SOCIAL PLAY IN THE SOUTH AMERICAN PUNARE

(<u>THRICHOMYS</u> <u>APEREOIDES</u>):

A TEST OF PLAY FUNCTION HYPOTHESES

by

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Thesis submitted to the Faculty of the

Virginia Polytechnic Institute and State University

in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

in

ZOOLOGY

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August, 1985

Blacksburg, Virginia

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(ABSTRACT)

The role of social play in juvenile behavioral development was examined in the punare (<u>Thrichomys</u> <u>apereoides</u>). Three proposed functions of social play were evaluated: 1. play serves to develop agonistic skills, 2. play has a role in the onset of weaning and 3. play establishes dominance relationships among participants.

Eight litters consisting of three juveniles and both parents were observed from birth until eight weeks of age, and the content, sequence and duration of parental and play behaviors were recorded. Adult agonism was characterized in paired encounters between unfamiliar adults. Encounters between unfamiliar juvenile dyads were conducted and compared to littermate play.

Sex specific differences in social play were concordant with observed differences in adult agonistic interactions.

Play bouts between male juveniles were more frequent, of greater duration and incorporated more dominance reinforcement behaviors than bouts between females. Mothers tended to avoid playing with offspring, while paternal play was frequent. Self-handicapping was observed during father-daughter play. Dominance relationships were evident during play, with strong, stable hierarchies established among male juveniles. Adult males dominated all offspring and juvenile males dominated female littermates. Unfamiliar juvenile play bouts were shorter in duration and more frequently resulted in avoidance than bouts among littermates.

These results suggest that punare social play functions to develop agonistic skills while concurrently establishing dominance relationships. The early establishment of dominance relationships may serve as a non-injurous means of precipitating male-biased post-weaning dispersal.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

The ontogeny of behavior is a topic of fundamental interest in the study of ethology, and juvenile play is thought to have an essential role in this development. Play has proved an enigmatic topic of investigation, and its adaptive value remains unclear due to the descriptive, highly subjective and often biased nature of earlier play research. Recent reviews by Fagen (1981) and Smith (1982) have identified a multitude of hypotheses concerning the function of juvenile play, but both conceded that quantitative support for most of the hypotheses is weak and often conflicting. Investigation of the evolutionary significance of play has been handicapped by futile attempts to pinpoint a single function for all forms of play across all species (Byers, 1984). Byers suggested that play, in the form of locomotor movements, evolved as motor training, and this ancestral function persists to varying extents in present-day species. The specific structure and content of juvenile play have been uniquely shaped by the selective forces acting on each species. Therefore, investigations of the role of play in behavioral development must consider the ecology of the model species.

The punare (<u>Thrichomys</u> <u>apereoides</u>) is an ideal species for a detailed study of juvenile play. Young are born highly precocial, yet the period of maternal dependence

extends beyond nutritional independence (Streilein, 1982a), facilitating extended juvenile play. Within hours of birth, juvenile movements are well coordinated, allowing the precise discrimination of play behaviors. The punare's play behavior repertoire is limited to a small number of easily differentiated behavior patterns, making it possible to collect objective data which are easily quantified.

The punare (<u>Thrichomys apereoides</u>), a medium-sized Echimyid rodent, is native to central and southern Brazil and Paraguay (Nowak and Paradise, 1983). It is strictly associated with rocky, thickly vegetated habitat (Mares et al.,1981; Melo, 1977; Streilein, 1982c), where thorn-scrub and cacti are the predominant vegetative forms (Lacher, 1982). The climate within the punare's range is semiarid, and is characterized by high temperatures and extremely unpredictable rainfall, with extensive flooding and prolonged periods of drought (Streilein, 1982a). As a result, the species' habitat is restricted to granitic outcroppings, which remain relatively mesic during periods of drought.

Punares are reported to be solitary, with adults defending individual territories against same-sexed conspecifics. Although territorial, overlap exists between animals of opposite sexes (Streilein, 1982b). Intraspecific agonistic behavior of wild-caught animals, described by

Streilein (1982d), consisted predominantly of upright displays, and conflicts tended to be resolved by avoidance rather than aggression. Encounters between adult males resulted in the highest frequency of agonism, while behavioral tolerance was greatest among opposite-sexed dyads. Streilein (1982b) reported a ratio of two adult females for every adult male, implying a polygynous mating system.

The current study investigated the role of social play in the behavioral development of juvenile punares and the extent to which the various proposed functions of play have shaped its content. Paired adult agonistic interactions were conducted and compared with juvenile social play. Parental influences on the behavioral development of juveniles were characterized, and social play within family groups and between unfamiliar juveniles was examined. Finally, the social interactions of a group of adults and juveniles were observed in a large, seminatural enclosure and compared to initial observations conducted in the smaller observation arena. Three proposed functions of juvenile social play were then evaluated: 1. play serves to develop agonistic skills, 2. play has a role in the onset of weaning, and 3. play establishes dominance relationships between participants.

Play has been hypothesized to enhance agonistic skills

by providing opportunities for juveniles to safely coordinate and perfect behaviors which otherwise might only be performed in emergency situations. The agonistic skill development hypothesis predicts close similarities between the components of social play and agonism (Smith, 1982). Sex specific differences in play should parallel dimorphism in adult roles (Biben, 1982; Smith, 1982). This hypothesis also predicts that play partners should be chosen on the basis of the potential practice benefits. In Siberian ibex (*Capra ibex sibirica*), where male juveniles play more frequently and intensely than females, males are the preferred play partners (Byers, 1980). Related partners should be preferred, and differences in play frequency, duration and content between related and unrelated juveniles are predicted (Bekoff, 1978; Smith, 1982; Symons 1978a).

A second proposed function of play is the regulation of developmental rates. The behavior of juveniles may act as cues to other individuals, resulting in developmental transitions. Anecdotal observations of domestic cats and several species of wild cats suggested that play might accelerate weaning through harassment of the mother (Fagen, 1981). This hypothesis predicts that the frequency of play should be high at weaning, and that parental females should respond to the increase in play with increased avoidance of the juveniles, thereby limiting their opportunities to

suckle.

Play may also serve to develop and reinforce dominance relationships. The dominance hypothesis predicts that behavioral components which determine dominance should appear in play (Poirer and Smith, 1974), that the interaction should result in an identifiable winner and loser, and that the outcome should be nonrandom and stable over time (Smith, 1982). Play should be most frequent among the sex for which dominance relationships are most important in adulthood (Fagen, 1981). For polygynous species with intense male-male competition, play should be most frequent among male juveniles. Male juveniles should preferentially play with other males, their future competitors, and adult males should exert dominance over juveniles in play bouts (Byers, 1980). If play is indeed serving to establish dominance relationships, the frequency of play should be greatest when dominance relationships are being determined, and should decrease when dominance relationships are stable (Smith, 1982).

The form and content of juvenile play has undoubtably been shaped by a great number of factors which vary from species to species. The role that play serves in the ontogeny of behavior is complex, and can only be elucidated through thorough, quantitative studies which take into account the many functions which play may serve. The

results of this study will provide information about the development of mammalian play behavior, clarify the importance of play in establishing dominance relationships and evaluate several current hypotheses of the evolutionary significance of play in punares.

LITERATURE REVIEW

The punáre (<u>Thrichomys</u> <u>apereoides</u>), a medium-sized Echimyid rodent, is native to central and southern Brazil and Paraguay (Nowak and Paradise, 1983). It is strictly associated with rocky, thickly vegetated habitat (Mares et al.,1981; Melo, 1977; Streilein, 1982c), where thorn-scrub and cacti are the predominant vegetative forms (Lacher, 1982). The climate within the punare's range is semiarid, and is characterized by high temperatures and extremely unpredictable rainfall, with extensive flooding and prolonged periods of drought (Streilein, 1982a). As a result, the species' habitat is restricted to granitic outcroppings, which remain relatively mesic during periods of drought.

Punares are scansorial, and move with agility through the rock-strewn, thickly vegetated habitat. They are herbivorous and frugivorous, feeding on cotton seeds and fruits, coconuts and cacti (Nowak and Paradise, 1983). Punares are generally nocturnal, with crepuscular activity peaks observed in the field (Mares et al., 1981), although the V.P.I. & S.U. Biology Department colony is most active during the mid-portion of the dark phase of the light cycle. They are reported to be solitary, with adults defending individual territories against same-sexed conspecifics. While territorial, overlap exists between animals of

7

opposite sexes (Streilein, 1982b). Intraspecific agonistic behavior of wild-caught animals, described by Streilein (1982d), consisted predominantly of upright displays, and conflicts tended to be resolved by avoidance rather than aggression. Encounters between adult males resulted in the highest frequency of agonism, while behavioral tolerance was greatest among opposite-sexed dyads.

Streilein (1982b) reported a ratio of two adult females for every adult male, suggesting a polygynous mating system. Reproduction is relatively synchronous (Mares et al., 1981), but some reproduction occurs throughout the year. Females exhibit a post-partum estrus and produce two to three litters per year (Streilein, 1982b). Litter size ranges from one to seven, with a mean of 3.1 reported from field data (Streilein, 1982b) and 3.4 reported from the National Zoological Park colony (Kleiman et al., 1979).

Juvenile punares are highly precocial. At birth, their eyes are open and they are fully furred and ambulatory. Within hours of birth their movements are well coordinated, and they have been observed to consume solid food (Streilein, 1982a). In spite of their precociality, juvenile punares have a prolonged period of maternal dependency. Although juveniles can be artificially weaned shortly after birth, nursing persists for three to four weeks.

This pattern of precocial young with delayed weaning is typical of the suborder Hystricomorpha. As a result of bearing precocial young, the parental behavior of Hystricomorphs is markedly different from that of altricial forms. Behaviors which maintain social bonds tend to be the main components of parent-offspring interactions, while direct care behaviors are relatively infrequent. In many species, mothers and young maintain contact through frequent vocalization (Kleiman, 1974). Wilson (1982) observed that body nosing was the predominant parental behavior in degus (Octodon degus). Maternal nest building and retrieval, however, are relatively infrequent (Kleiman, 1972). Paternal involvement in offspring care is widespread among Hystricomorphs (Kleiman, 1974). Males typically scent mark neonates by perineal dragging or enurination, thus minimizing the scent differences between father and young, and aiding in offspring recognition. Paternal care commonly takes the form of grooming, huddling and sleeping with the young. Several species of hystricomorphs have been observed to engage in vigorous social play with their offspring. Wilson (1982) speculated that such behavior in degus greatly influenced juvenile social development.

The ontogeny of behavior is a topic of fundamental interest in the study of ethology, and juvenile play behavior is thought to have an essential role in this

development. Play, although easily recognized and described, has proved an enigmatic topic of investigation, since its specific benefits remain unclear. This lack of an obvious function has hampered attempts to define play, and has caused several researchers to question whether play is a valid behavioral category. Lazar and Beckhorn (1974) and Taylor (1980) advanced the view that behaviors commonly refered to as play are undeveloped agonistic behaviors of immature animals. There is a great deal of evidence, however, that play can be reliably considered a distinct behavioral category on the basis of its structural components.

Although play bears a strong resemblance to other behaviors, such as agonism and predatory behavior, it has several distinguishing features. The sequence in which behavioral components occur may be reordered (Poole and Fish, 1975) or less predictable (Bekoff, 1974). Certain behaviors may be repeated more frequently in play (Henry and Herrero, 1974), and some occur solely within the context of play. These include species specific solicitation behaviors (Bekoff, 1972; Symons, 1978a) and the open-mouthed play face, which is common to a variety of taxa (canids, Bekoff, 1972; polecats, Poole, 1978; common marmosets, Stevenson and Poole, 1982; rhesus macaques, Symons, 1978a). Another distinguishing feature of play is the absence of agonistic

communication signals (Henry and Herrero, 1974; Owens, 1975b; Symons, 1978a). While juvenile play clearly differs from adult agonism, it has been argued that no distinctions exist between play and juvenile agonism. Several studies dispute this view. In canids (Bekoff, 1974) and baboons (Owens, 1975b), juveniles are fully capable of performing species typical agonistic behavior sequences as well as play. Therefore, play is not merely undeveloped agonistic behavior. At any point in an individual's life history, play and agonism are structurally distinct and reliably distinguishable.

There has been much speculation on the possible functions of play. Fagen (1981) and Smith (1982) recognized several basic categories of play function hypotheses, including skill development, the regulation of developmental transitions, aggressive competition, social bonding, and the formation of dominance hierarchies. Few play studies have rigorously investigated these hypotheses, and most of their documentation and support is anectdotal.

The skill development hypotheses suggest that play serves to develop physical, social and cognitive skills through practice. Four hypotheses may be grouped under the general heading of skill development: physical training, learning communication skills, developing cognitive skills and refining competitive social skills.

The physical training hypothesis, first proposed by Brownlee (1954), suggests that the function of play is to promote optimal physiological development, including increased strength and endurance. Play provides exercise which has a beneficial effect on the muscular and cardiovascular development of juveniles. In play, juveniles might gain the opportunity to exercise muscle groups which otherwise might only be used in emergency situations, such as predator avoidance.

The physical training hypothesis predicts that a large portion of a juvenile's physical exercise should consist of play. Locomotor play was indeed the predominant form of physical activity in juvenile ponies (Fagen and George, 1977) and giraffes (Pratt and Anderson, 1979).

Optimal development of strength and endurance is achieved when muscles are exercised to near exhaustion, therefore the physical training hypothesis predicts that the distribution of play bout durations should deviate from the negative exponential distribution expected if play bout lengths are determined by random events. Such deviations were found in the locomotor play of ponies (Fagen and George, 1977) and domestic cats (Fagen, 1981). However, the durations of California ground squirrel (McDonald, 1977) and rhesus macaque (Fagen, 1981) social play bouts did not differ from expected.

The hypothesis also predicts that play will occur preferentially on terrain which is optimal for the development of physical skills (Fagen, 1981). In the Siberian ibex, which inhabits mountainous terrain, social play of female kids and locomotor play of both sexes was concentrated on steeply sloped surfaces (Byers, 1977), while the social play of male kids was more frequent on flat terrain, suggesting a function other than physical training.

Although there are few rigorous tests of the physical training hypothesis, there is some evidence that locomotor play may have a role in contributing to the optimal physiological development of juveniles. This hypothesis fails, however, to explain the function of social play.

Poirer and Smith (1974) proposed that, in social play, juveniles learn species specific communication skills. Smith (1982) noted that no experimental support for this hypothesis exists, but several studies refute the ability of social play to familiarize the participants with communications signals. Most common communication signals were performed predominantly or solely outside the context of social play in olive baboons (Chalmers, 1980). Symons (1974) noted that agonistic signals did not occur during play in rhesus macaques, and that the communications signals which were exhibited in play did not appear in other contexts. Normal communication skills developed in a troop

of squirrel monkeys in which play did not occur (Baldwin and Baldwin, 1974). It therefore appears that the learning of communication skills is not an important function of social play.

Einon et al. (1978) proposed that play might be a mechanism for developing cognitive skills. In a series of experiments, the quality of juvenile rat social interactions was manipulated by pairing otherwise isolated rats with drugged or undrugged juveniles. Rats whose only social contact had been with drugged companions showed hyperarousal and had difficulty in switching from one behavior pattern to another. In contrast, rats whose play partners were normal showed more behavioral flexibility. They concluded that juvenile play experience, which involves rapid role reversal among the participants, is necessary for adult behavioral flexibility. Smith (1982) noted, however, that the cognitive skills which are increased through play are of uncertain significance in the natural environment. He concluded that the cognitive benefits of play are most likely incidental and are not major functions of play.

The competitive skill development hypothesis proposes that social play provides an opportunity for juveniles to safely coordinate and perfect behaviors which otherwise are only performed in emergency situations. Specific competitive skills which play has been proposed to provide

practice for include agonism, predation and predator avoidance.

In most species, the social play of juveniles bears a striking resemblance to the agonistic behaviors of adults. Juvenile ungulates often engage in play-butting which is similar to the aggressive sparring of adults (Fagen, 1981). In contrast, species in which the primary form of adult fighting consists of grappling and biting, such as the rhesus monkey, exhibit wrestling, grappling and inhibited biting during play interactions (Symons,1978a). Poole (1966) argued that, since agonistic behaviors remained unmodified in form throughout development in polecats, play could not serve to perfect agonistic skills. Play, however, might result in subtle changes in behavior which might be of great importance in encounters between closely matched individuals (Smith, 1982).

This hypothesis predicts that the sex which exhibits the greatest amount of intraspecific competition should play more frequently. In polygynous species, where male-male competition for resources and mates is often intense, practice afforded by play might be of crucial importance in later agonistic contests among males. Sex specific differences in play frequency have been reported in a variety of taxa, including rats (Poole and Fish, 1976; Meaney and Stewart, 1981), rhesus macaques (Symons, 1978a),

olive baboons (Owens, 1975a), ibex (Byers, 1977) and sea
lions (Gentry, 1974). As predicted, no sex differences in
play were found in several species for which adult agonistic
roles were similar, such as canids (Bekoff, 1974; Biben,
1983), ferrets (Biben, 1982) and grasshopper mice (Davies
and Kemble, 1983).

The design features of play also support its ability to
serve as practice for agonism. Behaviors comparable to
adult agonism were the predominant components of social play
in rats (Poole and Fish, 1975). In several species, social
play was similar to agonism in its goal, to "bite without
being bitten" (Gentry, 1974; Owens, 1975a; Symons 1978a).

There is also evidence that juveniles prefer to play
with partners which provide them with the greatest
opportunity for developing their skills. Preference for
similarly aged partners was noted in olive baboons (Owens,
1975a) and Siberian ibex (Byers, 1980). Ibex juveniles also
prefer to play with other males, who provide an opportunity
for more forceful play. Preference for siblings, who are
not only presumably better matched as play partners but who
also provide the opportunity for increasing the juvenile's
inclusive fitness, was reported in common marmosets
(Stevenson and Poole, 1982) and ibex (Byers, 1980).
Juveniles may also prefer to play on terrain which is most
suitable for developing specific skills. Although juvenile

ibex exhibit a preference for engaging in locomotor play on steeply sloped terrain, level terrain is prefered by males for social play. While sloped terrain appears optimal for physical development, it probably hampers efforts to practice combat skills.

A resemblance between social play and predatory behavior has been noted by many researchers. Behaviors similar to those used in prey-killing sequences appeared in the play of canids (Biben, 1983; Vincent and Bekoff, 1978), felids (Ewer, 1973) and grasshopper mice (Davies and Kemble, 1983). Ewer noted that interspecific differences in feline predatory behavior, such as the forepaw "slap" used by cheetahs in prey capture, are mirrored in the play of juveniles.

Correlational analyses have attempted to evaluate the relationship between play and predatory skill. Chalmers and Locke-Haydon (1984) reported a correlation between social play frequency and adeptness in two measures of food aquisition skill in the common marmoset. This effect was short-lived, and specific to the time of weaning. They further noted that the correlation did not pinpoint relationship directionality, and that it was possible that play frequency and food-aquisition were controlled by a third, unidentified underlying factor. Other such research has shown little relationship between social play and

predatory skill. Vincent and Bekoff (1978) found no relationship between coyote play frequency and later prey capture skill. Likewise, play frequency measures in grasshopper mice were not correlated with cricket killing or consumption frequency (Davies and Kemble, 1983). Caro (1979) found no more correlations between kitten play and predatory skill than would be expected by chance alone. In no instance was skill in a particular aspect of predation correlated to the frequency of that element in play. There is no conclusive evidence that social play enhances predatory skill.

It has been postulated that locomotor play might serve as practice for predator avoidance. Locomotor play in several species, particularly rodents, strongly resembles the species typical predator avoidance behaviors (Wilson and Kleiman, 1974). A general relationship between the level of predation and the frequency of locomotor play was noted in several species. In species where predation risks were high, such as rodents and ungulates, locomotor play formed a significant portion of the entire play repertoire, while species having little predator pressure, such as seals and pandas, rarely exhibited locomotor movements in play.

The competitive skill developement hypothesis, although well supported by experimental evidence, can not account for all types of play behavior. Play between adults, the gentle

play which often occurs between a female and her young, and bullying play are not adequately explained (Fagen, 1981). As a result of these limitations, several other hypotheses have been advanced.

An possible alternate function of play is the regulation of developmental transitions. The behavior of juveniles may act as cues to other individuals, resulting in developmental changes. Anecdotal observations of domestic cats and several species of wild cats suggested that play might accelerate weaning through harassment of the mother (Fagen, 1981). As predicted by this hypothesis, both kitten social play and object play peak at the time of weaning (Barrett and Bateson, 1978). More recent studies have called this hypothesis into question. Kittens artificially weaned at an early age either by separation from the mother (Bateson and Young, 1981) or by interupting lactation with an injection of bromocriptine (Bateson et al., 1981) showed greater levels of play than kittens permitted to continue nursing. Rather than play triggering weaning, it appeared that weaning permitted increased play.

Most hypotheses assume that play is a cooperative behavior, benefitting both participants. Geist (1978), however, proposed that play is actually aggressive competition, a method by which one individual could deny another access to certain resources and impair its future

competitive abilities. An analysis of the costs and benefits associated with adopting a strategy of damaging play suggested that this is not an evolutionary stable strategy (Fagen, 1981). The best strategy, if play is entirely aggressive competition, is not to engage in play at all. The greatest failing of Geist's hypothesis is that it does not explain why play behavior would ever evolve.

The social bonding hypothesis proposes that the function of play is to establish lasting social bonds between individuals. A general relationship between juvenile play and adult sociality has been shown in a variety of taxa, including rodents. Wilson (1973) observed a correspondence between the frequency of juvenile play and adult tolerance of other adults and juveniles. A similar correlation has been described among several species of marmots. In _Marmota monax_ (Barash, 1974a), a solitary, aggressive species, no juvenile play was observed. In contrast, juvenile social play was common in more social marmots such as _Marmota olympus_ (Barash, 1973a), _Marmota caligata_ (Barash, 1974b) and _Marmota marmota_ (Barash, 1976). The same trend was evident in two populations of _Marmota flaviventris_ at different altitudes (Barash, 1973b). At the lower altitude, juvenile play was infrequent, while, at the higher altitude, play was common. As predicted by the social bonding hypothesis, adults at the lower altitudes

were aggressive and intolerant, while at the higher altitudes, adult social groups were more cohesive.

The trend may be due to the differences in the physical proximities of playmates for the different species (Fagen, 1981), rather than the frequency of social play. In a solitary species, encounters with suitable playmates might be infrequent, resulting in fewer opportunities to engage in social play. A juvenile of a social species would have greater access to other juveniles, and as a result, more opportunities to play. In addition, there are many taxa in which the trend did not hold. Observations of the highly social bush dog (_Speothos venaticus_), the moderately social crab-eating fox (_Cerdocyon thous_) and the solitary maned wolf (_Chrysocyon brachyurus_) indicated that social play was not less frequent in the solitary species (Biben, 1983). The bush dog, in fact, had the most limited play repertoire.

Fagen (1981) was critical of this hypothesis' inability to explain the existence of juvenile social play in species in which young undergo post-weaning dispersal. Bekoff (1977) suggested that social ties developed during play might influence the timing of dispersal of juveniles within a litter. Prior to participating in frequent social play, juvenile coyotes engage in agonistic interactions which determine litter dominance status. The most dominant and most subordinate individuals were the least successful in

soliciting play, and, as a result, were involved in fewer play interactions. Bekoff predicted that the dominant and subordinate individuals, because of their potentially weaker ties to the social group, would disperse earliest. The social bonding hypothesis remains a possible primary function of play, but the lack of supporting evidence makes its importance difficult to assess.

Social play has also been suggested as a mechanism by which juveniles develop and reinforce dominance relationships. Although behavior patterns associated with dominance are frequent in play (Poirer and Smith, 1974), play has often been characterized as a reciprocal activity, with each participant assuming dominant and subordinate roles with equal frequency (Aldis, 1975). Detailed analyses of play bouts suggest that this may not be the case. Symons (1978a) noted that the animal which attained the most favorable position in rhesus macaque wrestling play was nonrandom. Heavy juveniles achieved advantageous positions over lighter juveniles, and male juveniles attained the more favorable postions over females. Dominance relationships within the play of juveniles have been reported in rats (Panksepp, 1981; Takahashi and Lore, 1983) and pronghorns (Kitchen, 1974). Takahashi and Lore, in a study of socially housed littermate rats, noted that individuals which were dominant as juvniles tended to retain their status in

adulthood. However, Adams and Boice (1983) observed that juvenile rats kept in a large outdoor enclosure formed unstable hierarchies which had no relationship to subsequent dominance status.

The validity of the dominance hypothesis in primates has been questioned by Symons (1978b), who noted that play was most frequent among animals whose rank was already established. A juvenile's rank within its peer group was largely determined by its mother's position in the social group, and juvenile females, which often were dominated in play by older sisters, assumed a ranking above their older siblings when they matured. Further lack of support was found by Bekoff (1978) in observations of coyotes, which established dominance relationships during agonistic interactions which preceded social play. Biben (1983) also reported a lack of any stable dominance relationships in three species of South American canids.

Although Symons (1978a) identified dominance relationships among playing rhesus macaques, he suggested that the learning of dominance information is fortuitous and not a primary function. Fagen (1981) conceded that more detailed analyses of the content and outcomes of juvenile play are necessary before the importance of learning dominance information during play can be assessed.

It is probable that no single hypothesis will explain

all types of play, and each function may not be of equal importance to all species. The specific functions play serves for a particular species will probably depend on the ecology of the species in question. In his review of ungulate play, Byers (1984) evaluated the possible functions of play based on interspecific differences and similarities in play. Locomotor movements were common to all species and the only form of play exhibited by some, leading Byers to postulate that play in ungulates evolved as physical training. As intraspecific competition became a more intense selection pressure, social play developed as practice for adult combat. Finally, Byers reviewed peccary herd play, a situation where play has possibly developed a secondary function of maintaining group cohesion.

The form and content of juvenile play has undoubtably been shaped by a great number of factors which vary from species to species. The role that play serves in the ontogeny of behavior is complex, and can only be elucidated through thorough, quantitative studies which take into account the many functions which play may serve.

METHODS AND MATERIALS

The Virginia Polytechnic Institute and State University punare colony was founded by five breeding pairs obtained from the National Zoological Park. Experimental animals were selected from this colony. The colony room was maintained on a 14L:10D photoperiod with a reversed light cycle (1800-0800 L, 0800-1800 D), permitting convenient nocturnal phase observation. Animals were acclimated to this photoperiod schedule for a minimum of five months prior to the onset of behavioral observations. During the nocturnal phase of the light cycle, the room was illuminated for observations with a single fluorescent tube covered with a red plastic filter. The red light provided a light intensity of .63 lumens/m^2. Breeding pairs and family groups were maintained in 28cm x 42cm x 34cm wire cages. Single animals were housed in 26cm x 48cm x 21cm polycarbonate shoebox cages with a sawdust substrate. Animals were fed a diet of Wayne Lab Blox laboratory chow and Roanoke City Mills rabbit pellets ad libitum, occasionally supplemented with fresh fruit and produce.

All animals were individually marked for identification purposes. Adults were permanently marked by ear tagging, juveniles by toe clipping. In addition, juvenile littermates were differentiated during observation periods by placing temporary white tape tags around their tails.

These tags were easily seen under red-light illumination, and were seldom removed by either juveniles or their parents. Prior to conducting systematic observations, an ethogram for the punare was compiled (Appendix 1).

Growth and physical development of juveniles were measured at weekly intervals from birth until 8 weeks of age. Total length, body length and tail length were measured to the nearest millimeter. Weight was determined to the nearest 0.1 gram on an O'Haus Triple Beam Balance. Female juveniles were examined daily, and the date at which the vaginal membrane first became perforate was noted. Since male Hystrichomorph rodents are nonscrotal and show no obvious external signs of sexual maturity, four juvenile males (two at 8 weeks of age, two at 12 weeks of age) were killed with chloroform in order to microscopically examine their testes. For each juvenile, both testes were removed, dissected and examined under a compound microscope at 400x for the presence of motile sperm.

Social interactions were conducted in a 1.0m x 0.5m x 0.5m plexiglass arena with a removable divider and sawdust substrate. All behavioral observations were conducted during the dark phase of the light cycle, under red-light illumination. Animals were placed in the arena 5 minutes before observations were begun in order to allow them to acclimate to the enclosure. Social interactions were

observed from a distance of one meter from the arena. Behaviors were recorded by hand in an abbreviated code. Durations of selected behaviors were determined with an Esterline Angus Minigraph 8-channel event recorder. Types of social interactions observed included unfamiliar adult dyads, family groups and unfamiliar juvenile dyads. Parametric statistical analyses were from Koopmans (1981) and nonparametric methods from Hollander and Wolfe (1973) and SAS Institute Inc. (1982). All means reported are mean plus or minus one standard deviation.

Interactions between randomly paired unfamiliar adults were staged in the neutral plexiglass arena. Encounter types and sample sizes were: male-male (14), female-female (14) and male-female (24). Each individual was used twice, once in a single sex trial and once in an encounter with an animal of the opposite sex. To minimize carry-over affects from previous encounters, no individual was used more than once within any two week period. A total of 56 animals were used in the encounters. Four pregnant females were removed from the sample following the female-female trials because it was feared that stress or injury during an encounter might result in spontaneous abortions.

Individuals were placed on opposite sides of the divided arena, and, after a five-minute adjustment period, the divider was removed and a 15-minute observation period

was begun. Focal sampling (Altmann, 1974) was the method of data collection, with the dyad serving as the focal group. All trials were conducted between 1100 and 1300 hours. Aspects of the encounters recorded include the frequencies of social behaviors, the initiator of each behavior, the sequence in which behaviors occurred, the duration in seconds of sparring bouts and the outcome of each trial in terms of dominance. In addition, physical parameters thought to affect dominance, such as body weight, age, total length and body length were recorded. Also, the reproductive condition of females was determined by noting whether the vaginal membrane was imperforate or perforate.

Dominance relationships within individual encounters were determined using the frequency of approach-retreat sequences. The individual whose approaches resulted in the greatest number of retreats by the conspecific was designated dominant. A factor analysis was used to obtain groupings of highly correlated behaviors. Behaviors and physical parameters within trial types and between single-sexed and mixed-sex trials were analyzed with a Wilcoxon Signed Rank test. Comparisons between male-male and female-female encounters were made using a Wilcoxon Rank Sum test. Sequences of behavior were analyzed using the method of McKinney (1961), which identifies significant linkages between behaviors.

Parental behavior and the ontogeny of play in juveniles were characterized by observing eight family groups composed of three juveniles and both parents. Litter compositions and sample sizes were: male-male-male (2), male-male-female (2), male-female-female (2) and female-female-female (2).

Family groups were observed from the day on which a litter was born until the litter reached eight weeks of age. During the first three weeks, each juvenile in a litter was observed twice daily in 15-minute focal observation periods (Altmann, 1974). The first daily observation session was conducted between 0800 and 1200 hours, and the second between 1300 and 1700 hours. Thereafter, observation sessions were conducted once daily, between 1300 and 1700 hours. Sampling frequency was increased during the initial three weeks because preliminary observations indicated that the greatest changes in behavioral development occurred during this interval. The order in which litters were observed during an observation session, and the order in which individual juveniles in a litter were observed were randomized. A total of 446.25 hours of family group observations were recorded.

During focal samples, all behaviors initiated by the focal juvenile and the recipient of each behavior were recorded. Also recorded were the sequences in which behaviors occurred, the durations in seconds of suckling

bouts and the duration in minutes of huddling bouts. Durations were recorded for all family groups with the exception of one male-female-female litter. In addition, all parental behaviors directed towards the focal juvenile were recorded.

Parental behaviors were summed by week to make ontogenetic trends more clear. Changes in parental behavior over time were evaluated with Pearson correlations. The frequency of maternal and paternal behaviors were compared using a Friedman's test.

All occurrences of play bouts were recorded during the 45-minute time period in which the three juveniles in a litter were being observed. Specific aspects of play bouts recorded include the initiator of each bout, the recipient, the duration of the bout in seconds, the sequence of behaviors within the bout, the outcome of the bout and the resulting dominance relationship. For purposes of this study, a play bout was defined as two juveniles boxing, followed by one of the participants turning away from the interaction, retreating or being pushed over onto the substrate. Each new act of boxing, even if performed by the same two individuals, was considered a discrete bout. The duration of a bout was measured from the onset of boxing to the onset of turning away, retreating or pushing over. Different combinations of participants resulted in seven

play bout types: male-male, male-female, female-female, parental male-male, parental male-female, parental female-male and parental female-female.

"Winners" and "losers" of play bouts were determined on the basis of the behaviors following boxing. Individuals which were pushed over by their opponent, or which turned away or retreated were designated as "losers". Dominance relationships were determined using the relative frequencies of push overs as the criterion. For each sibling pair, the juvenile with the greatest number of push overs was designated as dominant. If the frequency of push overs was too low to enable dominance relationships to be determined, all outcomes were utilized to determine dominance. Mounting behavior was used as a second measure of dominance. The extent of dominance was evaluated using a Chi-square test. Dominance hierarchies within litters were considered stable if all relationships remained unchanged for two or more consecutive weeks. The relationship between reversals in dominance relationships between sibling pairs and the frequency of play was evaluated using a Spearman correlation. Data were grouped by bout type, and the absolute values of play frequency were transformed to proportions of total play. Sex specific differences in juvenile play bouts were analyzed using a Wilcoxon Rank Sum test. Play bout durations were compared with an analysis of

variance and Fisher's LSD. The number of consecutive play bouts was compared between sexes using a Savage test. Outcomes of play bouts and behaviors following bout resolution were analyzed using a Chi-square test.

Interactions between unfamiliar pairs of juveniles were conducted in a manner similar to adult interactions. Juveniles from different litters born within nine days of each other were randomly paired and observed in 15-minute focal samples (Altmann, 1974), with the dyad serving as the focal group. All trials were conducted between 1100 and 1300 hours. Each individual was observed once or twice weekly from birth until eight weeks of age paired with different juveniles. The frequency with which juveniles were utilized in encounters depended on the availability of suitable unfamiliar juveniles. Due to the small number of similar-aged juveniles, it was necessary to repeat pairings, however, no individual pairing was repeated within any three week period. Fifteen of the 34 juveniles used in the unfamiliar dyad observations were concurrently observed in family group encounters. Juveniles which were concurrently being observed with family groups in the arena were termed residents, while juveniles which were less familiar to the arena were termed intruders. This resulted in three dyad types with repect to familiarity with the arena: resident-resident, resident-intruder and intruder-intruder.

As in unfamiliar adult encounters, the frequency of social behaviors, the initiator of each behavior, the sequence in which behaviors occurred and the durations of both sparring and boxing bouts were recorded. A total of 184 unfamiliar juvenile encounters were conducted.

The effects of bout and dyad types were evaluated using a Chi-square test. Durations of play bouts involving familiar and unfamiliar juveniles were compared with an analysis of variance and Fisher's LSD, and outcomes were compared using Spearman correlations and a Chi-square test. For each bout type, behavior sequences were consructed using the method of McKinney (1961).

Social interactions of a larger group of animals were observed in a large, semi-natural enclosure. The enclosure, measuring 2.4m x 2.4m x 2.4m, was equipped with a plexiglass wall through which observations could be made. The enclosure was maintained on a reversed light cycle identical to that of the main colony room. Between 1800 and 0800 hours, the enclosure was illuminated by two 60 watt light bulbs suspended from the ceiling of the enclosure. During the dark phase of the light cycle, the enclosure was illuminated by a single fluorescent light tube covered with a red plastic filter. The red light provided a light intensity of .63 lumens/m^2. Saw dust was used as a substrate, with large rocks and sturdy branches for climbing

provided to simulate the punare's natural habitat. The enclosure was also furnished with four wooden nest boxes, one food bowl, and two water bottles. Animals were fed a diet of Wayne Lab Blox ad libitum.

A family group consisting of the parents and a newborn litter composed of two males and one female was released into the enclosure, together with an unfamiliar adult male and an unfamiliar adult female. Juveniles were marked with hair dye (Clairol Born Blonde) for identification purposes. Adults were individually identifiable by physical characteristics. The group was observed from the day after the litter was born until the litter reached eight weeks of age. Focal sampling techniques (Altmann, 1974) were used to observe each individual in the group for 15 minutes daily. The order in which individuals were observed was randomized. Observation sessions were conducted between 1300 and 1700 hours, under red light illumination. A total of 73.5 hours of observations were recorded in the large enclosure.

During focal samples, all behaviors initiated by the focal individual and the recipient of each behavior were recorded. The sequence in which behaviors occurred and the duration in seconds of play, huddling and suckling bouts were recorded. Durations were measured using an Esterline Angus 20-channel event recorder.

Sequences of adult interactions were analyzed using the

method of McKinney (1961). Parental behaviors were summed
by week and changes over time were evaluated with Pearson
correlations. Differences between individuals in the
frequencies of behaviors were compared using a Chi-square
test pooled across juveniles. Durations of play bouts were
analyzed and compared to those in the small arena using an
analysis of variance. Outcomes of play bouts were compared
using a Chi-square test. Dominance relationships within the
litter and the stability of those dominance relationships
were analyzed using the same methods used for litters in the
small arena.

RESULTS

Growth and Development

Juvenile growth was linear within and across all
litters from birth to the end of the 8-week observation
period (Figure 1, minimum r=.985). The mean age at which
female juveniles first became perforate was 43.7 ± 3.8 days.
Males reached sexual maturity later, as neither of the
8-week-old males and only one of the 12-week-old males
exhibited motile sperm.

Unfamiliar Adult Interactions

Four basic categories of behavior were identified by
factor analysis, and were subjectively labeled Initial
Contact and Contact Promoting Behaviors, Agonistic
Behaviors, Transition Behaviors and Retreat Behaviors (Table
1). Behaviors within particular categories tended to be
sequentially linked (Figures 2-4). Sequences were highly
similar between encounter types. Male-male encounters
differed from other encounter types in the presence of two
behaviors: ground pat, which served as a transition between
Initial Contact and Contact Promoting Behaviors and
Agonistic Behaviors, and mounting, which served as a
transition out of Agonistic Behaviors. The transition
behavior category was entirely absent from mixed-sex and

female-female encounters. Encounter types also differed in the point at which conflicts were resolved. Male-male encounters typically progressed to the most intense agonistic behaviors, push over and chest kick, before one individual retreated. Female-female encounters occasionally progressed to this point, but often retreating occurred following upright posturing. Mixed-sex encounters rarely progressed to push over and chest kick, with retreats typically following sparring.

Agonism was observed in 86 percent of male-male encounters, 71 percent of male-female encounters and 64 percent of female-female encounters. Sparring was present in 57 percent of male-male encounters, 25 percent of male-female encounters and 43 percent of female-female encounters.

Dominance in male-male encounters was not associated with age ($Z=0.157, p=0.875$), total length ($Z=0.314, p=0.754$), body length ($Z=0.000, p=1.000$) or body weight ($Z=0.235, p=0.814$). Dominant individuals differed greatly from subordinates in the frequency of several behaviors. Initial Contact and Contact Promoting Behaviors, chest kick and mount were more frequently performed by dominant individuals, while subordinates more frequently retreated (Table 2).

Dominance in female-female encounters was not

associated with age (Z=0.178, p=0.859), total length (Z=0.711, p=0.477) or body length (Z=1.303, p=0.193), but body weight had a significant effect. Weight differences of fewer than 60g did not influence dominance (T=13, p=0.344), however when body weights differed by more than 60g, the heavier female was dominant significantly more often (T=15, p=0.031). Few behavioral differences were observed between dominant and subordinate females. Dominant females approached and followed more frequently and retreated less often than subordinates (Table 2).

Physical parameters were strongly associated with dominance in male-female encounters. Total length (Z=4.286, p<0.001), body length (Z=4.286, p<0.001) and body weight (Z=3.457, p=0.001) were positively correlated to dominance, but no relationship was found between dominance and age (Z=1.277, p=0.201). Sex was also a factor, with males typically dominating females (Sign test, B=19, p=0.003). Since adult punares are sexually dimorphic with males being larger, these factors are highly intercorrelated. In four of five trials in which females dominated males, the males were larger, suggesting that sex, not body size, had the greatest influence on encounter outcomes. Differences between the sexes in the frequencies of behaviors indicated that mixed-sex encounters were dominated by males. Behavioral differences between the sexes corresponded with

differences between dominant and subordinate individuals in male-male encounters. Males in mixed-sex encounters exhibited more Initial Contact and Contact Promoting Behavior and less retreating than did females (Table 2). No behavioral differences were observed in either sex with respect to female reproductive status.

Behavioral comparisons between encounter types indicated that male-male encounters incorporated more Agonistic and Transition Behavior than female-female encounters, and more Agonistic Behavior than male-female encounters (Table 3). Female-female and male-female encounters did not differ in the frequency of any recorded behavior. The duration of sparring bouts did not differ between encounter types.

Parental Behavior

Both parents interacted frequently with juveniles, with nose-to-cheek the predominant parental behavior. Most maternal behaviors declined with time as reflected by correlation coefficients (Table 4), while paternal behaviors tended to increase or had no relationship with the age of the litter. Nursing and grooming tended to extinguish after three to four weeks, while all other behaviors persisted over the 8 week observation period (Figure 5). The mean age at which nursing ceased was 21.67 ± 6.13 days.

Three maternal behaviors, approach, nose-to-cheek and nose-to-body, showed a rapid, significant decline from week 1 to week 2 (minimum T=36, p=0.004). As a result, in comparisons between parental females and parental males these behaviors were analyzed in two time periods. Parental females exhibited significantly more nose-to-cheek and nose-to-body during week 1 (B=24, p<0.001) and more nose-to-cheek during weeks 2-8 (B=16, p=0.026). Parental males exhibited more nose-to-body during weeks 2-8 (B=19, p=0.003). No significant differences between parents were observed for approaching during either time period (maximum B=15, p>0.10).

The remaining parental behaviors were compared over the entire 8-week period. Behaviors performed predominantly or exclusively by the parental female included nurse (B=24, p<0.001), groom (B=19, p<0.001), follow (B=11, p=0.003) and turn away (B=16, p=0.067). Behaviors performed significantly more often by parental males were crawl over (B=15, p=0.021), push away (B=16, p=0.047), box (B=14, p<0.001), push over (B=14, p<0.001) and mount (B=14, p<0.001).

Juvenile and Parental Social Play

All juveniles, all parental males and five of eight parental females were observed to engage in social play.

The frequency of juvenile and parental play over time is depicted in Figures 6 and 7, respectively. Virtually all juvenile play was dyadic, with less than one percent (2/3505) being triadic.

Play onset was significantly influenced by the litter composition (F=4.65,df=3,p=0.013). The age at which play was first exhibited was dependent on the number of males in the litter, with all male litters exhibiting play earliest and all female litters showing play behavior latest (Table 5).

Sex specific differences were observed in several aspects of juvenile play. Male juveniles initiated more play bouts than did female juveniles (Figure 8A, F=17.17, df=1, p=0.001) and tended to initiate a larger proportion of the bouts that they participated in (Figure 8B, F=31.33, df=1, p<0.001). Males more frequently followed play bouts with mounts (X²=14.3, df=1, p<0.001). In mixed-sex litters, males initiated play more frequently with other male juveniles (X²=16.41, df=1, p<0.001).

Bout type had a significant effect on play bout duration, outcome and the number of consecutive bouts. Among bouts involving two juveniles, male-male bouts were longest in duration, followed by male-female bouts, with female-female bouts being shortest (Table 6, F=8.51, df=6, p<0.001). Male-male play bouts were significantly more

likely to terminate in pushing over than either male-female or female-female bouts (X^2=41.52 and 26.96 respectively, df=1, p<0.001), and were less likely to terminate in turning away or retreating (minimum X^2=8.35, df=1, p<0.005). No differences in outcome with respect to bout type were observed for male-female and female-female bouts. Male-male play bouts were most likely to result in several successive bouts, and females had the lowest frequency of bout repetition, with mixed-sex bouts intermediate (Table 7, X^2=26.26, df=4, p<0.001).

Sex specific differences were also evident in parental play. Parental males initiated play more often than did parental females (Figure 9A, B=18, p<0.001) and tended to initiate a larger proportion of the bouts that they participated in (Figure 9B, B=18, p<0.001). Although parental males were more likely to be initiators of play bouts than were parental females, the majority of parent-offspring play was initiated by the offspring. In mixed sex litters, parental males initiated play somewhat more often with male offspring than with female offspring (X^2=3.49, df=1, 0.05<p<0.10). Parents occasionally intervened in juvenile play bouts, terminating the play bouts by separating the juveniles. Parental males intervened more frequently than did parental females (B=10, p=0.019).

During parent-offspring play, parental females were

much more likely to terminate play bouts by turning away or retreating than were parental males. Bouts between parental females and offspring resulted in the female turning away or retreating 83 percent (20/24) of the time, while bouts between parental males and offspring resulted in the male turning away or retreating 34 percent (84/247) of the time. While females tended to avoid play, juvenile play was uncorrelated with increased avoidance of the juveniles by the parental female (r=-0.072, p=0.306).

The duration of parent-offspring play bouts varied both with parent and offspring sex (Table 6, F=8.51, df=6, p<0.001). Durations of bouts between parental males and female offspring were significantly longer than any other parent-offspring comparison. Bouts between parental males and male offspring were longer in duration than those between parental females and female offspring. Bouts involving parental females and male offspring did not differ significantly from either parental male-male offspring bouts or parental female-female offspring bouts.

"Winners" were identified for 94 percent (3391/3605) of all play bouts. The three methods used to determine play bout "winners" (juveniles which pushed over their opponents, or whose opponents turned away or retreated) were highly correlated (minimum r=0.799, p<0.001). Juveniles which were frequently pushed over tended to turn away and retreat more

from interactions. Two behaviors, vertical hop and mount, frequently followed the resolution of juvenile play bouts, and both behaviors were performed significantly more often by the juvenile designated as the bout "winner" (X^2=42.09 and 138.19 respectively, df=1, p<0.001). Mounting followed pushing over significantly more frequently than any other outcome (X^2=41.78, df=2, p<0.001). Mounting was rarely associated with play among parental males and their offspring, as fewer than 1 percent (2/244) of all bouts were followed by mounts.

Dominance hierarchies based on the relative frequencies of push overs could be determined for five of the eight litters (Figure 10) For the remainder, predominantly female litters, the frequency of push overs was too low to construct hierarchies, so a pooled value of push over, turn away and retreat was used (Figure 11). The frequency of play in one male-female-female litter was too low to construct a hierarchy by either method. Hierarchies were linear over most of the eight week period, however in several instances triangular relationships resulted. Six of eight litters met the stability criterion at some point in time, but only litters with one or more male juveniles exceeded the criterion. Both male-male-male litters, one male-male-female litter and one male-female-female litter were highly stable over the last three weeks of the eight

week observation period. During this period, the frequency of pushing over was significantly greater for the the dominant member of 11 of 12 sibling pairs (minimum $X^2=7.41$, df=1, p<0.01). The exception was a female sibling pair in which push overs were too infrequent to result in a significant comparison. In all mixed-sex litters for which dominance hierarchies could be constructed, male juveniles dominated female littermates.

Periods of relative instability in dominance relationships varied by bout type (Figure 12). In male-male bouts, dominance relationships changed most during week 5, then rapidly became more stable. Male-female dominance relationships achieved stability by week 6. Instability in dominance relationships among females tended to increase with time. The frequency of reversals in dominance relationships within a bout type was significantly correlated to the frequency of play (r=0.335, p=.043).

Dominance relationships based on the frequency of mounting following play bouts generally agreed with relationships based on the frequency of pushing over. Notable exceptions occurred in both male-male-male litters, with the most subordinate male on occasion mounting its dominant siblings more frequently than it was mounted in return. In four instances, the juvenile designated as the "loser" of a bout mounted the "winner". In all these cases,

the juvenile which mounted had been a subordinate for several previous weeks.

In all litters, parental males dominated all offspring. Parental males "won" a significantly larger proportion of the bouts they participated in ($X^2=24.00$, df=1, p<0.001), bouts which they initiated ($X^2=83.18$, df=1, p<0.001) and bouts which resulted in push overs ($X^2=89.04$, df=1, p<0.001).

Unfamiliar Juvenile Interactions

Interactions between unfamiliar juveniles frequently incorporated social play, but unlike play between siblings, social encounters between unfamiliar juveniles occasionally escalated into agonism. Agonism was easily differentiated from play by the presence of chatter vocalizations, upright posturing, chest kicks and retreating by the subordinate juvenile. Behavioral sequences in unfamiliar juvenile encounters were very similar to those in adult encounters (Figure 13) with the additional presence of play.

Residence status had a significant effect on the frequency of play and agonism (Table 8), with both occurring more frequently among pairs of resident juveniles. Both play and agonism were inhibited when both juveniles were unfamiliar to the enclosure. No significant differences in the frequency of play or agonism were observed in

comparisons of male-male and male-female encounters. Female-female juvenile encounters were excluded from the analysis due to the small number of encounters and the infrequent occurance of boxing and sparring. In encounters in which one juvenile was a resident and the other was an intruder, the resident emerged dominant in play interactions significantly more often (B=10, p=0.006). This residence effect was strong enough to reverse the effect of juvenile sex on dominance. Resident females matched with intruder males "won" play bouts more frequently than when matched with resident males ($X^2=5.61$, df=1, p<0.025).

Social play among unfamiliar juveniles differed in several respects from play among siblings. Play bouts between unfamiliar juveniles were significantly shorter in duration than those between siblings (F=9.03, df=1, p=0.003), and terminated in turning away and retreating more often ($X^2=9.33$ and 12.51 respectively, df=1, p<0.005), and pushing over less often ($X^2=12.81$, df=1, p<0.001) than bouts between siblings. Unlike the case within family groups, among unfamiliar juveniles there was a trend (athough not statistically significant) for juveniles which "won" play bouts on the basis of push overs to turn away or retreat from further play interactions with unfamiliar juveniles (r=-0.243, p=0.276). The mean number of successive play bouts did not differ by unfamiliar bout type or between

unfamiliar and littermate play (Table 7).

Large Enclosure Observations

Although agonistic behavior among adults was observered throughout, no clear pattern could be constructed, since sequences tended to be fragmented. The only behavioral transition which was significant was retreating eliciting a following response from a conspecific.

All adults were observed interacting with juveniles, however the frequency of interaction was considerably lower in the large enclosure than in the small arena, resulting in fewer significant trends and comparisons. The frequency of interaction with juveniles tended to decline with time for both the parental and nonparental female (Table 9). Most correlations were similar in sign and magnitude to those observed for parental females in the small arena (Table 4). Change over time in behaviors exhibited by the parental and nonparental males is shown in Table 9. Correlations for the parental male are similar in sign and magnitude to those observed in the small arena, while those of the nonparental male often differed. The parental female exhibited more nose-to-body than the parental male ($X^2=7.35$, df=1, $p<0.01$), while the parental male exhibited more boxing ($X^2=26.47$, df=1, $p<0.001$) and pushing over ($X^2=7.00$, df=1, $p<0.01$). No significant behavioral differences were observed between the

parental female and nonparental female, or between the parental female and nonparental male. The parental male exhibited less approaching, nose-to-body and following than did the nonparental male (X^2=9.00, 11.57 and 10.00, df=1, p<0.005, 0.001 and 0.001 respectively), but boxed and pushed over juveniles more frequently (X^2=32.00 and 7.00, df=1, p<0.001 and 0.01 respectively).

Juvenile play in the large enclosure tended to be most frequent during the middle weeks of the 8-week observation period (Figure 14). Play bouts tended to be somewhat longer in duration than bouts in the small arena (F=4.83, df=7, p<0.001). One juvenile was dominant during the entire 8-week period, and during the final three weeks had significantly more push overs than did the subordinate juvenile (X^2=4.00, df=1, p<0.05). Mounting following play bouts generally agreed with dominance relationships determined through the frequency of push overs, although during weeks 5 and 8 the subordinate mounted the dominant juvenile more frequently.

The parental male played with the juveniles significantly more often than any other adult (minimum X^2=13.24, df=1, p<0.001). The parental female initiated one play bout with the juveniles, while neither nonparental adult initiated play. As in the small arena, adults occasionally intervened in juvenile play bouts. Six

instances of intervention were observed, four by the parental male and two by the nonparental male. The only play bout between the parental female and her offspring for which an outcome could be determined terminated in the female turning away, while only 17 percent (5/30) of bouts involving the parental male terminated in the male turning away or retreating. The parental male dominated both juveniles in play interactions, and was designated as the "winner" in 80 percent (24/30) of all play bouts, 94 percent (15/16) of bouts initiated by the parental male and 100 percent (10/10) of bouts ending in push overs.

DISCUSSION

Punares are born highly precocial, yet do not quickly achieve nutritional or social independence. Suckling persists for approximately three weeks, and sexual maturity in females is not reached until about six weeks of age, with sperm production in males delayed further. Porter, Cavallaro and Moore (1980) suggested that an extended period of social contact in species with precocial young may have non-nutritive functions, permitting prolonged social interaction and littermate play. This reasoning is supported by this study, where a high degree of social interaction with parents and littermates occurred throughout the 8-week observation period. Social play was observed during the week following birth, and most play occurred prior to sexual maturity. Social play was a significant component of juvenile social interactions. Littermate and parent-offspring play were common, and play persisted in encounters between unfamiliar juveniles and in a larger social group in a seminatural enclosure.

Play, which was easily distinguishable from agonism, consisted of one basic behavioral component, boxing, followed by a limited number of discrete outcomes. Virtually all social play was dyadic, allowing accurate discrimination of play bout initiators and recipients. "Winners" and "losers" were easily identifiable on the basis

51

of the behaviors following boxing.

Adult Agonism

Encounters between unfamiliar pairs of adults characterized the agonistic behavioral repertoire and differences in adult roles. Factor analysis grouped behaviors occurring within encounters into four major categories, three of which were common to all encounter types. The presence of transition behaviors (ground pat and mount) solely within the context of male-male encounters reflects the higher agonistic levels of male-male encounters. Ground pat occurred as a transition between initial contact behaviors and agonism, and may be a displacement behavior indicative of higher levels of aggression, or may function as warning behavior. Mounting was exhibited following the resolution of agonistic conflict, and appeared to reinforce the preceding dominance decision.

Behaviors within categories identified by factor analysis were sequentially linked, and sequences were highly ritualized, with little variation between encounter types. Facial nosing immediately followed an initial approaches, and tended to be mutual and repeated, indicating that it might function in recognition and familiarization. Transitions to agonistic behavior followed nosing, further

supporting the role of nosing in recognition.

Agonistic behavior in adults typically began with upright posturing, which was reciprocal and repeated. Upright posturing may provide unfamiliar individuals an opportunity to assess their opponents before engaging in further agonism. Female agonistic encounters were often resolved at this point, with one female retreating. Since female-female encounters are significantly influenced by body weight differences, recoprocal posturing would provide a means of evaluating relative opponent size. Agonistic behavior tended to be sequentially similar between encounter types, but the behavior at which encounters were resolved differed. In contrast to single-sex encounters, male-female encounters usually ended with retreats following sparring and rarely progressed to the most intense agonistic behaviors, chest kick and push over. This earlier resolution point reflects the higher levels of submissiveness by females in mixed-sex encounters.

Retreating had a very high probability (.70 and greater) of eliciting a following response from a conspecific in all encounter types. This interaction then progressed into a repeated cycle of behaviors. Repetitive biting in both single-sex encounter types and mounting in male-male encounters indicate this cyclic pattern apparently functions in dominance reinforcement. Biting was not

incorporated into the cyclic behaviors in mixed sex encounters. Mounting in male-female encounters appeared to be sexual, and was therefore grouped with initial contact and contact promoting behaviors by factor analysis. These behavioral sequences then serve two different functions depending on context, promoting sexual contact in mixed-sex encounters and dominance reinforcement in single-sex encounters.

Adult interactions in a large enclosure failed to show clear behavioral sequences. Sequences were fragmented, with few significant linkages between behaviors noted. Two factors could have caused this result. Observations in the large enclosure were not undertaken until the day following introduction of the group into the enclosure. Initial interactions could have been more highly ritualized, with dominance relationships established on the first night, resulting in subsequent encounters being less stereotypic. Also, the small arena reduced a conspecfic's ability to flee, forcing further stereotypic interactions. The only consistent sequence of behavior observed in the large enclosure was retreating which elicited a following response from the conspecific. This pattern was also one of the most predictable transitions in the small arena, and the stability of this sequence indicates its importance in both the reinforcement of dominance and as a component of sexual

behavior.

Differences in behavioral frequencies between encounter types were similar to those reported by Streilein (1982d), except that the frequencies of agonism and sparring were somewhat higher in this study. Lower levels of agonism observed by Streilein may reflect methodological differences, as his were conducted in a larger arena ($1.5m^2$) and for a shorter time period (5 minutes). Streilein's encounters were conducted between wild-caught animals trapped in the same location and prior relationships between individuals were unknown. Therefore, they may have had prior social contact or been related, both of which would result in lower agonistic encounter rates. Streilein proposed that initial encounters between individuals were of greatest intensity, and subsequent encounters would show reduced agonism, therefore prior familiarity between experimental animals may have contributed to the reduced levels of agonism exhibited in his study. Animals in the present study were of known relationships and had no prior social contact, therefore higher frequencies of agonism would be expected.

Steilein observed agonism in 50 percent of male-male, 22 percent of female-female and 37 percent of male-female encounters, compared to 86, 64 and 71 percent respectively in this study. In both studies, agonism occurred with

greatest frequency in male-male encounters. Sparring, a high intensity agonistic behavior, occurred in 36 percent of male-male, 17 percent of female-female and 15 percent of male-female encounters in Streilein's study, compared to 57, 43 and 25 percent respectively in the present study. In both studies, male-male encounters showed the greatest amounts of sparring, mixed-sex encounters exhibited the least and female-female encounters were intermediate.

This pattern of differences in agonistic intensity between encounter types was reflected in many aspects of paired adult encounters. Male-male encounters had greater frequencies of agonistic and transition behaviors than male-female or female-female encounters and were also more likely to progress to the most intense agonistic behaviors before resolution. Male-male encounters incorporated more dominance related mounting behaviors and dominance relationships were more evident than in the other encounter types. Dominant and subordinate males significantly differed in several behavioral aspects and encounters were not resolved by physical characteristics. Slight differences in competetive social skills, possibly as a result of play, might have been of great importance. Encounters between females, in contrast, were often resolved by differences in the weights of the participants, and few dominance related behavioral differences were noted between

conspecifics.

Behavioral tolerance was greatest in male-female encounters, and encounter outcomes were strongly influenced by the sex of the participants, with males tending to dominate. Males exhibited higher frequencies of social investigatory behaviors such as nose-to-cheek, paw and follow, which may help males to assesss the reproductive status of females. Females were basically passive, exhibiting more retreating. Female retreating was strongly linked to following and mounting of males, and the repeated nature of the this cycle may have permitted familiarization of the pair prior to copulation.

Sex specific differences in paired adult encounters were consistent with adult roles inferred from field studies (Streilein, 1982a,b,c). Reports of little territorial overlap between same-sexed conspecifics were supported by the relatively higher levels of agonism in male-male and female-female encounters. The low agonism exhibited in mixed sex encounters supports field observations of high territorial overlap and presumed polygynous mating system with intense male-male competition for territories and mates, and low levels of agonistic interaction between sexes.

Parental Behavior

Parental behavior of the punare was similar to that of other Hystricomorphs (Kleiman, 1972; Kleiman, 1974; Wilson, 1982). Body-nosing predominated in interactions between parents and offspring, as observed in degus (Wilson, 1982). Parental behavior tended to fall into two major categories on the basis of apparent function and profile over time. Direct care behaviors, nursing and grooming, tended to extinguish as the juveniles matured and became increasingly capable of feeding and grooming themselves. Other social behaviors, nosing, pawing and social play, had a role in the formation and maintenance of social bonds between parents and juveniles, and/or influenced the juveniles' social development and persisted over time.

The importance of parental nosing in social recognition is shown by a lack of systematic differences in the frequencies of these behaviors. Apart from week 1, where maternal nosing exceeded paternal nosing, there were no obvious patterns in comparisons of nosing frequency between parents. Parental females showed more cheek-nosing, while parental males exhibited more body-nosing, but rump-nosing rates did not differ. Parental nosing in the large enclosure differed only in nose-to-body frequency between the parents. Maternal nosing declined significantly from week 1 to week 2, then stabilized. This is consistent with

the formation of social bonds and preliminary familiarization period between mother and offspring as has been proposed to occur during this time period (Kleiman, 1972). Father-offspring nosing, in contrast, was initially low in frequency and increased over time. This pattern could be due to the reported increased aggression of female Hystricomorphs after the birth of offspring (Kleiman, 1972), which might disrupt interactions between a parental male and offspring. High maternal aggression during the early developmental period might also account for the tendency of paternal behaviors to show an increase over time. Paternal-juvenile interaction would be lowest post-partum, when maternal aggression is high, and would increase as maternal aggression decreased. Low initial rates of father-offspring interactions may also be the result of the post-partum estrus exhibited by females. During the post-partum period, a male would maximize his fitness by first mating with the female and delaying interaction with the newborn young.

The greater frequency of crawling over juveniles by parental males may reflect differences in a social familiarization mechanism. Crawling over by the male could result in scent transfer to offspring, either by urine dribbling or glandular secretion (Kleiman, 1974). This would result in a greater degree of scent similarity between father and young, and would aid in later recognition. This

is probably unnecessary for maternal recognition of offspring, as offspring scents are, to a large degree, dependent upon the diet of the mother and are transferred to the young via maternal milk (Porter, et al., 1981). Differences between the sexes in the targets of parental nosing further support this view. Maternal nosing is primarily directed at the cheek regions, which are in direct contact with mammary tissue during nursing, resulting in scent transfer. Also, glandular regions in the cheek area might produce identifying scents. Parental males, in contrast, differentially nose the bodies of juveniles, enabling them to detect scents deposited by paternal crawling over.

Differences in maternal and paternal roles potentially have a significant influence on juvenile behavioral development. Parental females were basically nurturant and nonactive in social play, rarely initiating play and frequently terminating play bouts. Parental females also exhibited the least forceful avoidance behavior, tending to turn away from interactions, while parental males tended to push away juveniles. Paternal males took a more active role in vigorous social interaction with juveniles, more frequently mounting, pushing away, pushing over and boxing with their offspring. Through social interactions such as these, parental males could directly influence the social

development of offspring and assert dominance over them.

A high degree of paternal involvement is not unusual among Hystricomorphs (Kleiman, 1974), and would be facilitated by the ecology of the punare. Males are likely to be in frequent contact with juveniles due to the territorial overlap of males and females and the highly mobile nature of the precocial young. The post-partum estrus of the female also increases the probability that a male would come into contact with newborn young. Thus scent marking of the juveniles by the male could occur, increasing the probability of subsequent offspring recognition. Because of territorial overlap between males and females and territory stability (Streilein, 1982c), juveniles born within a male's territory are likely to be the male's offspring. The high probability of parenthood, potential for frequent social contact and mechanism for social recognition significantly increase the probability of paternal investment and potential benefits to juvenile development.

The lower frequency of parent-offspring interaction in the large enclosure than in the small arena could have resulted from several factors. First, since much of mother-young interaction took place inside nestboxes where the parental female's body obstructed the opening, it was impossible to observe behaviors within the box. This

obstruction could account for the absence of the rapid decline in maternal nosing during week 1 and the smaller number of behavioral differences between the parental female and the parental male. The greater area of the large enclosure and the presence of more conspecifics to interact with could also have resulted lower interaction rates. Sex specific differences in parental behavior which were evident were consistent with those in the small arena, with boxing and pushing over occurring more frequently in the paternal male. Correlations of parental behaviors with time also were consistent with small arena observations, with maternal behaviors tending to decrease in frequency and paternal behaviors tending to increase or show no relationship with time.

Parental behavior in the large enclosure was not limited to biological parents, with both non-parental adults taking an active interest in the juveniles. The non-parental female did not differ from the parental female in the frequency of any non-nutritive behavior measured, and showed highly similar trends in the frequency of behaviors over time. Under natural conditions, an adult female would have reduced opportunities for contact with unrelated juveniles due to the territorial nature of females and the reported high levels of female Hystricomorph post-partum aggression (Kleiman, 1972).

The non-parental male interacted with the juveniles, showing similar frequencies of social behavior as the parental female with more approaching, body-nosing and following than exhibited by the parental male. The non-parental male differed from the parental male in the sign and magnitude of the correlations of social behaviors with time. Although play occurred between all paternal males and their offspring in both enclosure types, it was never observed between the non-parental male and juveniles in the large enclosure. These differences in behavior between parental and non-parental males may be the result of housing conditions prior to introduction into the large enclosure. The paternal male had been housed continuously with his mate, and was present during the birth of the litter, allowing opportunity for social familiarization and scent marking of the juveniles, thereby increasing the degree of paternal certainty. Paternal behavior clearly was not a small arena artifact, since the degree of paternal involvement remained high even in the large enclosure.

Social Play

Encounters with peers and parents largely shape juvenile behavioral development, and clear-cut sex specific differences in punare adult agonistic roles indicate the potential for play to significantly influence social

development. Play may have its greatest impact among
juvenile males, where competition as adults would be intense
and combat skills, rather than physical attributes, are the
decisive factors in agonistic competition.

Play and agonism in the punare were easily
discriminated on the basis of behavioral components and
sequences. Agonism differed from play in the presence of
chatter vocalizations, upright posturing and chest kicking.
Preceding agonism, there was a sequence of repeated,
reciprocal behaviors including upright posturing and paw
front, accompanied by chatter vocalizations which tended to
extend the interval between initial approaches and sparring.
During social play, in contrast, approaches were immediately
followed by boxing. Vocalizations and upright posturing may
serve as communication signals and attempts to divert
escalation of conflicts by providing opportunities for the
assessment of opponents, as in unfamiliar adult female
encounters. These behaviors would not be expected to occur
in play because the presence of agonistic signals might
directly precipitate escalation into agonism. Chest
kicking, present exclusively during agonism, could
potentially result in serious injury (Streilein, 1982d).
Performed during play, it might ultimately cause a decrease
in inclusive fitness if the play partner was a relative, and
in any case would make that individual unattractive as a

potential play partner due to the risk of injury. Two behavioral elements, turn away and vertical hop, were present in social play but not agonism. Vertical hop is a locomotor play pattern (Wilson & Kleiman, 1974) and is indicative of the nonagonistic nature of boxing. The tendency of boxing to lead to turning away rather than retreating, as in sparring, further illustrates the distinctions between the two behavioral categories. Juveniles rarely departed from play interactions, while avoidance was common during agonistic encounters. The distinction between play and agonism was present in juveniles as well as adults, and attests to the distinct functions of play.

Although structurally and sequentially distinct from agonism, play incorporated several important elements of both agonism and determination of dominance relationships. Social play would be inadequate for coordinating agonistic behaviors, however, due to the dissimilarity in behavioral elements and sequences. Many components of agonism were absent from play, however boxing could potentially provide the practice necessary for developing skill at sparring. Social play incorporated all the elements of adult dominance determination and reinforcement, in particular push over and mount, and the sequence in which the dominance reinforcement cycle of behaviors occured during unfamiliar juvenile play

interactions closely resembled that of unfamiliar adults. Social play clearly has the potential to develop and reinforce relationships between juveniles.

Sex specific differences in juvenile play and play partner preferences were supportive of both the development of competitive skills and dominance hypotheses. Play was most prevelant among male juveniles, and sex specific differences were evident in all aspects of play measured. Male juveniles initiated more play bouts, engaged in more successive bouts, and exhibited play at a younger age than females. Male juveniles tended to take an active role in play, being initiators of play bouts more often than recipients. Bouts involving male juveniles were longest in duration of all bouts among juveniles, and incorporated more dominance determination and reinforcment behaviors such as push over and mount. Male juveniles initiated play significantly more often with other male juveniles. Male juveniles may have been prefered play partners due to the more forceful nature of play between male juveniles, which would result in more efficient practice of agonistic behaviors. Alternately, the preference of male juveniles for other males may have resulted from more intense competition for dominance status among males. While play was most frequent and vigorous among males, mixed-sex play was intermediate in most respects. This potentially has

great implications for female juvenile development. If play improves agonistic skills, then female juveniles with male littermates would have the benefit of more frequent and forceful practice, thus increasing their future competitive skills. These females would have a competetitive advantage in obtaining resources, resulting in increased reproductive success.

The regulation of developmental transitions hypothesis was not supported data obtained in this thesis. Neither male-female nor female-female play increased near the time of weaning. The frequency of bouts between males did not peak until well after weaning, and the steep increase in male-male play after weaning indicates that weaning possibly permitted more frequent play. Although parental females avoided play with offspring, there was no evidence that juvenile play resulted in harrassment of the mother. Maternal avoidance was unrelated to the frequency of play, and parental females rarely attempted to intervene and terminate play bouts between juveniles.

The structure of juvenile social play is highly supportive of play serving to establish dominance relationships. "Winners" were identifible in 94 percent of all play bouts, and the resulting dominance relationships were statistically significant, linear and stable during weeks 6-8 in male juveniles. As predicted, parental males

dominated offspring during play interactions and initiated play more often with male juveniles. Sex biased play initiation is possibly the result of greater competition among males. Since male juveniles are future competitors, parental males can assert dominance during early play interactions and continue to reinforce their status as parent-offspring play increases with time. In this manner, adult males may hasten dispersal of young males, preventing further competition for resources between father and offspring and increasing the representation of the adult male's genes in other populations. Parental male intervention in juvenile play bouts further supports this interpretation. By breaking up play interactions between juveniles, parental males prevent juveniles from asserting dominance among themselves while reinforcing their own dominance status. Changes in the frequency of play over time also indicate that dominance relationships were established during play. Play frequency was highest during periods of frequent changes in dominance relationships among juveniles, and as dominance relationships stabilized, the frequency of play sharply declined. The incorporation of mounting in juvenile play interactions further supports the role of play in the formation of dominance relationships. Pushing over, a behavior which resulted in an obvious "winner"-"loser" relationship, was significantly linked to

mounting. Mounting was performed more frequently by the "winner" of a play bout and, in unfamiliar juvenile encounters among males, led directly into a cyclical pattern of behavior identical to the dominance reinforcement pattern of unfamiliar adults. Dominance relationships based on the frequency of mounting in males were identical to relationships based on the frequency of push overs with few exceptions. In all instances where subordinates more frequently mounted dominant juveniles and play bout "losers" mounted "winners", litter dominance relationships were well established and not in question. This observation suggests that dominant juveniles were permitting subordinate siblings to gain experience performing dominance reinforcement behaviors. Alternately, mounting by extreme subordinates may be a conflict behavior, since it was only exhibited in the most stressful of social situations, by the lowest ranking male in all male litters. Although dominance relationships were evident in paternal play with offspring, mounting was not incorporated into father-young play bouts. Since parental males dominated juveniles in virtually all play bouts, the additional presence of mounting in play may have suppressed further father-offspring play.

Other aspects of social play were also supportive of a development of competitive social skills function. Parental male-juvenile female play bouts were longest in duration of

all bout types, indicating that parental males were not using their full physical abilities. This self-handicapping by the parental males may serve to increase the amount of competitive social skill practice time among juvenile females, compensating for the lower frequency of social play. Parental males appeared to use a different strategy to promote play among juvenile males. By intervening in male juvenile play bouts, the parental male efeectively delayed the establishment of dominance relationships, permitting further play. Differences in play between related and unrelated participants were also supportive of the development of agonistic skills hypothesis. Play was shorter in duration among unfamiliar juveniles, and did not occur between juveniles and an unrelated adult male. The greater extent of play among related individuals may serve to increase each juveniles inclusive fitness, while play among unrelated juveniles would increase the fitness of a future competitor.

Differences in social play between related and unrelated juveniles indicate that the formation of dominance relationships occurs concurrently with the development of competitive social skills. If play serves both functions, the best possible strategy would be for a juvenile to attempt to gain dominance in all its social play bouts and to engage in play more frequently with relatives. If it

could not achieve dominance, then the best general strategy would be to decrease the opponent's ability to achieve dominance by terminating the play interaction or by injuring its opponent. If however, the juvenile plays with a littermate which it cannot dominate, this purely selfish strategy would result in a decrease in its own inclusive fitness. In such a situation, it would be most advantageous for the juvenile to allow its sibling to assume dominance, rather than depriving it of play or injuring it (Bekoff, 1978).

This interaction between the two hypotheses is strongly supported by observations of juvenile punares. Escalation into agonism, never observed in 3605 play bout interactions among littermates, was a significant component of encounters among unrelated juveniles. Among male littermates, "losers" tended to break off play interactions by retreating or turning away, while among unfamiliar male juveniles turning away and retreating tended to be performed more frequently by the juvenile designated as dominant based on the frequency of push overs. Unfamiliar male juveniles terminated play bouts more often by turning away or retreating than did littermates. This behavior indicates that, among unfamiliar juveniles, the primary purpose of play is the establishment of dominance relationships, and once dominance relationships have been decided, the dominant

juvenile avoids further interaction with the subordinate. Play continues, however, among littermates to perfect and coordinate competitive social skills.

The structure and content of punare social play suggests that it serves an integral role in juvenile social development. All aspects of punare play were consistent with a function of developing competitive social skills while concurrently establishing dominance relationships. Play serves to prepare juveniles for adult roles by permitting practice of agonistic and dominance reinforcement behavior. Among males, where competition was intense and agonism and dominance relationships were most prevalent, juvenile play was most frequent and forceful. Females, which were more passive as adults, showed lower levels of juvenile social play. Paternal males were extensively involved in social interactions with juveniles, and asserted their dominance over juveniles through social play. Stable dominance relationships were evident among littermates and persisted over time. Residence status had a significant effect on dominance and the frequency of agonism among unfamiliar juveniles, suggesting a territorial basis for juvenile play competition similar to that in adult agonism. These aspects of dominance relationships suggest that the ultimate function of dominance hierarchy formation during juvenile social play may be in promoting juvenile dispersal.

Male-biased dispersal is predicted in the punare due to the presumed polygynous mating system (Dobson, 1982) and intense male-male competition. Establishment of dominance relationships among littermates resulted in decreased play frequency and may cause a similar decrease in the frequencies of other social interactions, thus weakening littermate social bonds (Bekoff, 1977). Through the early establishment of dominance relationships between parental males and offspring, juvenile social play may function as a non-injurous means of precipitating dispersal of juveniles without the potential decrease in inclusive fitness inherent in agonistic competition between father and offspring. The ancestral function of juvenile social play appears to be the development of agonistic skills, however in punares it has assumed a secondary function of establishing dominance relationships, thereby precipitating male-biased post-weaning dispersal.

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APPENDIX 1.

An Ethogram for the South American Punare
(_Thrichomys apereoides_)

This ethogram consists of a comprehensive description of behavioral patterns observed in the South American punare (_Thrichomys apereoides_). Several agonistic behavior patterns have been described by Streilein (1982d), however, this ethogram is the first description of the punare's complete behavioral repertoire. The ethogram was derived from 60 hours of recorded observations on a colony of 100 individuals maintained at Virginia Polytechnic Institute and State University. Adult and juvenile animals were observed in a variety of social situations, familiar and novel enclosures, and during all portions of the light cycle. This ethogram is believed to be reasonably complete, as all reported behaviors were observed on more than one occasion. Ethograms published by Eisenberg (1968) and Wemmer et al. (1983) served as models in the preparation of the ethogram for _Thrichomys apereoides_.

ETHOGRAM

GENERAL MAINTENANCE BEHAVIORS

Sleep and Rest: Common resting postures include sitting with the forelegs straightened keeping the chest above the substrate, lying with the forelegs extended anteriorly with the ventrum resting on the substrate, and lying with the forelegs extended anteriorly and the hind legs stretched out to one side. The tail may be extended posteriorly, curled around the legs, or curled over the back. Animals may rest solitarily or huddled in a group. In adults, the eyes remain partially open during rest, while, in juveniles, the eyes are frequently closed.

Locomotion: Punares exhibit quadrupedal walking, running, jumping and climbing. Occasionally, upright bipedal walking is observed during exploration.

Care of the Body Surface and Comfort Movements:

Groom: Grooming begins with the muzzle, and progresses posteriorly. The nose is wiped with the forepaws, either alternately or simultaneously. The

forepaws, used in synchrony, are then drawn across the sides of the face from behind the ears towards the muzzle, and through the vibrissae. Fur on the sides and belly is licked and nibbled. At the same time, the fur is combed with the forepaws. The tail is held with the forepaws while the tail fur is licked and nibbled. After the remainder of the body fur has been groomed, the toenails of the forepaws and hind feet are nibbled. During toenail grooming, the forepaw being groomed is held by the alternate forepaw.

Sandbathe: The animal rubs its hindquarters in the substrate by vigorously kicking both hind legs out to one side. This is occasionally followed by rolling over the back and rubbing the back in the substrate. Sandbathing often occurs in conjunction with scentmarking.

Scratch: With the hindlegs. Scratching is usually directed at the face, neck shoulders or anterior sides.

Sneeze: Forceful expulsion of air through the nose. During a sneeze, the eyes are closed. Sneezing is often accompanied by head shaking, and is frequently followed by wiping the nose with the

forepaws.

Cough: Förceful expulsion of air through the mouth.

Yawn: With the mouth open, the tongue extended and the eyes closed. Yawning often occurs during the transition from resting to activity resumption.

Stretch: First the head and neck are extended anteriorly, then forelegs, and finally hind legs are extended one at a time posteriorly. Stretching frequently follows Yawning.

Food Gathering, Ingestion and Egestion:

Food Carry: Items are transported in the mouth held by the incisors.

Food Steal: Juveniles often remove food from the forepaws or mouths of adults. Juveniles stand on their hindlegs and grasp the food item with their incisors, while pushing the adult away with their forepaws. Adults usually quickly relinquish the food item.

Manipulation of Food Items: With the forepaws.

Eat: Consists of gnawing with the incisors, chewing with the molars, and swallowing.

Drink: Liquids are lapped with the tongue.

Urination: No special posture for urination was observed. Dribbling of urine may be associated with scentmarking.

Defecation: No special posture for defecation was observed, except during Copraphagy. Often fecal pellets are dropped during locomotion. Defecation may be associated with scentmarking.

Coprophagy: During reingestion of fecal pellets, the animal assumes a sitting position, with the head curled toward the anus. Fecal pellets are removed from the anus with the incisors or the forepaws.

Exploratory Behaviors:

Elongate Posture: The head is extended anteriorly and the tail is extended stiffly backwards.

Exploratory Upright Posture: The animal stands on the hind legs, often resting the forepaws on objects for support.

Sniff: Investigation of objects or surfaces in the environment or the air.

Nibble: Investigation of objects or surfaces in the environment with the lips and teeth.

Digging: The substrate is scooped under the body using alternate forepaws, then is kicked backwards by the hind legs.

Predator Avoidance:

Vertical Jump: From a quadrupedal standing position, the animal leaps straight upwards. This closely resembles the Frisky Hops performed by juveniles during play.

Spin: When grasped by the tail, the animal rotates its hips in a 360 circle, which can result in the tail breaking off near its point of attachment to the body.

SOCIAL BEHAVIORS

Initial Contact and Contact Promoting Behaviors:

Approach: Movement to within one body length of another animal.

Nose-to-nose: Contact of the nasal area of one animal with the nasal area of another.

Nose-to-cheek: Contact of the nasal area of one animal with the side of the muzzle of another.

Nose-to-body: Contact between the muzzle of one animal and the back, shoulders or sides of another.

Nose-to-rump: Contact between the muzzle of one animal and the area surrounding the tail of another.

Nose-to-side: Contact, usually prolonged, between the muzzle of a juvenile and the teat region of its mother.

Paw: The animal contacts the body of another with its forepaws. Pawing is usually directed towards the sides or rump.

Piggyback: One animal perches on the back of another. Piggyback is predominantly a juvenile behavior pattern.

Crawl Under: The animal crawls underneath the body of another. Crawl under is exhibited most frequently by juveniles.

Roll Over: After Crawling Under an adult, juveniles often roll onto their backs, exposing their anogenital regions. The adult frequently responds by Allogrooming the juvenile.

Crawl Under Chin: The animal walks underneath the head of another, rubbing its dorsal surface against the underside of the other animal's chin. Crawl under chin is typically performed by juveniles and directed at adults. Adults frequently respond by Allogrooming the juvenile.

Crawl Over: The animal passes over the body of another, rubbing its ventral surface against the dorsal surface of the other animal. Crawling over may be associated with scentmarking.

Follow: The animal attempts to Approach a Retreating animal.

Huddle: Resting in contact with one or more other animals. Juveniles huddle in a heap, often with an adult crouched over them. Adults huddle with their sides or rumps in contact.

Agonistic Behaviors:

Ground Pat: Drumming against the ground with alternate

forepaws.

Paw Wave: Waving alternate forepaws in the air while assuming an Agonistic Upright Posture.

"Rhumba": Keeping the forepart of the body stationary, the hindquarters are rotated in a semi-circle around the forelegs.

Tail Wag: The animal swishes its tail back and forth through a wide arc.

Agonistic Yawn: The animal opens its mouth and exposes its teeth. Yawning occurs during agonistic approaches.

Hind Foot Thump: The animal slaps the substrate with both hind legs in unison.

Tail Up: The tail is held nearly vertically or curled over the back.

Agonistic Paw Front: The animal bats a forepaw at the face of its opponent.

Agonistic Upright Posture: The animal stands on its hind legs, with its back hunched and forelegs raised to chest level. This may be distinguished from the Exploratory Upright Posture by the hunched back and tense body tone.

Spar: The animals grapple in an upright position, using forepaws to push against each other's shoulders or chests.

Chest Kick: An individual in Upright Posture or during Sparring kicks with both hindlegs at the chest of its upright opponent.

Wrestle: The animals grapple while lying on the substrate, with one animal attempting to gain a position on top of its opponent.

Push over: Following Sparring, one animal pushes the other from a bipedal, upright position to a quadrupedal stance or onto its back or side.

Mount: The animal rests the front portion of its body on the back of another, with its forelegs gripping the other animal just anterior to the hind legs.

Cower: The animal assumes a crouched position, with its head flattened against the substrate.

Bite: Self-explanatory. Directed at the back, rump or facial area of opponent.

Turn Away: The animal rotates its body to face away from another animal.

Push Away: The animal bats another animal away with its forepaw. Pushing is typically directed at the opponents shoulders or sides.

Retreat: Movement which increases the distance between two animals to more than one body length.

Chase: One animal attempts to Approach at a run, while the other animal flees.

Sexual Behaviors:

Male Patterns:

Mount: The male rests the front portion of its body on the back of the female, while clasping with its forelegs just anterior to the female's hind legs.

Nose-to-nape: The male's muzzle makes contact with the nape of the female.

Copulate: Copulation follows the pattern of intromission, pelvic thrusting and

ejaculation, with repeated copulations.

Female Patterns:

Lordosis: The female raises her anogenital region above the substrate.

Stand: The female remains stationary and permits the male to Mount.

Patterns of Both Sexes:

Post-copulatory Groom: In a sitting position, the animal licks its ventrum and anogenital area.

Parental Behaviors:

Parturition: The female squats with her head bent between her hind legs. The neonate emerges head first, and is withdrawn by the female using her forepaws. The female severes the umbilical cord with her incisors and licks the nasal region of the neonoate. The paternal male may assist in the grooming of the neonate.

Nurse: The nursing female crouches quadrupedally or with one foreleg raised, and arches her back slightly.

Allogroom: The juvenile is licked and nuzzled. Adults

often manipulate the juvenile with their forepaws while allogrooming. Most allogrooming is directed at the juvenile's anogenital and facial regions.

Carry: With the incisors, the female grasps her young by the scruff of the neck, ears, legs or base of the tail.

PLAY BEHAVIORS

Solitary Locomotor Play:

Run: A rapid, bouncy gait characterized by sudden stops and starts.

Climb: Self-explanatory. Often performed in association with Running and Jumping.

Jump: From a quadrupedal standing position, the animal leaps forward and upward.

Vertical Hop: From a quadrupedal or bipedal standing position, the animal leaps directly upwards. Vertical hops are often repeated many times in succession. Vertical hops may be distinguished from Jumps in that little or no horizontal

distance is travelled.

Object Manipulation:

Bite Ear: The animal pulls on another animal's ear with its incisors.

Bite Tail: The animal pulls on another animal's tail with its incisors.

Pull Tail: The animal grasps another animal's tail with its forepaws.

Interactive Social Play:

Playful Paw Front: The animal bats its forepaw at the head of another animal. This is distinguished from an Agonistic Paw Front by the lack of Chatter vocalizations.

Playful Upright Posture: The animal assumes a bipedal stance. This is distinguished from an Exploratory Upright Posture by the social context, and from an Agonistic Upright Posture by the loose body tone and lack of Chatter vocalizations.

Jump Over: The animal leaps over another animal without making physical contact.

Crawl Over: The animal passes over another animal, making physical contact. Crawling over in a play context is most often preceded and followed by Running.

Pounce: The animal jumps towards another animal, making contact with its forepaws. In contrast to Crawl Over, pouncing is not followed by Running.

Box: Animals grapple in a bipedal position, pushing against each other's shoulders with their forepaws. This is distinguished from Sparring by the lack of low intensity agonistic behaviors and Chatter vocalizations.

Push Over: Following Boxing, one animal pushes the other from an upright position to a quadrupedal stance or onto its back.

Mount: The animal rests the front portion of its body on the back of another, with its forelegs gripping the other animal just anterior to the hindlegs.

SCENTMARKING BEHAVIORS

Perineal Drag: The animal walks forward with the forelegs while dragging the anogenital region along the substrate or over the body of another animal.

Cheek Rub: The animal repeatedly rubs the vibrissae and cheek area against objects in the environment or over the body of another animal. Males may cheek rub the dorsal surfaces of females while Mounted.

VOCALIZATIONS

Chatter: A rapid chitter vocalization. Chatters accompany low intensity agonistic behaviors, such as Ground Pat, Paw Wave, "Rhumba", Tail Wag, Hind Foot Thump, Tail Up, Paw Front and Agonistic Upright Posture.

Wheet: A sharp, high-pitched call given by juveniles when isolated from their mothers, or when handled roughly.

Chip: A sharp, high-pitched call given by adults.

Eee: A prolonged wail given by the subordinate animal in the later stages of an agonistic encounter.

Whir: A low-pitched, growling vocalization given by the dominant animal in the later stages of an agonistic encounter.

Gurgle: A low intensity vocalization given by animals when injured. It is probably associated with pain.

Table 1. Categories of adult agonistic behavior identified by factor analysis and the percent of variance explained by each.factor. Overall variance explained is 63%.

Factor 1 (30.8%)	Factor 2 (13.6%)	Factor 3 (10.3%)	Factor 4 (8.3%)
Initial Contact and Contact Promoting Behaviors	Agonistic Behaviors	Transition Behaviors	Retreat Behaviors
Approach	Paw Front	Ground Pat	Retreat
Nose-to-nose	Upright Posture	Mount	
Nose-to-cheek	Spar		
Nose-to-body	Push Over		
Nose-to-rump	Chest Kick		
Paw			
Follow			
Mount*			

* in male-female encounters

98

Table 2. Comparisons of behavioral frequencies within unfamiliar adult encounter types.
Behaviors not listed did not differ in frequency within encounter types.

Encounter Type	Male-Male N=12		Female-Female N=11		Male-Female N=24	
	dominant	subordinate	dominant	subordinate	male	female
Behaviors Exhibited With Greater Frequency	Approach** Z=3.06		Approach** Z=2.76		Approach** Z=1.98	
	Nose-to-body** Z=2.47				Nose-to-cheek* Z=1.75	
	Nose-to-rump** Z=2.52					
	Paw** Z=2.65				Paw** Z=1.97	
	Follow** Z=2.80		Follow** Z=1.91		Follow** Z=2.13	
	Chest Kick* Z=1.83					
	Mount* Z=1.68				Mount** Z=2.67	
		Retreat** Z=2.85		Retreat** Z=2.71		Retreat** Z=2.42

* p<0.10
** p<0.05

Table 3. Comparisons of behavioral frequencies between unfamiliar adult encounter types. Behaviors not listed did not differ in frequency between encounter types. Female-female and male-female encounters did not differ in the frequency of any recorded behavior.

Comparison	N=23		N=24	
	Male-Male	Female-Female	Male-Male	Male-Female
Behaviors Exhibited With Greater Frequency	Paw Front* $Z=1.85$		Paw Front* $Z=1.92$	
			Spar* $Z=1.79$	
	Mount** $Z=2.18$			

* $p<0.10$

** $p<0.05$

Table 4. Correlation coefficients of maternal and paternal behaviors over time.

Behavior		Correlation Coefficients	
		Parental Female	Parental Male
Approach		-0.311**	0.077
Nose-to-cheek		-0.488***	-0.085
Nose-to-body		-0.508***	-0.360***
Nose-to-rump		-0.383***	-0.380***
Groom		-0.532***	-0.411***
Paw		-0.189	-0.339**
Follow		-0.393***	-0.034
Box		0.142	0.283*
Push Over		0.074	0.249*
Mount		0.172	0.427***

* p<0.05

** p<0.01

*** p<0.005

Table 5. Comparison of play onset by litter compsosition. Play was defined as the first day on which social play was observed in a juvenile, and is expressed as the mean day ± 1 standard deviation for all juveniles within a litter type.

Litter Composition	Play Onset	Grouping*
Male-Male-Male	1.33 ± 1.21	A
Male-Male-Female	2.50 ± 1.63	A
Male-Female-Female	4.33 ± 1.86	B
Female-Female-Female	6.17 ± 0.41	C

* Fisher's LSD; values with the same letter were not statistically different

Table 6. Comparison of play bout durations between bout types, where J=Juvenile, P=Parental, ♂=Male and ♀=Female.

Bout Type	Duration	Grouping*
J♂J♂	4.36 ± 1.66	A
J♂J♀	3.51 ± 3.11	B
J♀J♀	2.19 ± 1.52	C
P♂J♂	3.39 ± 3.50	B
P♂J♀	4.93 ± 6.58	A
P♀J♂	2.39 ± 0.88	B C
P♀J♀	2.03 ± 1.05	C

* Fisher's LSD; values with the same letter were not statistically different

Table 7. Comparison of the number of successive play bouts by familiarity and bout type. See Table 6 for symbol definitions. Values are means ± 1 standard deviation.

Bout Type	Successive Bouts	Grouping*		
Littermate ♂♂	1.49 ± 1.25	A		
Littermate ♂♀	1.36 ± 0.91		B	
Littermate ♀♀	1.13 ± 0.66			C
Unfamiliar ♂♂	1.44 ± 1.06	A	B	
Unfamiliar ♂♀	1.26 ± 0.65		B	C

* Savage Test; values with the same letter were not statistically different

Table 8. Effect of bout type and residence status on unfamiliar juvenile encounters. See Table 6 for symbol definitions.

		Bout Type	
		♂J♂J♂	♂J♂J♀
	N	42	13
Resident-Resident	Boxing	240*	60*
	Sparring	14*	2
	N	20	41
Resident-Intruder	Boxing	3	8
	Sparring	0	0
	N	16	34
Intruder-Intruder	Boxing	0	0
	Sparring	0	0

* p<0.001

Table 9. Correlation coefficients of adult behavioral interactions with juveniles in the large enclosure.

Behavior	Parental Female	Correlation Coefficients Nonparental Female	Parental Male	Nonparental Male
Approach	-0.502	-0.169	0.148	0.063
Nose-to-cheek	0.645	0.151	0.601	0.085
Nose-to-body	-0.457	-0.850*	0.507	0.035
Nose-to-rump	-0.080	-0.474	0.000	0.258
Groom	-0.507	-0.402	0.000	0.000
Paw	0.507	0.516	0.169	-0.115
Follow	-0.577	-0.135	-0.258	-0.233
Box	0.507	0.258	0.258	0.000
Push Over	0.000	0.000	0.044	0.000
Mount	0.000	0.000	0.507	0.000

* $p < 0.01$
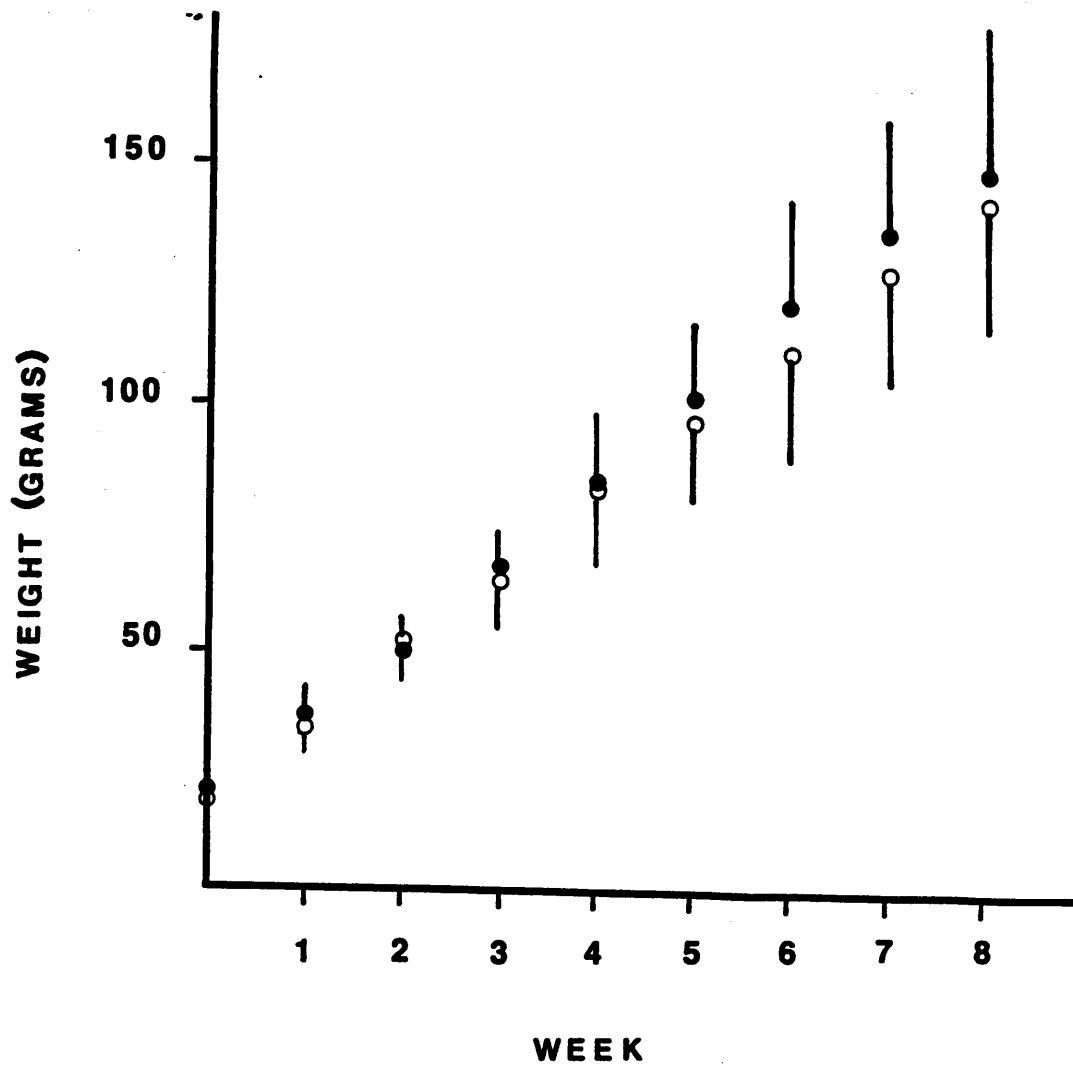
Figure 1. Mean body weight from birth until eight weeks of age for males (●) and females (O). The plotted values represent the mean ± 1 standard deviation.
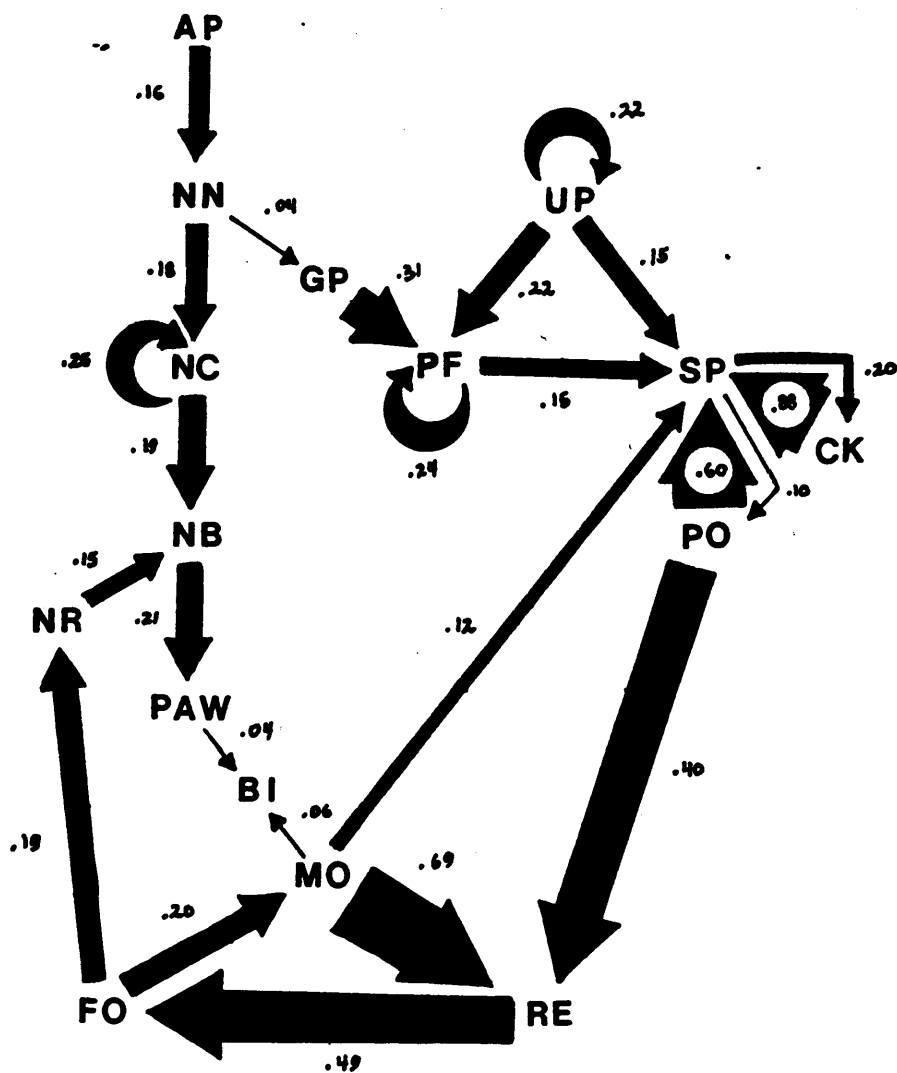
Figure 2. Behavior sequences and transition probabilities for unfamiliar adult male-male encounters. AP=Approach, NN=Nose-to-nose, NC=Nose-to-cheek, NB=Nose-to-body, NR=Nose-to-rump, PAW=Paw, BI=Bite, MO=Mount, FO=Follow, GP=Ground Pat, PF=Paw Front, UP=Upright Posture, SP=Spar, CK=Chest Kick, PO=Push Over and RE=Retreat.
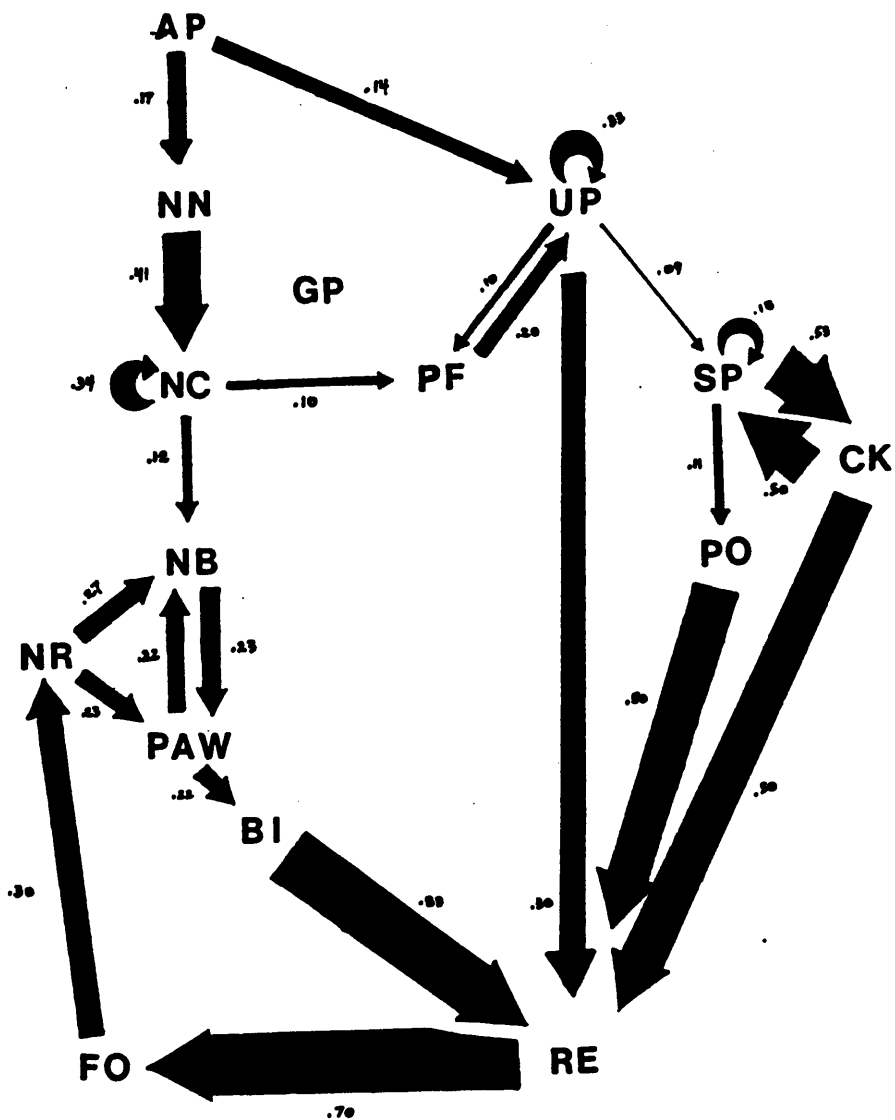
Figure 3. Behavior sequences and transition probabilities for unfamiliar adult female-female encounters. See Figure 2 for symbol definitions.
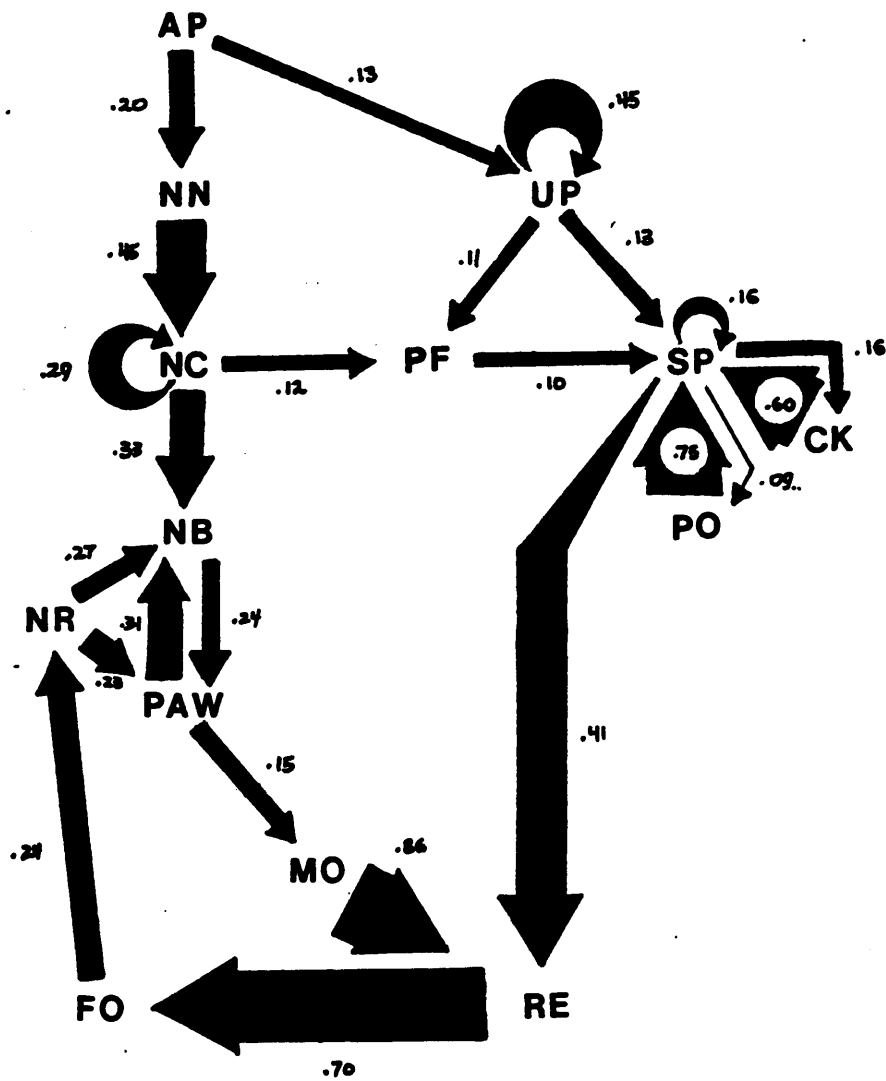
Figure 4. Behavior sequences and transition probabilities for unfamiliar adult male-female encounters. See Figure 2 for symbol definitions.
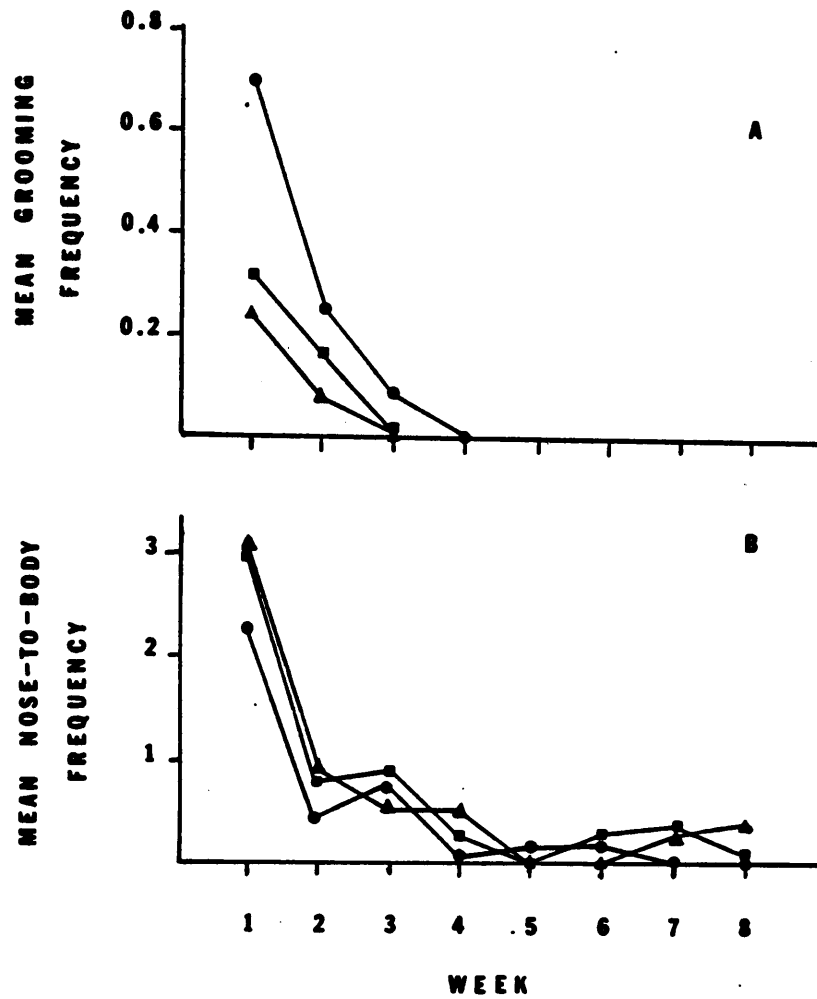
Figure 5. Mean frequencies of maternal grooming (A) and nose-to-body (B) over time for a representative litter. Each juvenile is represented by a different symbol.
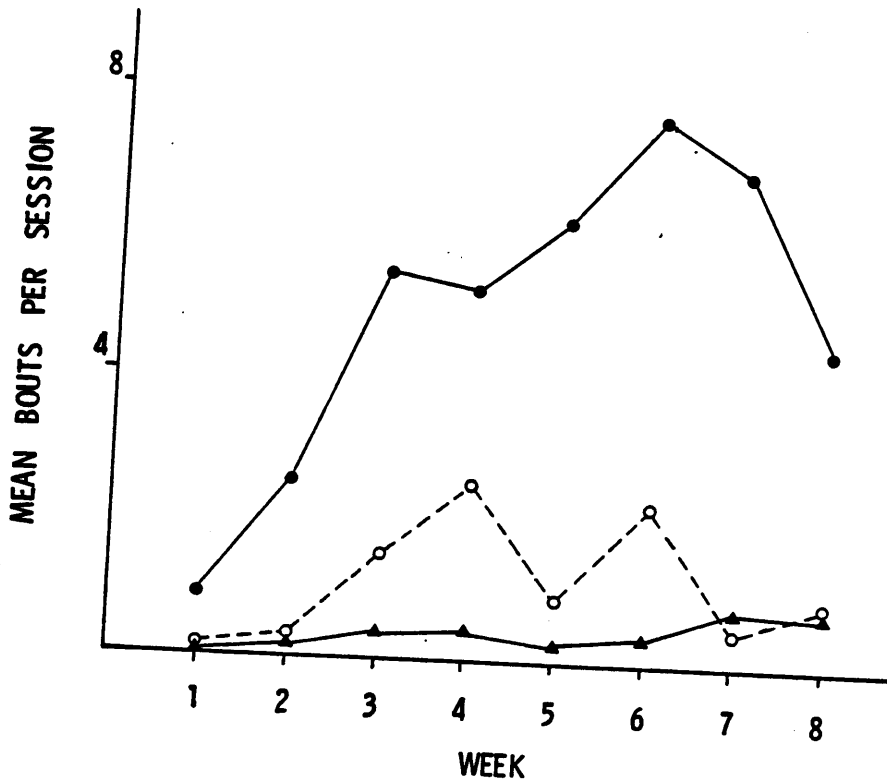
Figure 6. Play bout occurance over time for male-male (●), male-female (○) and female-female (▲) bouts.
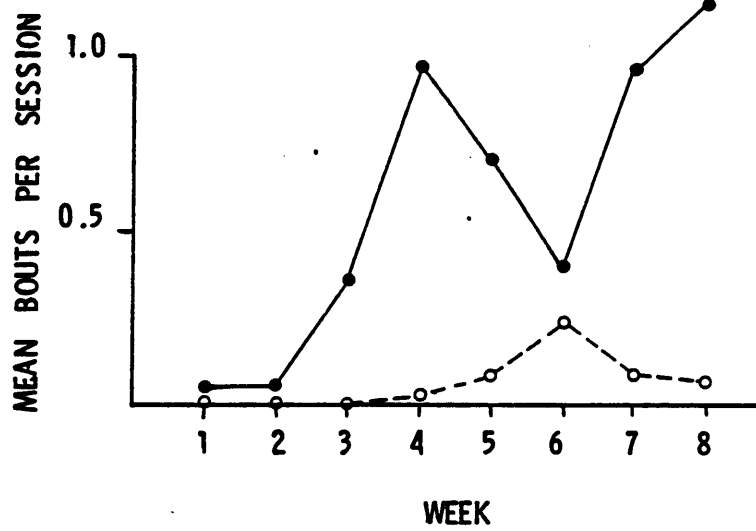
Figure 7. Play bout occurance over time for parental males
(●) and parental females (○).
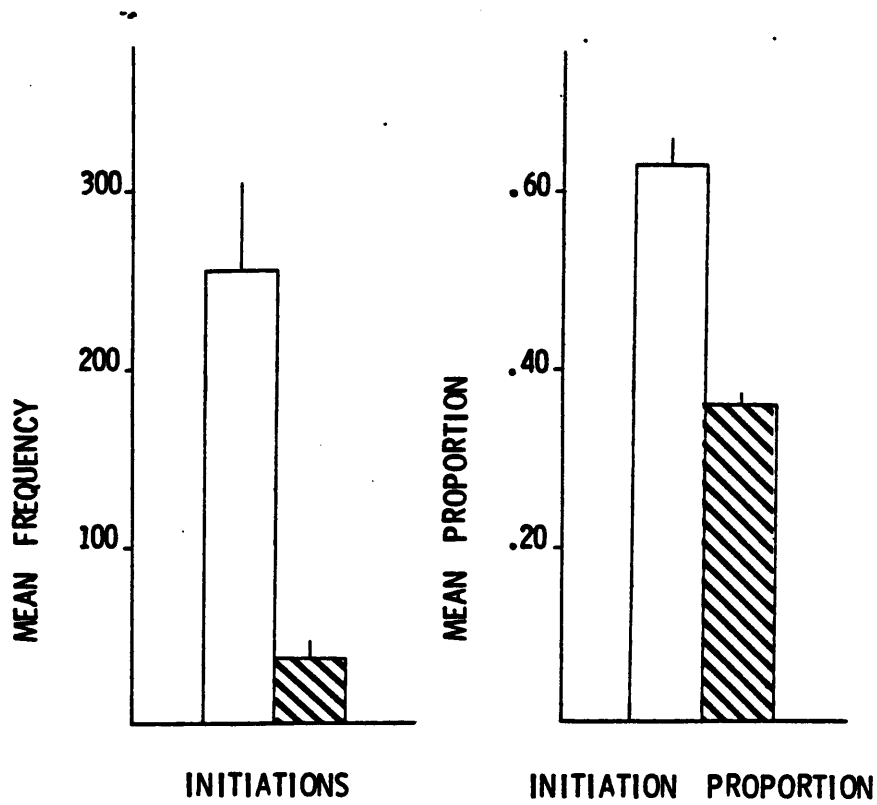
Figure 8. Comparison of play bout initiations (A) and the proportion of total play bouts initiated (B) for male (☐) and female (◨) juveniles.
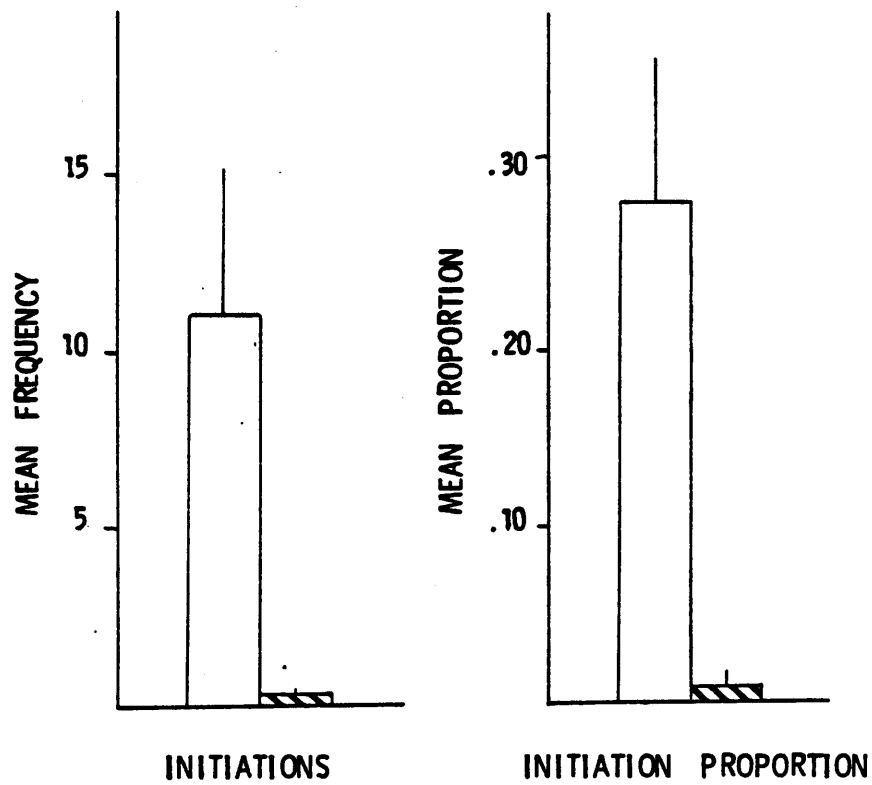
Figure 9. Comparison of play bout initiations (A) and the proportion of total play bouts initiated (B) for parental males (☐) and parental females (☒).
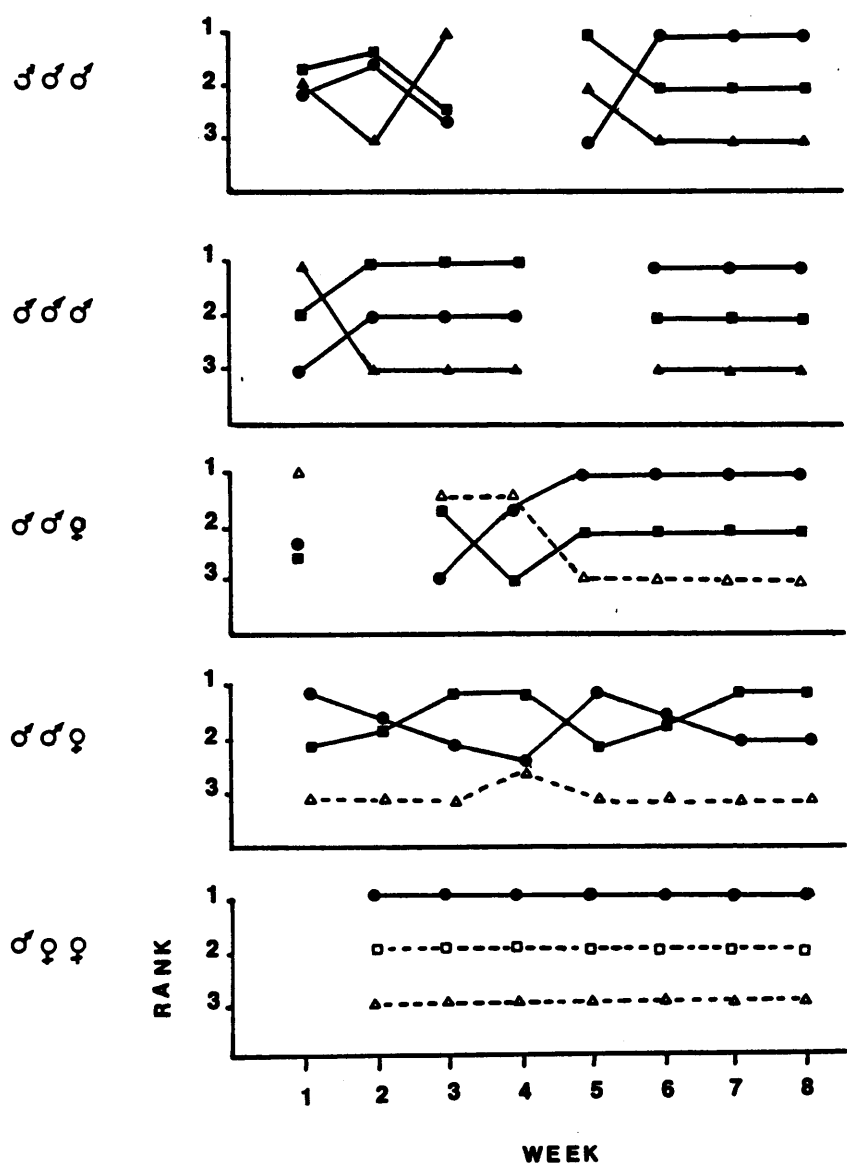
Figure 10. Dominance hierarchies within litters constructed using push over frequency. For weeks in which the hierarchies were non-linear, no points are plotted. Solid symbols denote male juveniles and open symbols denote female juveniles.
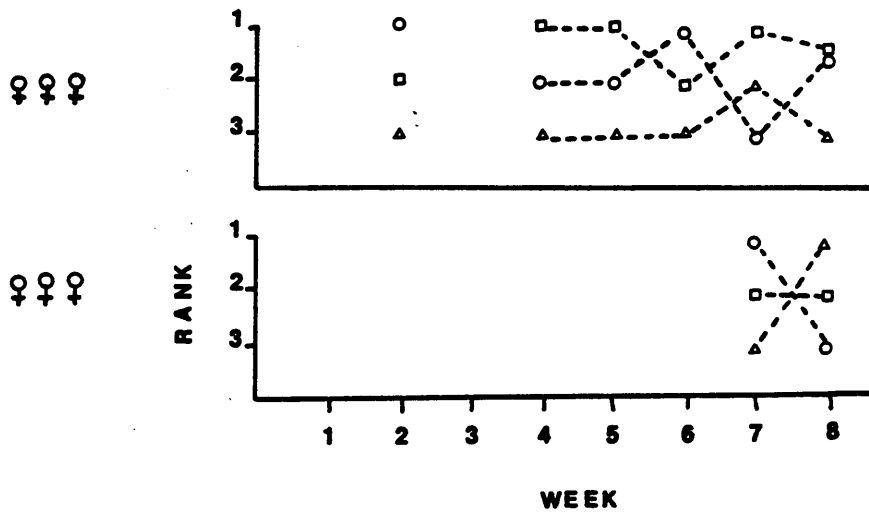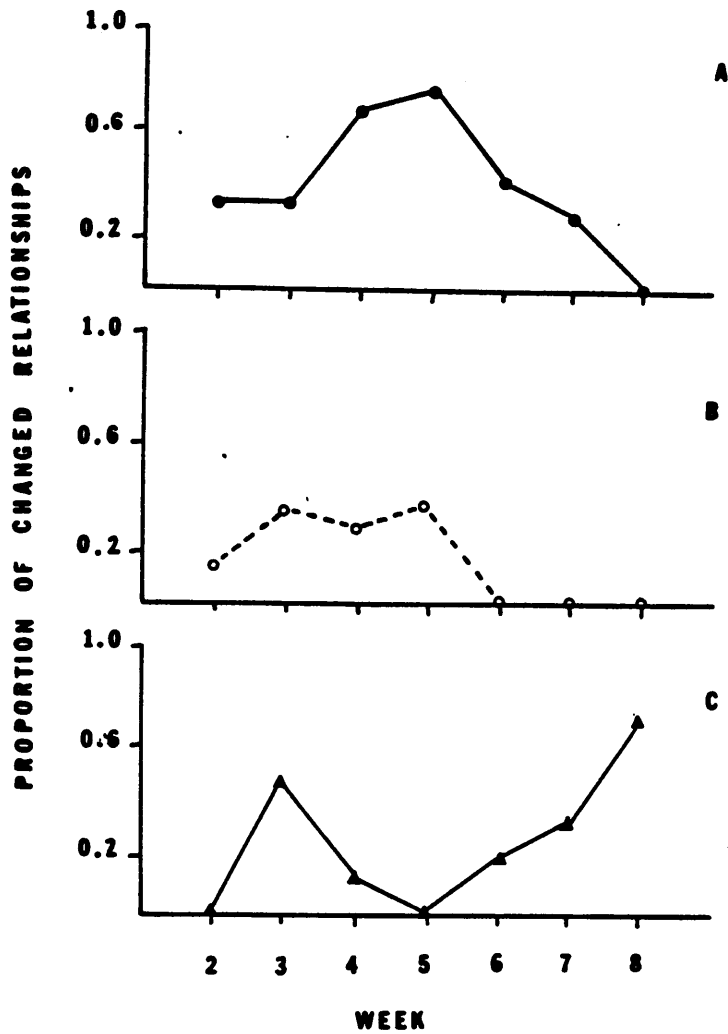
Figure 11. Dominance hierarchies within litters constructed using the combined frequencies of push overs, turn aways and retreats. For weeks in which the hierarchies were non-linear, no points are plotted. Solid symbols denote male juveniles while open symbols denote female juveniles.

Figure 12. Proportion of changes in dominance relationships over time for male-male (A), male-female (B) and female-female (C) sibling pairs.
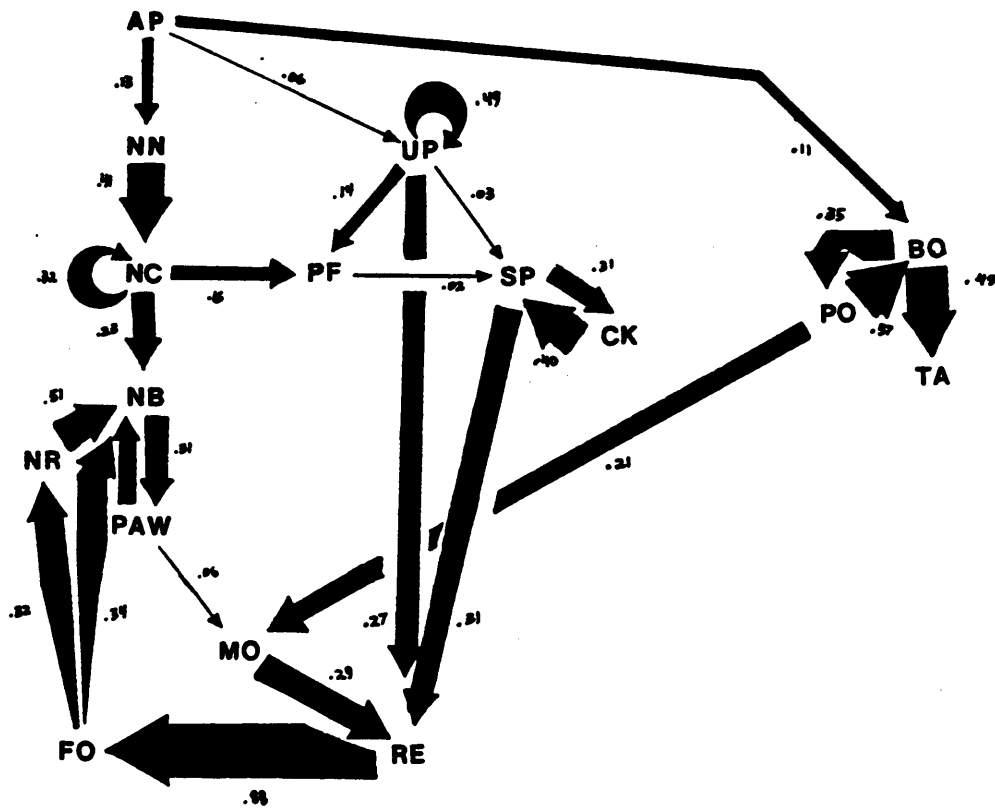
Figure 13. Sequences of behavior and transition
probabilities for unfamiliar juvenile male-male encounters.
BO=Box and TA=Turn Away. See Figure 2 for additional symbol
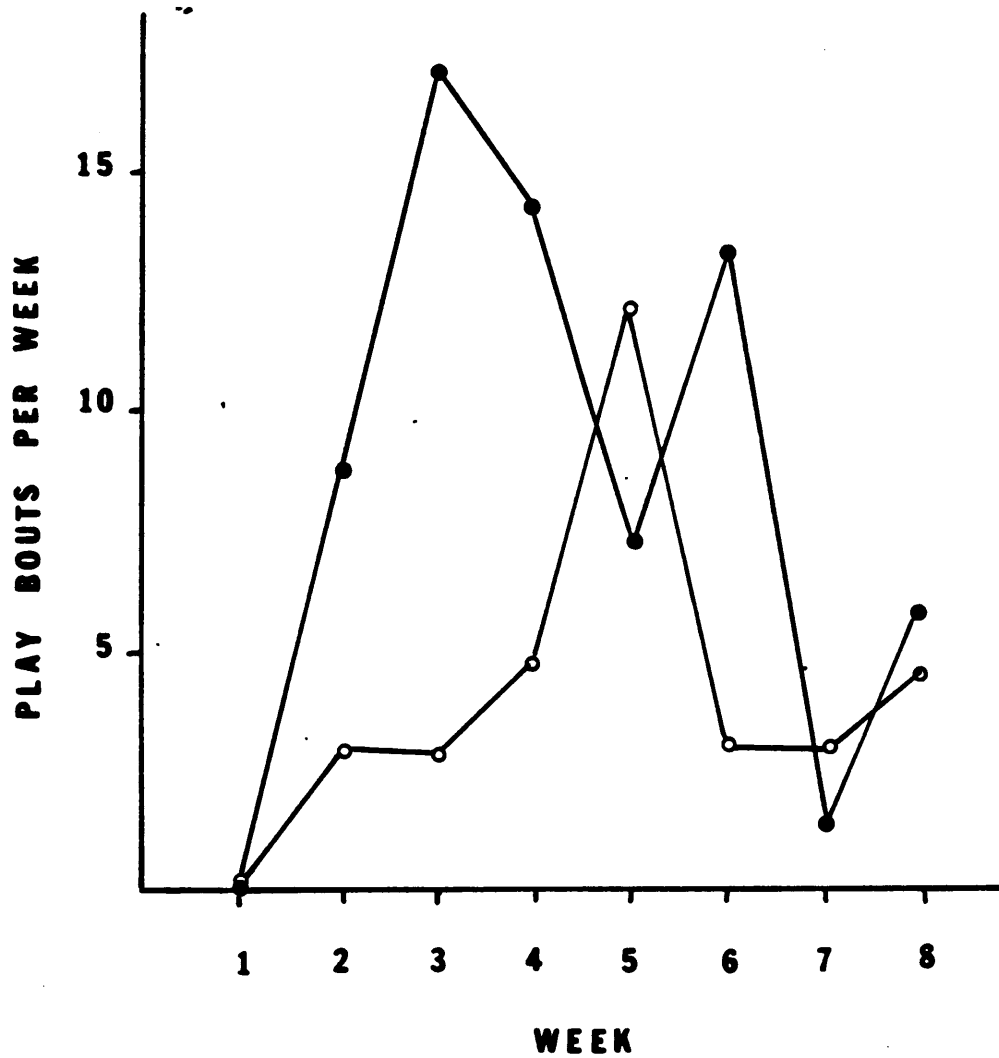definitions.

Figure 14. Frequency of play bout initiations by week for juveniles in the large enclosure. The two juveniles are represented by different symbols.