT SEX	0.00 0.04	0.03 0.04	27 79	0.00 1.25	1.00 0.22

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

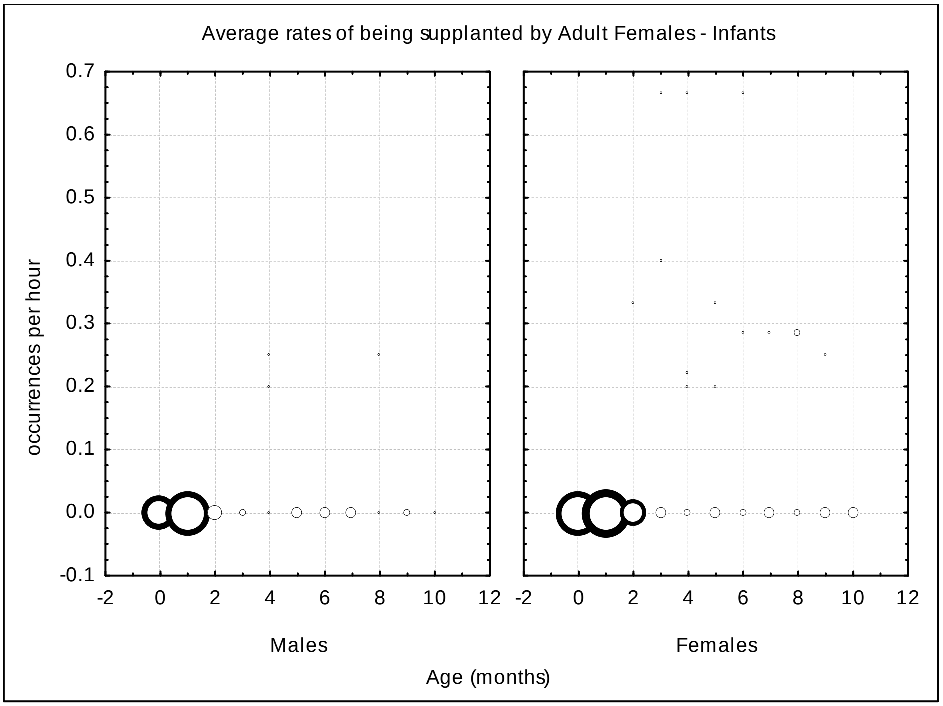


Fig. 6-5. Average rates of being supplanted by adult females for infants.

Juveniles

There are no juvenile sex differences in overall rates of overt aggression received, or in rates of aggression received from adult males and females. However, juvenile females receive significantly more aggression from their mothers than do juvenile males (Table 6-5, Fig. 6-6).

TABLE 6-5. Model parameter estimates for rates of aggression received from others for juveniles.

Age	Variable	Model	Effect	est.	SE	DF	t	p
JUV	TOT Aggression received	random int. LMEM	INT	0.40	0.12	7	3.43	0.01*
			SEX	0.23	0.16	83	1.39	0.17
		mean RP	INT	0.34	0.09	7	3.83	0.006*
			SEX	0.09	0.13	7	0.75	0.48
JUV	Aggression from MOM	random int. LMEM	INT	0.03	0.03	7	1.00	0.35
			SEX	0.13	0.05	83	2.74	0.007*
		mean RP	INT	0.04	0.04	7	0.92	0.39
			SEX	0.12	0.06	7	2.08	0.08†
JUV	Aggression from AF	random int. LMEM	INT	0.25	0.10	7	2.56	0.04*
			SEX	0.09	0.14	83	0.63	0.53
		mean RP	INT	0.22	0.06	7	3.37	0.01*
			SEX	0.06	0.09	7	0.60	0.57
JUV	Aggression from AM	mean RP	INT	0.08	0.03	7	2.79	0.03*
			SEX	-0.01	0.04	7	-0.14	0.89

* p ≤ 0.05; † 0.05 < p ≤ 0.10

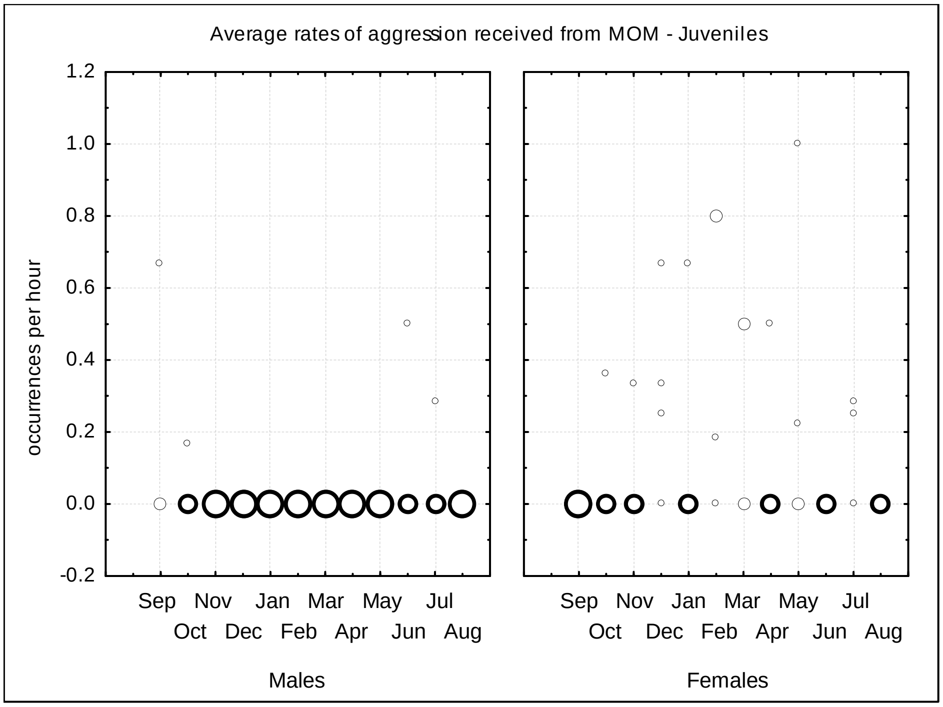


Fig. 6-6. Average rates of receiving aggression from mother for juveniles.

There are no juvenile sex differences in rates of being supplanted, either overall, or by adults of different sex classes (Table 6-6).

TABLE 6-6. Model parameter estimates for rates of supplants received from others for juveniles.

Age	Variable	Model	Effect	est.	SE	DF	t	p
JUV	TOT Supplants received	random int. LMEM	INT	0.83	0.31	7	2.69	0.03*
			SEX	-0.50	0.46	83	-1.08	0.28
		mean RP	INT	0.35	0.07	7	4.92	0.002*
			SEX	-0.03	0.10	7	-0.31	0.76
JUV	Supplants from MOM	random int. LMEM	INT	0.04	0.02	7	1.76	0.12
			SEX	-0.01	0.03	83	-0.19	0.85
		mean RP	INT	0.04	0.03	7	1.18	0.28
			SEX	0.01	0.04	7	0.27	0.79
JUV	Supplants from AF	mean RP	INT	0.13	0.03	7	4.09	0.005*
			SEX	0.03	0.05	7	0.71	0.50
JUV	Supplants from AM	mean RP	INT	0.10	0.02	7	4.16	0.004*
			SEX	-0.05	0.03	7	-1.41	0.20

* $p \leq 0.05$

EXTRINSIC SOCIAL INTERACTIONS – SUMMARY

There is little evidence that extrinsic, sexually differentiation social interactions are important in the development of adult sex-typed behavior in *Lemur catta*, because there is very little evidence that extrinsic, sexually differentiated social interactions occur. Infants are not treated in sex-differential ways by others except for the possibility that infant females are supplanted more often by adult females than infant males are (Table 6-7). Similarly, juveniles do not experience sex differential treatment by adults except in that juvenile females receive more aggression from their mothers than do juvenile males (Table 6-8). These patterns of interaction are not simply the result of sex differences in proximity patterns to adult females and mothers, however, because infant females are not significantly more often in proximity to adult females than infant males (Table 5-26) and juvenile females are not significantly more often in proximity to their mothers than juvenile males (Table 5-27). Thus, these sex differential interactions with mothers and non-maternal adult females may represent real sex differences in treatment by other group members of potential import for the development of later behavior.

TABLE 6-7. Summary of sex differences in extrinsic social behavior received by infants.

Age	Extrinsic behavior	Partner type	Sex difference or bias		Time effect	
INF	Groomed overall	n/a	·		♀ –	♂ –
	Groomed	MOM	·	·	♀ –	♂ –
		Adult ♀	·	·	♀ ⍰	♂ ⍰
		Adult ♂	·	·	♀ –	·
		Juvenile ♀	·	·	·	·
		Juvenile ♂	·	·	·	·
	Overt aggression overall	n/a	·		·	·
	Overt aggression	MOM	·	·	·	·
		Adult ♀	·	·	·	·
		Adult ♂	·	·	·	·
		Juvenile ♀	·	·	·	·
		Juvenile ♂	·	·	·	·
	Supplants overall	n/a	·		·	·
	Supplants	MOM	·	·	·	·
		Adult ♀	♀ +	·	·	·
		Adult ♂	·	·	·	·
		Juvenile ♀	n/a			
		Juvenile ♂	·	·	·	·

Sex-typed bias: + significantly more than opposite sex or than expected at random
· no difference from opposite sex or from expected at random
Time effects: – decrease with time
⍰ quadratic effect (– with time, + with time^2);
· no effect

TABLE 6-8. Summary of sex differences in extrinsic social behavior received by juveniles.

Age	Extrinsic behavior	Partner type	Sex difference or bias		Time effect	
JUV	Groomed overall	n/a	·		·	·
	Groomed	MOM	·	·	·	·
		Adult ♀	·	·	·	·
		Adult ♂	·	·	·	·
	Overt aggression overall	n/a	·		·	·
	Overt aggression	MOM	♀ +	·	·	·
		Adult ♀	·	·	·	·
		Adult ♂	·	·	·	·
	Supplants	MOM	·	·	·	·
		Adult ♀	·	·	·	·
		Adult ♂	·	·	·	·

Sex difference: + significantly greater
Time effects: · no effect

SEX DIFFERENTIAL ECOLOGY

An animal's ecological needs will determine where it should be in space and time, and as such, will affect the number, sex, and ages of the conspecifics with which that individual can or must interact [Altmann 1980]. Whenever males and females are foraging at different times, in different places, or are focusing on different resources, they will necessarily have access to a different set of social partners, and they may face different constraints on their interactions with those social partners. In such cases, sex-differential social behavior may be an artifact of sex-differential niche use. Further complicating the issue, some authors [Agostini and Visalberghi 2005] have proposed that the initial development of ecological niche divergence may sometimes stem from social causes, rather than the reverse.

The simplest way to control for the effects of sex differences in ecology on sex-differential social behavior is to examine behavior that occurs before sexual differentiation in ecology. However, many juvenile primates exhibit sex-typical resource use patterns prior to sexual maturation [Grassi 2002], and mothers of some species might even base their own foraging choices on the sex of their dependent infant [Bercovitch 2002]. Detailed studies of diet at early ages should reveal whether young animals that are foraging in different places among different social partners actually differ in their diets. If not, such patterns would suggest that diverging dietary needs are not responsible for motivating sex-differential foraging behavior even if they are associated with time engaged in foraging.

Unfortunately, the developmental timeline of sexual differentiation in feeding ecology of *Lemur catta* is still unknown, and if it were generally known, yearly seasonal variation would call for a documentation of early dietary shifts in this particular sample in order to fully address this issue. A detailed investigation of the diets of the particular subadults sampled here was beyond the scope of this project. However, it is only the effects of dietary divergence on social divergence that is of interest here, and not dietary divergence, *per se*. Therefore, I have investigated subadult sex differences in social proximity during foraging. If sex differences in social proximity during foraging are present, they cannot reliably be attributed to either dietary or social sex differentiation by this study. But, if there are no sex differences in social proximity during foraging, dietary divergence is probably not driving sex differences in intrinsic social behavior.

Feeding time

While sex differences in amount of time spent feeding will not necessarily influence the set of social partners available to subadults in sex differential ways, it would affect the amount of time subadults have to express intrinsic behavioral sex differences. However, neither infants nor juveniles exhibit sex differences in the amount of time they spend feeding (Table 6-9).

TABLE 6-9. Model parameter estimates for time spent feeding by subadults.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	Time feeding	random int. LMEM	INT	2.73	0.80	25	3.41	0.002*
			SEX	0.36	1.09	78	0.33	0.74
		quad. RP	INT	0.22	0.17	25	1.32	0.20
			SEX	-0.24	0.22	25	-1.11	0.28
			TIME	1.77	0.27	74	6.58	<.0001*
			$TIME^2$	-0.11	0.03	74	-3.43	0.001*
			SEX*TIME	0.35	0.34	74	1.02	0.31
			$SEX*TIME^2$	-0.04	0.04	74	-1.13	0.26
JUV	Time feeding	random int. LMEM	INT	6.03	0.40	7	14.93	<.0001*
			SEX	-0.95	0.58	83	-1.64	0.11
		mean RP	INT	6.03	0.46	7	13.09	<.0001*
			SEX	-0.94	0.66	7	-1.43	0.20

* $p \leq 0.05$

SEX DIFFERENCES IN PROXIMITY DURING FEEDING/FORAGING

Dietary sex divergence can occur in at least two ways—either through modeling of same-sex others or as a result of an intrinsic need to utilize sex-typed resources. This study cannot distinguish between them, but in either case, sex differences, if present, should be reflected in individuals' nearest neighbor distributions during feeding. If subadults are achieving dietary sexual differentiation through same-sex modeling, they should be closer to and more overtly attentive to same-sex adults. If they are simply driven to dietary sex differentiation by an underlying need to consume sexually differentiated food resources, they should find themselves in close proximity to other same-sex individuals who have the same underlying dietary needs. Therefore, to assess whether gross dietary sex differentiation is an important potential cause underlying the intrinsic subadult sex differences in social behavior documented in this study, the only measure of proximity during feeding and foraging investigated here was nearest neighbor identity.

Infants

There is no evidence of an infant sex difference in foraging time spent with adult females as nearest neighbors, but patterns of nearest neighbor association with mother and adult males during feeding are less clear (Table 6-10). The most complex LMEMs that could be fit were random intercepts models. Those indicate that there is no sex difference in foraging time spent with mother as a nearest neighbor, but an overall tendency for infant females to spend less foraging time with adult males as nearest neighbors than infant males do. In contrast, the best fit RP models are quadratic and account for temporal changes throughout the year. These suggest that there is a sex*time interaction with regard to foraging time spent with mother as a nearest neighbor in which females spend more of their foraging time with mother as a nearest neighbor as the observation year progresses, and that there is no sex difference with regard to foraging time spent with adult males as nearest neighbors. Examination of the scatterplots and individual OLS plots reveal that there is little reason to conclude that infant females are spending significantly more of their foraging time with mother as a nearest neighbors as time progresses (Figures 6-7, 6-8) and that there may be good reason to conclude that infant females, on average, tend to spend less of their foraging time with adult males than infant males do (Figures 6-9, 6-10). Because the LMEMs partially account for inter-individual variation and because their results are supported by a qualitative examination of the individual OLS regressions, I conclude that there is no sex difference in terms of infant feeding time spent with mother as a nearest neighbor but a tendency for infant females to spend less of their foraging time with adult males than infant males do. Incidentally, one of the three infant males for which good longitudinal data are available exhibits a different pattern from all other infants with regard to how much of his foraging time he spent as a nearest neighbor of adult males (08M155). This was not the infant whose mother was ill, so I have no reason to think that his unusual spatial patterning resulted from pathological processes.

TABLE 6-10. Model parameter estimates for deviations from expected time spent feeding with nearest neighbors at random for infants by adult partner type.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	Dev feed nearest MOM	random int. LMEM	INT	0.84	0.22	25	3.87	0.0007*
			SEX	0.09	0.29	78	0.33	0.75
		quad. RP	INT	0.26	0.14	25	1.87	0.07†
			SEX	-0.20	0.18	25	-1.11	0.28
			TIME	0.22	0.12	74	1.92	0.06†
			TIME^2	-0.02	0.01	74	-1.76	0.08†
			SEX*TIME	0.32	0.14	74	2.28	0.03*
			SEX*TIME^2	-0.03	0.02	74	-1.88	0.06†
INF	Dev feed nearest AF	random int. LMEM	INT	-0.40	0.14	25	-2.79	0.01*
			SEX	-0.04	0.19	78	-0.22	0.83
		linear RP	INT	-0.11	0.06	25	-1.85	0.08†
			TIME	-0.11	0.03	76	-3.55	0.0007*
			SEX	0.07	0.08	25	0.88	0.39
			TIME*SEX	0.02	0.04	76	0.48	0.63
INF	Dev feed nearest AM	random int. LMEM	INT	-0.64	0.14	25	-4.60	0.0001*
			SEX	-0.32	0.18	78	-1.80	0.08†
		quad. RP	INT	-0.08	0.05	25	-1.82	0.08†
			SEX	0.09	0.06	25	1.51	0.14
			TIME	-0.39	0.07	74	-5.46	<.0001*
			TIME^2	0.04	0.01	74	3.73	0.0004*
			SEX*TIME	-0.12	0.09	74	-1.32	0.19
			SEX*TIME^2	0.00	0.01	74	0.00	1.00

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

Dev indicates deviation from time expected at random

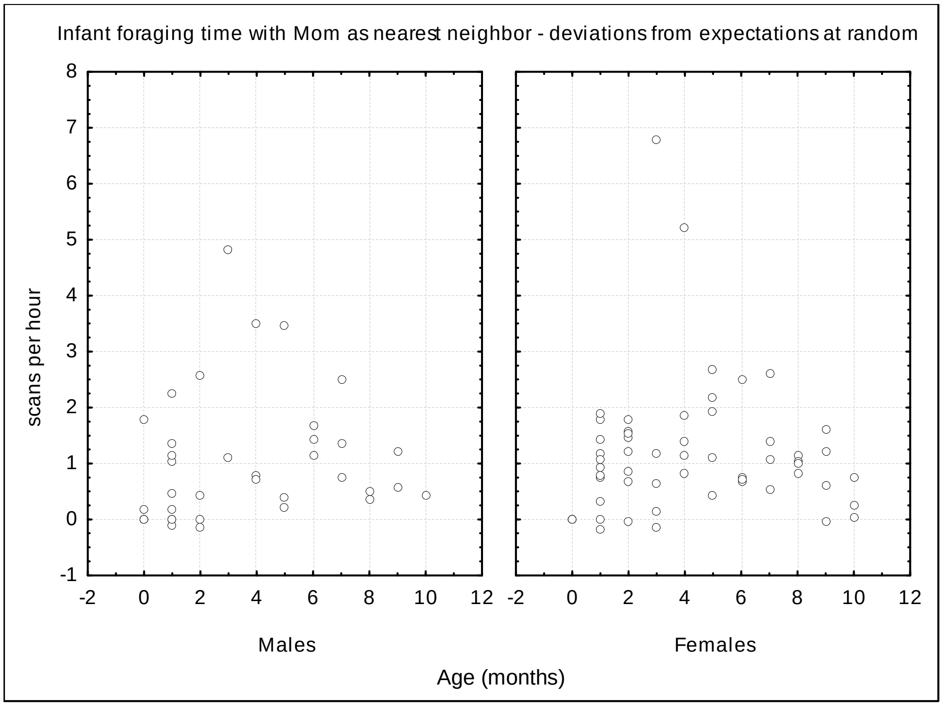


Fig. 6-7. Deviations from expected time foraging with mother as a nearest neighbor at random for infants.

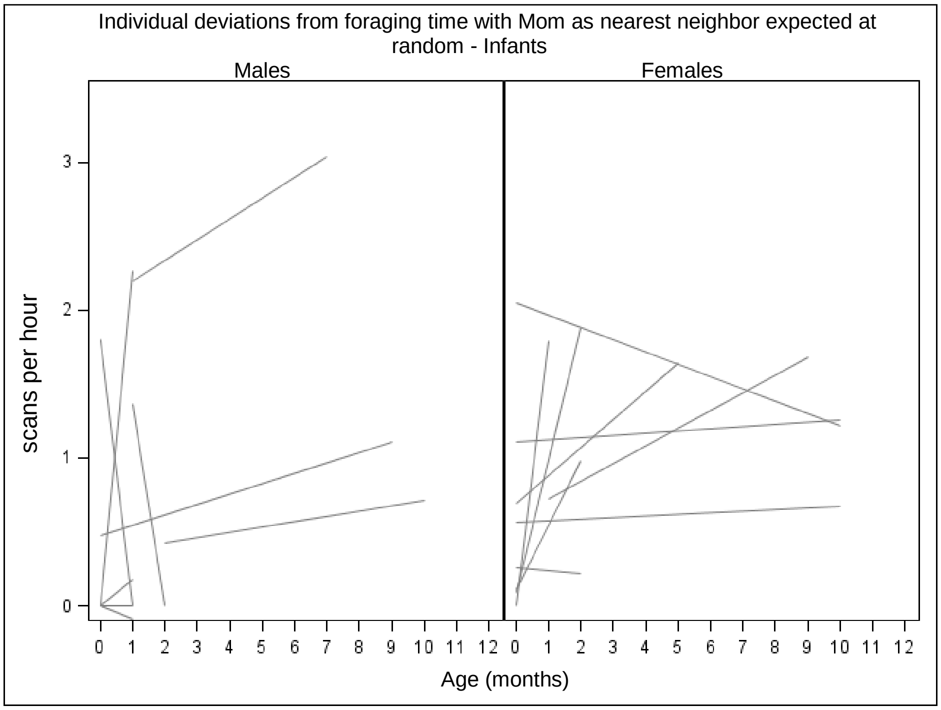


Fig. 6-8. Individual OLS regressions of deviations from expected time foraging with mother as a nearest neighbor at random for infants.

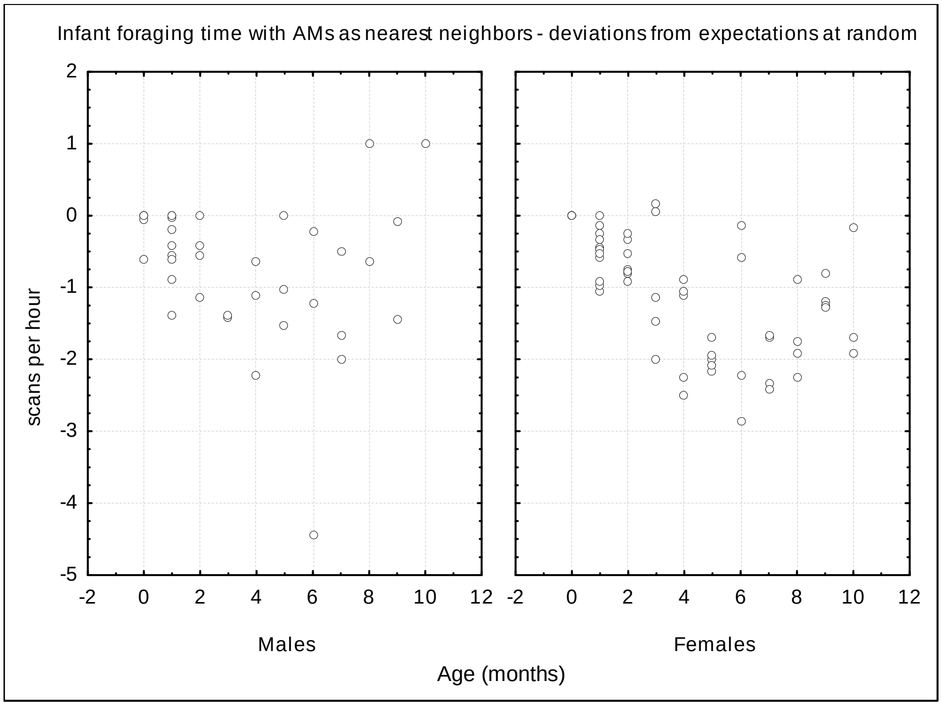


Fig. 6-9. Deviations from expected time foraging with adult males as nearest neighbors at random for infants.

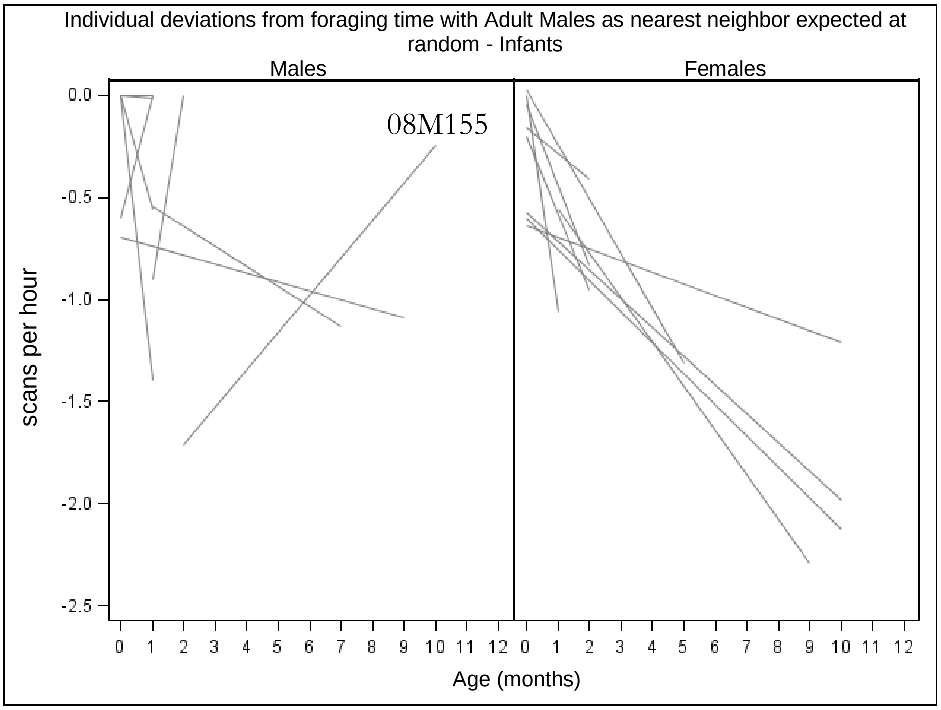


Fig. 6-10. Individual OLS regressions of deviations from expected time foraging with mother as a nearest neighbor at random for infants.

There are no infant sex differences in foraging time spent with juveniles or other infants as nearest neighbors (Table 6-11).

TABLE 6-11. Model parameter estimates for deviations from expected time spent feeding with nearest neighbors at random for infants by subadult partner type.

Age	Variable	Model	Effect	est.	SE	DF	t	p
INF	Dev feed nearest JF	random int. LMEM	INT	0.03	0.05	25	0.52	0.61
			SEX	0.01	0.07	78	0.15	0.88
INF	Dev feed nearest JM	mean RP	INT	0.00	0.00	25	-1.70	0.10†
			SEX	0.00	0.00	25	0.91	0.37
INF	Dev feed nearest INFs	random int. LMEM	INT	-0.09	0.07	25	-1.27	0.22
			SEX	0.13	0.10	78	1.28	0.20
		mean RP	INT	-0.045	0.03	25	-1.57	0.13
			SEX	0.0115	0.04	25	0.30	0.77

† $0.05 < p \leq 0.10$

Juveniles

There are no juvenile sex differences in feeding time spent with adult males and non-maternal adult females as nearest neighbors, but there is some suggestion that juvenile females tend to spend more of their feeding time with their mothers as nearest neighbors than juvenile males do (Table 6-12, Fig. 6-11). Qualitative examination of the individual OLS regressions (Fig. 6-12) indicate that only two of four juvenile males spend less feeding time with their mothers as nearest neighbors than the juvenile female group does. Therefore, I conclude that there is no strong evidence that juveniles exhibit a sex difference in their feeding time spent with their mothers as nearest neighbors, but suggest that this pattern deserves future investigation.

TABLE 6-12. Model parameter estimates for deviations from expected time spent feeding with nearest neighbors at random for juveniles by adult partner type.

Age	Variable	Model	Effect	est.	SE	DF	t	p
JUV	Dev feed nearest MOM	random int. LMEM	INT	-0.07	0.16	7	-0.44	0.68
			SEX	0.40	0.23	83	1.72	0.09†
		mean RP	INT	-0.08	0.18	7	-0.42	0.68
			SEX	0.41	0.26	7	1.54	0.17
JUV	Dev feed nearest AF	random int. LMEM	INT	0.28	0.24	7	1.15	0.29
			SEX	-0.36	0.35	83	-1.04	0.30
		mean RP	INT	-0.12	0.16	7	-0.71	0.50
			SEX	0.08	0.23	7	0.34	0.75
JUV	Dev feed nearest AM	random int. LMEM	INT	-0.86	0.14	7	-5.96	0.0006*
			SEX	-0.06	0.21	83	-0.31	0.76
		mean RP	INT	-0.87	0.16	7	-5.26	0.001*
			SEX	-0.06	0.24	7	-0.24	0.82

* p ≤ 0.05; † 0.05 < p ≤ 0.10

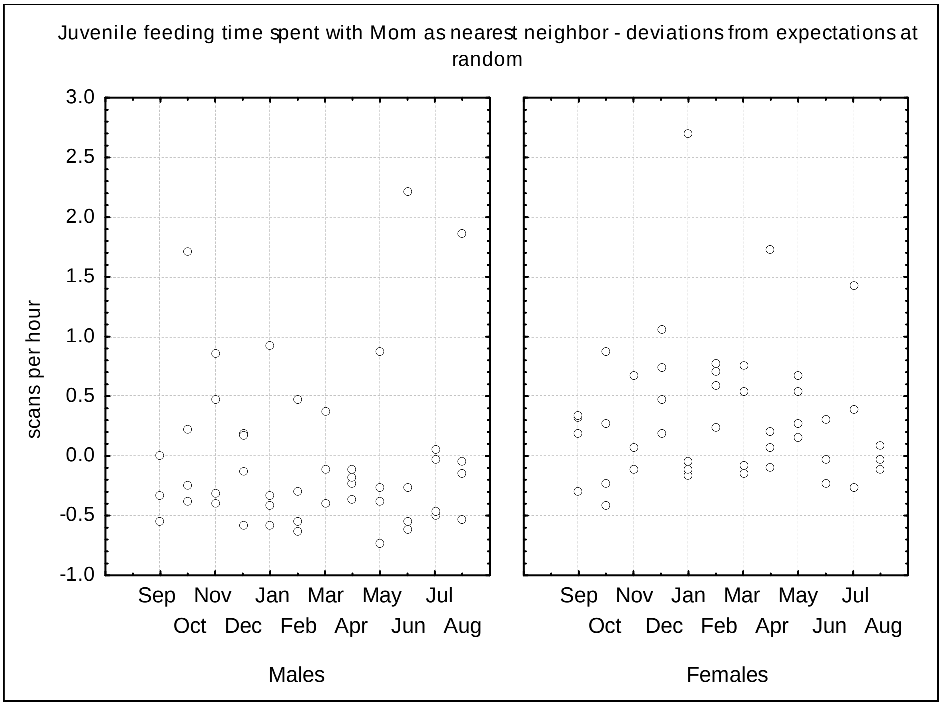


Fig. 6-11. Deviations from expected time foraging with mother as a nearest neighbor at random for juveniles.

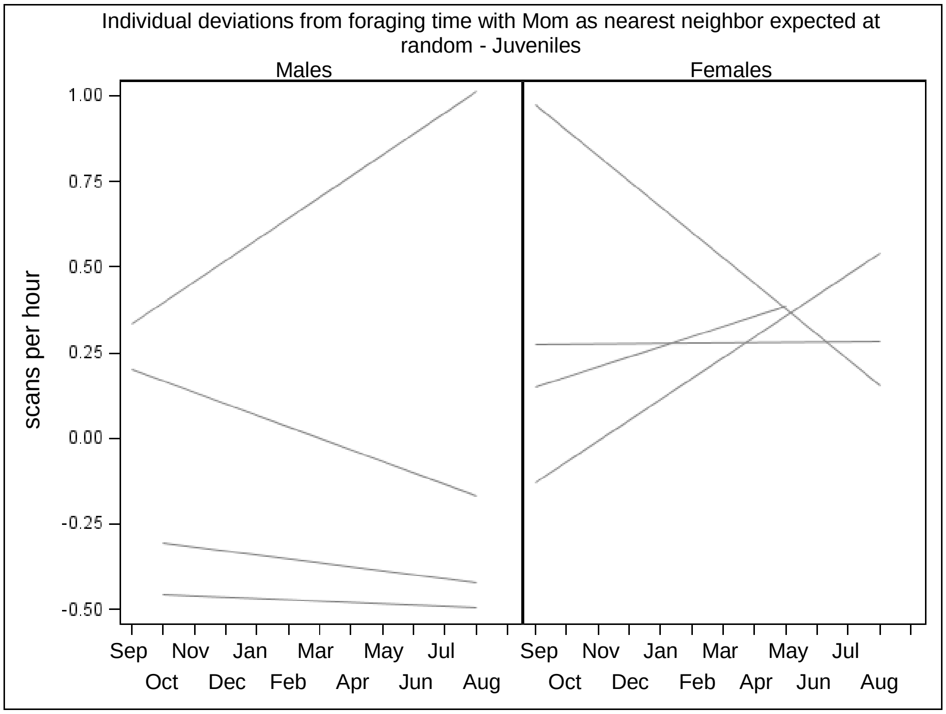


Fig. 6-12. Individual OLS regressions of deviations from expected time foraging with mother as a nearest neighbor at random for juveniles.

As with previous analyses of juvenile-juvenile interactions, the results of analyses of bias in feeding time spent with other juveniles are problematic. There is no evidence of a juvenile sex difference in feeding time spent with juvenile females as a nearest neighbor, but juvenile females apparently spend significantly more feeding time with a juvenile male as a nearest neighbor than juvenile males do (Table 6-13). Recall, though, that only two juvenile males had the opportunity to have a juvenile male nearest neighbor; all juvenile male-juvenile male interactions describe only those of this dyad, and my impression of this dyad was that their relationship was not particularly affiliative. Furthermore, examination of the scatterplot (Fig. 6-13) and individual OLS regressions (Fig. 6-14) show that the significant effect here is due solely to the feeding nearest neighbor patterns of only two of the juvenile females, and only due to feeding proximities late in the year. Therefore, I conclude that there is no good evidence that juveniles exhibit a sex difference in their tendency to feed near other juveniles. There is also no evidence that juveniles exhibit a sex difference in their feeding time spent with infants as nearest neighbors (Table 6-14).

TABLE 6-13. Model parameter estimates for deviations from expected time spent feeding with nearest neighbors at random for juveniles by subadult partner type.

Age	Variable	Model	Effect	est.	SE	DF	t	p
JUV	Dev feed nearest JF	random int. LMEM	INT	0.14	0.07	7	1.99	0.09†
			SEX	-0.08	0.10	83	-0.77	0.45
JUV	Dev feed nearest JM	mean RP	INT	0.03	0.03	7	1.12	0.30
			SEX	0.11	0.04	7	2.63	0.03*
JUV	Dev feed nearest INFs	linear RP	INT	-0.70	0.19	7	-3.70	0.008*
			TIME	0.09	0.03	81	2.79	0.007*
			SEX	0.18	0.27	7	0.64	0.54
			TIME*SEX	-0.05	0.05	81	-0.95	0.34

* $p \leq 0.05$; † $0.05 < p \leq 0.10$

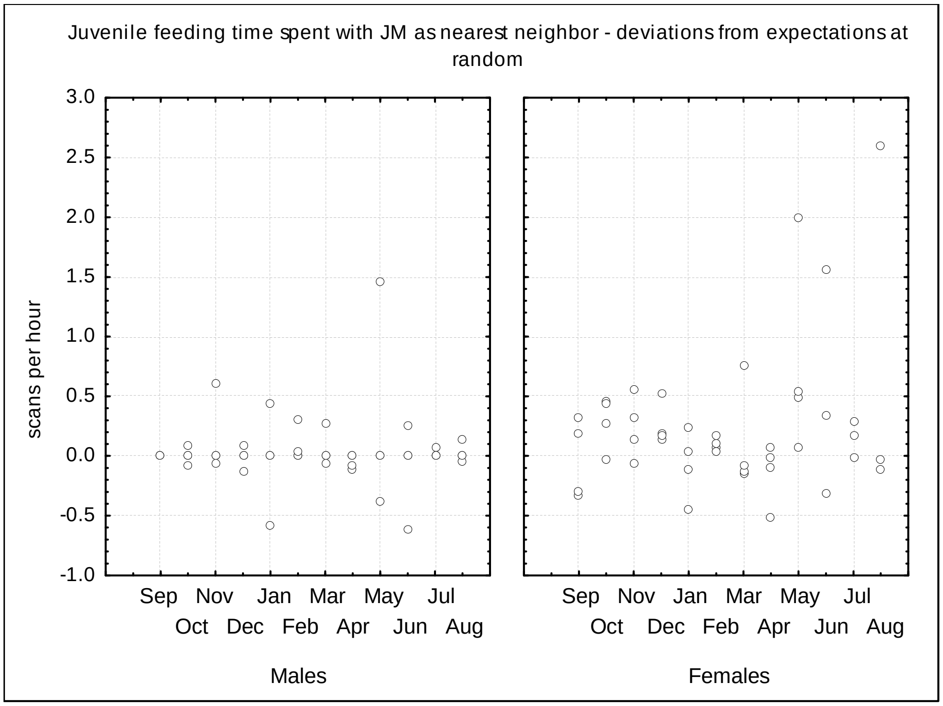


Fig. 6-13. Deviations from expected time foraging with juveniles males as nearest neighbors at random for juveniles.

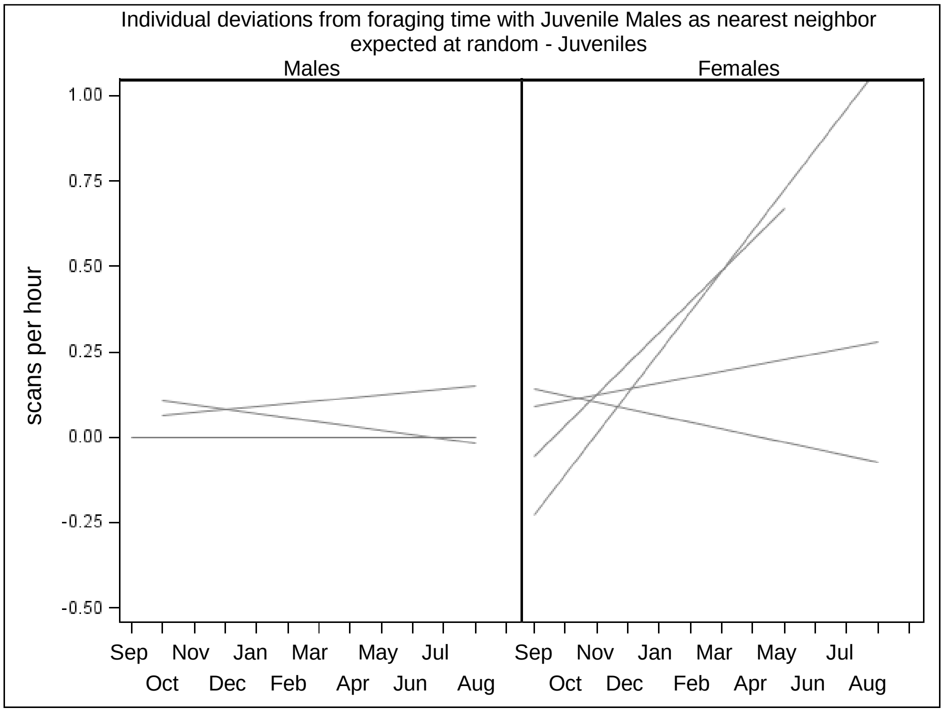


Fig. 6-14. Individual OLS regressions of deviations from expected time foraging with juveniles males as nearest neighbors at random for juveniles.

Ecological sex differences - Summary

Gross ecological factors do not seem to be key causal motivators of sexual differentiation in subadult intrinsic social behavior because there are no significant subadult sex differences in gross ecological measures (Table 6-14).

TABLE 6-14. Summary of subadult sex differences in socioecological measures.

Age	Ecological factor	Partner type	Sex-typed bias		Time effect	
INF	Time spent feeding	n/a	·	·	·	·
	Nearest neighbor when feeding	MOM	·	·	·	·
		AF	·	·	·	·
		AM	·	·	·	·
		JF	·	·	·	·
		JM	·	·	·	·
		INFs	·	·	·	·
JUV	Time spent feeding	n/a	·	·	·	·
	Nearest neighbor when feeding	MOM	·	·	·	·
		AF	·	·	·	·
		AM	·	·	·	·
		JF	·	·	·	·
		JM	·	·	·	·
		INFs	·	·	·	·

Sex-typed bias: · no difference from expected at random
Time effects: · no effect

SUMMARY - EXTRINSIC MOTIVATORS OF INTRINSIC SEXUAL DIFFERENTIATION

In sum, the only potential causal factor of subadult sexually differentiated behavioral development identified in this study is higher rates of aggression by mothers toward their juvenile daughters than toward their juvenile sons. Whether higher rates of maternal aggression toward juvenile daughters is a causal factor motivating juvenile sex differentiation in intrinsic social behavior depends on whether increased maternal aggression precedes intrinsic sex differences.

Unfortunately, the temporal resolution afforded by the data from this study is insufficient to address this point for several reasons. First, maternal aggression toward juveniles is not very common; second, there were only four juveniles of each sex in the collared population. The combination of these two factors results in poor temporal resolution of the development of this sex difference in the juvenile sample. Third, due to the sampling problems in the infant cohort at later ages, there is no reliable indication of what is happening with maternal aggression toward offspring in the months immediately preceding the data presented here on the juvenile cohort. In other words, unless good resolution on the development of this sex difference is also available for the period of 0-11 months, one cannot be certain that one has captured the onset of this sex difference. Resolution of this issue will have to wait for future study.

CHAPTER 7: DISCUSSION AND CONCLUSIONS

SEX-TYPED SOCIALIZATION

This study found essentially no evidence for extrinsic socialization of the development of sex-typed adult behavior in *Lemur catta*. Twenty-two quantifiable sex differential behaviors were identified in adults. As expected, infants were not found to exhibit adult patterns of behavioral sex differentiation for any of those twenty-two behaviors (*contra* Figure 2-1-A). Therefore, infants were not sexually differentiated in any of the adult sex-typed behaviors documented in this study, allowing for the possibility of a pre-pubertal developmental component to each (Figure 2-1-B).

However, only a portion of these adult sex-typed behaviors were found to differ by sex in the juvenile cohort—patterns of grooming of adult males and infants; some elements of patterns of proximity to adult females, adult males, and infants; and male-typical marking behaviors (Table 5-31). The rest presumably develop sometime after the age of 24 months, just prior to, at, or after sexual maturity, as in Figure 2-2. While these late-developing behaviors may depend on social input for their appearance and maintenance, it is difficult to make a case that they are not simply dependent on gonadal hormone input of instead. Therefore, only overall grooming rates and patterns of grooming of adult males and infants, patterns of proximity to adult females, adult males, and infants, and male-typical marking behaviors are considered potential targets of extrinsic socialization.

This study found evidence of sex differential treatment of subadults by others in only two behaviors—infant females are supplanted more often by adult females than infant males are, and juvenile females receive more aggression from their mothers than juvenile males do. Therefore, only two sex differential social interactions (one in infancy and one in juvenility) were potential socialization agents for eight sexually differentiated juvenile behaviors. Unfortunately, this study did not have the resolution necessary to assess the temporal relationships between these extrinsic sex differences and the intrinsic subadult sex differences they might have shaped. As a result, these two types of sex differential treatment by adults cannot be rejected as causal in the development of juvenile sex differences in intrinsic social behavior.

However, it is not immediately obvious how receiving more supplants from adult females and more aggression from one's mother would be expected to result in the particular set of juvenile sex differences found in this study. I cannot imagine a scenario in which being supplanted more often by adult females or receiving more aggression from mother would directly cause decreased proximity to and rates of grooming adult males or increased proximity to and rates of grooming infants on the part of juvenile females, or in increased rates of scent-marking related behavior on the part of juvenile males. An argument could be made that being supplanted more often by adult females or receiving more aggression from mother resulted in juvenile females seeking out allies or other "friends," resulting in their increased rates of overall grooming of others and increased proximity to adult females. However, coalitions are conspicuously absent in ring-tailed lemurs [Pereira 1995; Sauther et al. 1999], and interactions that could be interpreted as triadic averaged only five per month. Furthermore, only four triadic interactions recorded could be interpreted as third-party intervention on behalf of a juvenile. A more fine-grained investigation of this hypothesis might reveal that juvenile females are grooming and maintaining proximity to individuals other than those from whom they are receiving aggression, which would suggest that juvenile females are indeed seeking out “friends” in response to the aggression they receive. Until this investigation can be completed, I tentatively conclude that this study has produced no evidence that sex differential socialization by adults is an important driver of ring-tailed lemur sex-typed social development.

It is important to caution that even though this study found evidence for only two types of sex differential treatment of subadults by others, this does not indicate that other types of sex differential treatment of subadults do not occur. The limited sample sizes in this study only allowed for detection of sex differences with relatively large effect sizes and precluded the identification of subtle sex differences in treatment by others. This was especially true for the infant cohort in months 3-11, but characterized the sample overall. Due to the small sample sizes used here, sex differential treatment by others characterized by small effect sizes are invisible to this study.

This caveat is not just theoretical—relatively subtle sex differences in treatment of infants by others do occur in primates and have been documented in studies of other species with larger sample sizes. In captive rhesus macaques, mothers investigate the genitals of male infants more often than those of female infants [Goy et al. 1988] and are more responsive to male infants’ distress calls [Tomaszycki et al. 2001]. In free-ranging Barbary macaques, mothers choose social partners based on their own infants’ sex [Timme 1995]. In captive sooty mangabeys, non-maternal group members direct more types of social interaction toward female infants, engage in more types of contact behaviors with female infants, and larger numbers of non-maternal group members interact with female infants than with male infants [Deputte and Quris 1996]. In wild yellow baboons, high-ranking mothers initiate more changes in contact with their sons and nurse their daughters less [Nguyen et al. 2010]. In captive rhesus macaques, milk quality and composition (but not total milk energy available to offspring) differs according to infant sex [Hinde 2009]. None of this work can assess whether these sex differences in mother-infant interactions are driven by mothers or infants, but they illustrate the types of subtle but potentially important early sex-differential interactions that have been documented in studies of other primates but which, if they occur in *Lemur catta*, will have been missed by this one. Future work will investigate sex differences in more detailed aspects of subadult social interactions such as responsibility for proximity maintenance with mothers, responsibility for initiating grooming with particular age/sex classes, and further investigation of the contexts in which juveniles receive aggression from their mothers.

Therefore, despite the fact that this study found no support for the primacy of sex-differential treatment of subadults by adults in behavioral sex differentiation, the potential importance of sex-differential treatment by adults in that process is not negated for this species. Still, this study reveals that sex-typed treatment of subadults by adults is more subtle than the expression of sex-typed behavior on the part of juveniles, which, to me, suggests that juvenile sex differences are more likely dependent on some other proximate factor for their development. The two most likely candidates are sexually differentiated ecological demands and sexually differentiated organizational and activational hormone effects.

ECOLOGICAL CAUSES

I also found no evidence that sexual differentiation in feeding and foraging behavior, specifically, is driving the development of the behavioral sex differences documented in this study. However, my treatment of sexual differentiation in foraging behavior in this study was not sufficiently rigorous to conclusively rule out sex-differential ecology as a driver of pre-pubescent behavioral sex differentiation. A more rigorous investigation of this question would thoroughly investigate the timing of actual dietary sex differentiation, which proved to be beyond the scope of this study due to the impossibility of distinguishing many *Lemur catta* food plants from each other without both botanical training and the assistance of a Malagasy botanist familiar with those plants. Documentation of the timing of actual dietary divergence between males and females relative to sex divergence in other behavioral variables may rule out ecological constraints as a causal factor in behavioral sex differentiation—until there is sexual divergence in diet, ecological constraint cannot be argued to be responsible for sexual divergence in other arenas. Whenever dietary and social sex divergence co-vary, distinguishing causation becomes an intractable problem (just as when behavioral and hormonal sex differences co-occur). Further complicating the issue, just as dietary divergence may drive social sex differentiation, social sex differentiation may drive or facilitate dietary divergence [Agostini and Visalberghi 2005], and covariance between the two does not indicate that ecological constraint is the causal factor underlying both. It is not yet clear whether this is a problem for understanding the casual factors underlying behavioral sex differentiation in *Lemur catta*, as the temporal relationships among particular aspects of ecological and social behavior are still unknown. However, the findings of this study may support conceptualizing of this problem from an entirely different perspective that solves this conundrum (discussed below).

HORMONAL CAUSES

Impending work on the developmental profiles of total androgens and estradiol will soon address the role of postnatal hormones in the development of sex-typed behavior in this population. Developmental profiles of estradiol and total androgens will be created to test for changes in steroid hormone levels that correspond temporally to the appearance of the juvenile sex-typed behaviors found in this study and that can be inferred to be activating their development.

Some authors have previously suggested that the development of anogenital marking is under direct control of gonadal hormones because it corresponds with sexual maturation in captivity [Palagi et al. 2002; Pereira 2002]. The behavioral data here—no evidence of anogenital marking prior to 24 months of age in a population in which sexual maturation does not occur until at least 26 months of age [Pereira 1995]—are consistent with this hypothesis, and the hormonal data to directly address it will soon be produced by M. Teague O'Mara and myself.

The developmental schedule of other types of marking behavior suggests a potential role for prenatal organization of marking behavior. Despite the accelerated somatic and gonadal maturational schedules that characterize captive settings and that are reflected in the early onset of anogenital marking in captivity compared to the wild, the juvenile onset of brachial and antebrachial marking behavior at 12-13 months of age appears to be invariant across settings (Figure 7-1). This invariance suggests that the juvenile onset of brachial and antebrachial marking is unrelated to somatic growth. It bears resemblance to the onset of male-typical urinary behavior in domestic dogs, which is determined by prenatal and neonatal (but not postnatal) hormones [Ranson and Beach 1985]. Still, juvenile rates of brachial and antebrachial marking do not mirror adult rates, suggesting that juvenile and adult marking behaviors are motivated at least partially by different causal factors. Perhaps they come under the control of gonadal hormones at maturity even though they are not dependent on gonadal control in the juvenile period, as with male mounting behavior and female patterns of infant interest in rhesus and pig-tail macaques, respectively [Maestripieri and Zehr 1998; Wallen et al. 1991].

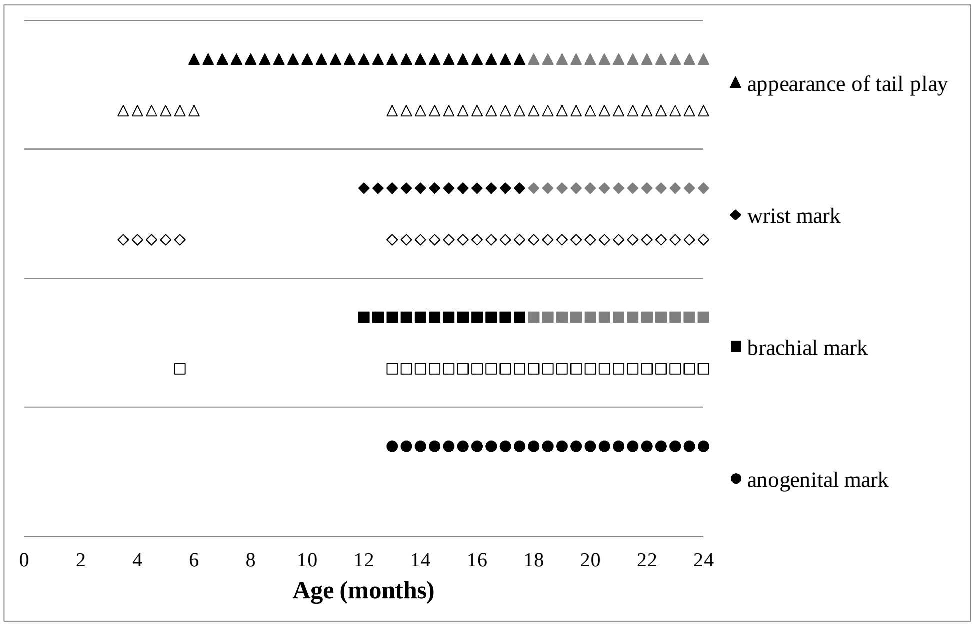


Fig. 7-1. Developmental timing of scent marking behaviors in captivity (solid symbols) and at Beza Mahafaly (open symbols). Tail play, wrist mark, and brachial mark data are from Palagi et al. [2002], which observed individuals only through the age of 18 months. These behaviors are marked in grey through 24 months because they are unlikely to have ceased between the ages of 18 and 24 months in captivity.

Unfortunately, aside from the inferences made above, investigating the role of prenatal hormones in lemur sex-typed development was well beyond the scope of this particular study and will have to wait for future research. Therefore, regardless of the outcomes of impending research on postnatal hormonal development, this study will never be able to rule out the hypothesis that juvenile lemur sexual differentiation is hormonally programmed in the womb, and that no kind of social input need be invoked to explain sexual differentiation. Certainly, much experimental work has established the important roles of both prenatal and postnatal hormones in the development of sex-typed behavior, and sexual differentiation does not proceed normally without their appropriate, sex-typed input in other primate species [Deputte and Goy 1991; Eisler et al. 1993; Goy and Phoenix 1971; Goy et al. 1988; Maestripieri and Zehr 1998; Pasterski et al. 2005; Pomerantz et al. 1986; Thornton and Goy 1986; Wallen 2001; Wallen et al. 1991; Wallen and Hassett 2009]. Still, while experimental work has shown that hormonal inputs are crucial to the normative development of sex-typed behavior, it has also shown—across many species and many behaviors—that the acquisition of the adult behavioral phenotype simultaneously relies on social input [Capitanio 1984; Champoux et al. 1992; Champoux et al. 1991; Goldfoot 1977; Harlow 1962; Harlow 1965; Harlow and Harlow 1962a; Harlow and Harlow 1962b; Maestripieri 2005a; Maestripieri et al. 2007; Mason 1978; Ruppenthal et al. 1976; Suomi 1997; Wallen 1996; Wallen 2005; Wallen et al. 1977; Wallen et al. 1981] and that social environment and/or experience can affect the expression of hormones that are typically thought to contribute to the development and expression of sex-typed behavior [e.g., Muller et al. 2009; Wobber et al. 2010]. Therefore, a position that envisions juvenile lemurs as prenatally hormonally programmed automatons is less reasonable than the alternative hypothesis I now put forward.

JUVENILE MODEL-SEEKING

This study conclusively demonstrates that sex-typed treatment of subadults by adults is uncommon (or, at most, subtle) compared to the expression of sex-typed behavior on the part of juveniles, which suggests that juvenile *Lemur catta* are likely the prime movers of their sexual differentiation, not adults. This is not to say that sexually differentiated interactions with adults are unimportant in the development of species typical sex-typed behavior. Even when sexually differentiated social interactions result from juvenile-driven sexually differentiated proximity patterns, those social interactions may be important for further shaping behavioral sex differences. The evidence produced by this study simply suggests that, ultimately, the sexually differentiated developmental process in *Lemur catta* is more "bottom-up" than it is "top-down"—that subadults make the first sexually differentiated moves in their sexually differentiated social feedback loops and, with respect to behaviors that are not due solely to hormonal organization and activation, are largely responsible for driving their own behavioral sex differentiation.

The portion of subadult behavioral sex differentiation that relies on social input may be driven primarily in ring-tailed lemurs by juvenile "model-seeking" [Agostini and Visalberghi 2005; Lonsdorf 2005; Pereira 1988; Schiel and Huber 2006], and the way that juveniles ensure that they have access to sex-appropriate models may be through their proximity maintenance to them [Pereira 1988]. This is not a new idea, but considered from this perspective, the sex-differential treatment of juveniles by mothers is more likely an outcome of patterns of proximity of juveniles to their mothers than a cause of juvenile behavioral sex differentiation, and juvenile proximity patterns are justifiably considered to be more intrinsically than extrinsically determined (although, granted, others will have some contribution to these patterns).

If juvenile model-seeking via proximity maintenance is important in behavioral sex differentiation, increased aggression by mothers to juvenile females is more likely to be a response to some element of juvenile female proximity to mothers rather than a cause of it. Although this study did not find sex differences in juvenile proximity to mothers in measures derived from scan data, *per se*, other juvenile female proximity and behavioral tendencies documented in this study likely bring juvenile females in closer proximity to their mothers. For example, compared to male peers, juvenile females are more often in proximity to and spend more time grooming infants. Sometimes, these infants would have been their siblings and would have been in close association with their (shared) mothers. Perhaps juvenile female proximity to and increased interactions with their own siblings made them more likely than juvenile males to attract their mothers' ire. There may be other measures of intrinsic juvenile behavior not yet quantified from these data that will help to assess this hypothesis of juvenile model-seeking via sexual differentiation in proximity, and the narrower (and quite different) focus of this question will direct further investigation of this dataset.

Juvenile seeking of adult behavioral models is to be expected in sexually differentiated systems. This type of bottom-up social learning would seem to be a more effective target of selection than top-down socialization, and a juvenile model-seeking process of behavioral sex differentiation is consistent with the rarity of teaching found in non-human animals [Whiten et al. 2003] but the commonness of social learning by imitation, goal emulation, and other mechanisms in which the responsibility for social learning rests with the learner [Galef and Laland 2005; Hoppitt and Laland 2008; Pike and Laland 2010; Webster and Laland 2008]. Juvenile model-seeking also seems to apply to the acquisition of sex-typed foraging behavior in primates [Agostini and Visalberghi 2005; Lonsdorf 2004; Lonsdorf 2005]. If juveniles acquire all of their socially influenced behavioral sex differences through model-seeking, then sexual differentiation in feeding and foraging behavior need not be considered a confound of sexual differentiation in non-foraging contexts; instead, both may be more appropriately considered parallel manifestations of the same underlying process of behavioral sex differentiation.

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