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# THE BEHAVIOURAL ONTOGENY OF THE COLUMBIAN GROUND SQUIRREL

by

© JANE-MARGARET WATERMAN

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SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
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# Abstract

The behavioural ontogeny of the Columbian ground squirrel (*Spermophilus columbianus*) was examined using live-trapped and marked individuals in a population in southwestern Alberta, Canada. Observations using scan and all-occurrence sampling recorded the activities and locations of individuals in order to study the development of spatial and behavioural patterns, with emphasis on social play.

Differences between sexes in the movement of juvenile Columbian ground squirrels were apparent after the first 10 days from first emergence from the natal burrow. Males travelled further from the natal burrow, had larger home ranges and shifted their activity centres more than did females. Females remained nearest their sisters and rates of play between sisters were the highest of all interacting pairs. Although there was no difference in the mean distance from the mother for males and females, females greeted their mothers three times more frequently than did brothers.

The structure of play varied with age, sex and relatedness of the interactors. Only in intrasexual play were differences apparent in sibling and non-sibling play. Male-male non-sibling play had fewer contact behaviours than sibling play; female-female non-sibling play had escalations in aggressive behaviours. Yearling play was longer and more aggressive than juvenile play. As well, reversals in wrestling were more common in yearling bouts.

These results suggest that males and females have different social experiences in early development. The consequences of such different experiences are discussed in light of female site fidelity and male dispersal. The possible benefits of social play are considered for the various categories of sex, age and relatedness. The differences noted between sibling and non-sibling intrasexual play suggests that more than just exercise or practice is involved in the social play of Columbian ground squirrels.

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# 1. General Introduction

The social organization of a species can be described in terms of the social interactions among members of a population relative to spatial and temporal characteristics of their environment (Pitelka *et al* 1974). As animals differ in their life history characteristics and habitats occupied, they also differ in their social organization. Evolutionary and ecological constraints on social organization can be examined in a number of ways, one of which is the study of the integration of young into the social group. The ontogeny of social patterns among immature animals may reveal some of the mechanisms influencing sociality.

Socialization is the sum of all social experiences that alter the development of an individual (Wilson 1975). In many mammals early social experiences often involve play. Most likely play has both physiological and social consequences. The suggested benefits of social play range from simple exercise to social bonding between individuals (Bekoff 1984; Fagen 1981). These benefits may vary depending on the age, sex, and relatedness of the participants and on environmental conditions (Bekoff 1984; Fagen 1981). Play has been studied in a variety of mammals, including cats (Caro 1981; West 1974), canids (Bekoff 1982), ferrets (Biben 1982), bighorn sheep (Berger 1980) and many species of primates (Fedigan 1982; Lee 1983) (see Fagen 1981, for a review). Many of these studies involved the study of captive animals. Research quantifying play between kin and non-kin are, however, rare in both field and laboratory studies.

The ground-dwelling sciurids (Rodentia:Marmotini) range from solitary species (eg. woodchuck, *Marmota monax*) to highly social species (eg. black-tailed prairie dogs, *Cynomys ludovicianus*) (Michener 1982). The social sciurids are ideal animals for studies of behavioural ontogeny. They are diurnal, easy to observe, and individuals can be easily marked and identified from year to year. Due to the proximity of littermates and their mothers, relationships among groups can be determined (albeit paternity is usually unknown). Thus not only can the development of behaviours of individuals be studied, but comparisons between sexes and relatedness can be made.

The Columbian ground squirrel, *Spermophilus columbianus*, of western North America is a relatively social species (Michener 1982). As with many sciurids, Columbian ground squirrels are characterized by sex-differential dispersal, in which females have greater site fidelity than males and often remain near the site of their birth (Murie and Harris 1984). According to King (1984), nepotism is an important component of the social organization of adult female Columbian ground squirrels. Michener (1982) suggests that familiarity through primary socialization is likely to be a proximate mechanism through which kin selection operates. Play is an important part of the social repertoire during the first two summers (as a juvenile and yearling) (Steiner 1971; Betts 1976). However, in this species in which female kin groups (King 1984) and sex differential dispersal may be characteristic, little is known about development of such patterns.

The aim of this study is to investigate the development of behaviour in the Columbian ground squirrel. In this thesis I firstly describe the development of spatial and behavioural patterns in juveniles. The development of sex differences in these patterns, and the possible effects that these differences have on opportunities for social interactions with other ground squirrels is examined (Chapter 2). Next I analyze the structure of play, concentrating on differential play between sexes, between siblings and non-siblings, and between juveniles and yearlings. The potential benefits of such play are discussed in light of the social organization of the species (Chapter 3).

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# 2. Behaviour and use of space by juvenile Columbian ground squirrels

## 2.1 Introduction

The social organization of animals is often analyzed in light of the spatial organization and social behaviour of adults. However this organization is maintained by the integration of young individuals into already existing social groups (Bekoff 1972, 1977, 1981, 1985). Clearly, in order to evaluate the significance of adult social behaviours, it is important to understand the development of such behaviours in immature animals (Tinbergen 1963, Bekoff 1978, Bekoff and Byers 1981).

The Columbian ground squirrel (*Spermophilus columbianus*) is a polygynous species, living in colonies in western North America (Manville 1959). Squirrels hibernate in underground burrows most of the year, emerging in the spring to breed, grow, and build up fat stores in a four month period before immergence in late summer (Boag and Murie 1981a). Sexual differences in behaviour and use of space are prevalent in the adult population. In the early spring, males usually maintain a territory which encompasses the ranges of more than one female (Murie and Harris 1978). Females defend areas during gestation and lactation but their active defense of space declines upon emergence of the young (Festa-Bianchet 1982, this study).

Michener (1982) suggests that amicability between neighbouring, most likely related, litters is important in the formation of cohesive multiple-family clusters of female kin. She suggests that this is the basis of the social organization of females. Thus, interactions between female littermates, and related non-littermates may be important in establishing and reinforcing amicable relationships among kin. The young of Columbian ground squirrels meet Bekoff's (1981) four criteria for the promotion of sibling interactions by familiarity. There is usually more than one individual per litter, and individuals are relatively immature at birth. Litters remain intact and isolated from other litters (for the first 30 days an individual remains in the natal burrow, interacting only with other siblings or the mother), and finally, social groups are relatively closed to outsiders and juvenile emigration is rare. King (1984) examined the spatial and social relationships in juvenile Columbian ground squirrel females and found evidence to suggest favouring of kin. Harris and Murie (1984) found that females often inherit the nest site of their mother. As a consequence of this inheritance, and the greater site fidelity of females (compared to males), related females would be apt to settle near each other. Favouring of kin would be unlikely in males, which disperse as yearlings (Boag and Murie 1981b) and thus face future social interactions with unknown and usually unrelated animals. They would not be expected to promote sibling interactions to the same extent as females.

The aim of this study was to describe the spatial patterns and social behaviours of juvenile Columbian ground squirrels and examine the development of sexual differences within them. The effect of such sex differences on the on the social organization of the Columbian ground squirrel were considered in light of female site fidelity and male dispersal.

## 2.2 Methods

The study site was located 15 km southwest of Longview, Alberta, Canada, in the foothills of the Rocky Mountains (50°33'N, 114°33'W; elevation 1295m).. The 2 ha area was surrounded by spruce *(Picea glauca)* and aspen *(Populus tremuloides)* forest. Dominant plants on the area varied throughout the season, but were mainly comprised of various grasses, windflower *(Anemone globosa)*, sticky purple geranium *(Geranium viscosissimum)*, prairie crocus *(Anemone patens)*, shrubby cinquefoil *(Potentilla fruticosa)*, yellow pucoon *(Lithospermum ruderale)*, strawberry *(Fragaria vesca)* and long-plumed avens *(Geum triflorum)* (Moss 1967). The area was grazed regularly by both horses and dairy cows, resulting in relatively good visibility for observing squirrels throughout the summer.

All squirrels on or adjacent to the study area were live-trapped using National live traps (15x15x50cm) baited with peanut butter. Individuals were marked for identification using numbered metal ear tags (National Band and Tag Co., Monel #1) and dye marks on the body using hair dye (Lady Clairol Nice N'Easy blue-black). In addition coloured plastic strips were attached to one eartag of each juvenile and yearling to aid in identification. All squirrels were weighed (±5g) with a Pesola spring scale, examined for sex and reproductive status, and released at the place of capture. In the first year of the study, the approximate ages (ie. either as a yearling or an adult) were estimated by weight based on Boag and Murie (1981a). In order to mark litters before they could intermix, juveniles were trapped within 3 days of first emergence using wire mesh traps placed over the burrow.

The study site was divided into two observation areas of one ha each. Coloured surveyors flags were used to mark the coordinates of a 10x10m grid. Squirrels were observed with 10x50 and 20x60 binoculars, or a 20x60 spotting scope from either a 3m (area 1) or a 2.5m (area 2) observation stand. Observations were made from 1 June to 17 August in 1982, and 5 May to 11 August in 1983. In total, 576 hours of behavioural observations were recorded.

In both years, the identity, location and activities of all squirrels were recorded every 1/2 hour using scan sampling (Altmann 1974, Lehner 1979). Due to good visibility most neighbouring squirrels could be sighted within 1 minute of each other. In 1982, scans at 15 minute intervals were also used to observe juveniles only. In 1983, all social interactions were recorded by all occurrences sampling (Altmann 1974). Behaviours for scan and all occurrences sampling were based on descriptions by Steiner (1970a,1970b) and Betts (1976). Nonsocial behaviours included feeding, sitting, grooming (included all scent marking), and nest maintenance (digging and collecting nest material). Social behaviours included play, "greeting", [illegible] (another individual), and being chased by another individual.

Sizes [illegible] home ranges were calculated by the minimum polygon method (Mohr 1947) using an APL program written by D. Fulton and W. Klenner of the University of Manitoba, Winnipeg. An animal's home range is usually defined as that area covered in normal daily activities (Lehner 1979). To calculate the home range, the approximate percentage of the outermost points which were outside normal daily usage areas had to be estimated and eliminated. By plotting area size against the percentage of outermost points dropped, it was apparent that at 80% the rate of decrease in area size was relatively small (see Appendix I). This indicated that animals spent most of their time within this range and thus 80% was used as an estimator of home range size. This is consistent with findings by Davis (1982a) in Richardson's ground squirrels, and King (pers. comm) in Columbian ground squirrels. The area of overlap between adjacent squirrels was calculated as the area of their home ranges that was mutual. The percent of their total home range that this encompassed was then calculated, as well as the percent of all sightings of each individual in the area of overlap.

Rates of play over the summer were calculated on the basis of individual pairs (dyads) in which the number of interactions of the dyad (from scan data) was divided by the number of times the two individuals were seen together in a scan (Michener 1980). However, in order to account for variability among dyads, rates were divided by the fraction of total time a squirrel spent in the area of overlap of the dyad.

Because activity levels declined throughout the summer, data were analyzed using 10 day intervals, the minimum amount of time necessary to obtain 20 sightings per individual. Where data were found to be normal and homoscedastic, parametric statistics were used (Sokal and Rohlf 1981; Kleinbaum and Kupper 1978); otherwise non-parametric statistics were employed (Siegel 1956; Conover 1980). The 0.05 probability level of a Type I error was considered significant. All figures are mean ± standard error, unless otherwise indicated.

## 2.3 Results

### 2.3.1 Demographic characteristics

The number of squirrels on the study area was similar in both years (Table 2.1). In 1982, the first litter emerged on 17 June and the last on the 10 July, a 21 day interval. In 1983, the first litter emerged on 13 June and the last on 25 June, a 13 day interval. Only two litters in 1982 and two litters in 1983 had mixed before being marked due to squirrels emerging on the same day and in neighbouring burrows. These squirrels were all on the periphery of the study site and were not included in sibling analyses. In all 72 juveniles (23 litters) emerged in 1982 and 86 (28 litters) in 1983. Mean litter size did not differ between years (1982, 2.78±0.83; 1983, 3.04±0.96; Mann-Whitney U-test P=0.75). The overall sex ratios of juveniles favoured females in 1982 (56.9% female) and males in 1983 (43.1% female) but did not differ significantly from a 1:1 ratio, nor did they differ significantly between years ($X^2$ contingency table,P=0.08). The percent males per litter, a measure indicating sex ratio within litters, did not differ between years (1982, 45.5±6.6%; 1983, 53.8± 6.1%; Mann-Whitney U-test P=0.41)

### 2.3.2 Use of space

The first day or two from initial emergence, juveniles usually remained within a few metres of their natal burrow (or an adjacent burrow). Within the first 10 days they began to move an average of 10m from the burrow (Figure 2.1). At this time there was no difference between sexes in the distances travelled from the natal burrows (Mann-Whitney U-test, P=0.112). Sex differences in distances appeared after the first 10 days and existed for the rest of the summer (Mann-Whitney U-test, P<0.001 for all intervals in both study years). The average distance that both males and females were observed from the natal burrow increased over the summer (1982: males r=0.473 P=0.001, females r=0.375 P=0.001; 1983: males r=0.575 P=0.001, females r=0.381 P=0.01). Movements were analyzed using a three way analysis of covariance to examine sex, year and seasonal effects. The increase in distances from the burrow were much higher for males than females (ANCOVA, F=21.07 P<0.000, N=331). Individuals of both sexes travelled further in 1982 than 1983; however the difference was greater for males than for females (ANCOVA, F=4.64 P=0.03, N=331). As result of these movement patterns, distances travelled from the natal burrow increased as the summer progressed, males moving farther than females.

The longer excursions of males were reflected by the size of their home ranges. Over the entire summer, males had much larger home ranges than did females (Table 2.2). As there were no differences between years, (3 way ANOVA, F=0.216 P=0.643, N=167) data were pooled. Examination of the change in the size of home ranges over the summer indicated only a trend for males to have larger home ranges than females, but this was not significant (ANOVA, F=2.04 P=0.102, N=167)(Figure 2.2). Both males and females more than doubled their home range size over the first twenty days above ground. Male ranges were the largest 30 to 40 days after emergence, and decreased just before immergence to a similar size as females.

Throughout the summer juveniles continued to return to their mother's burrow system and centred their activities within the mother's home range (Figure 2.3). Although males travelled further from the natal burrow than females, their overall activity centres were not further from their mothers activity centres than females (Males: 5.63 ± 1.07 (N=24); females: 7.09 ± 2.12(N=11); Mann-Whitney U-test P=0.82). There did not appear to be much independence from the natal area and the bulk of the juvenile activities remained fairly close to their first centre of activity. However, males shifted their activity centres further from their initial activity centre than did females (ANOVA, F=6.67 P=0.003, N=252)(Table 2.3). Thus, females seemed to centre their activity centres closer to the natal burrow than did males. As a result of remaining closer to the natal burrow, the distances between sisters during scans were smaller than those of brother or brother-sister dyads (3 way ANOVA, F=14.23 P<0.0001, N=4319)(Table 2.4). These distances did not increase over time (ANOVA, F=2.031 P=0.154, N=4319) even though home range and distances travelled increased over time. This indicates that individuals, especially males, were maintaining short distances between themselves and their siblings, even as they moved farther from the burrow. Females in 1983 were found closer to each other than those in 1982, possibly a result of small sample size. The lack of statistical independence among data for brother, brother-sister and sister groups necessitates cautious interpretation of such results, however.

Even though the overall home range size of males was larger than that of females, there was no difference in the percentage of home range overlap between brother, brother-sister and sister dyads (Mann-Whitney U-test P=0.37)(Figure 2.4). Thus, there appeared to be equal opportunity for a juvenile to interact with siblings of both sexes. The percentage of home range overlap with non-siblings was considerably less than that of siblings, regardless of the sexes in the dyads (Mann-Whitney U-test P<0.0001). However, the number of non-sibling juveniles overlapped with tended to be greater for males than females (Table 2.5). Males in 1982 overlapped more non-sibling males than did females, (Mann-Whitney U-test P=0.04). Although the trend was similar in 1983, it was not significant (Mann-Whitney U-test P=0.18), possibly because of the small number of females observed in 1983. In summary, although the percent overlap with non-siblings was as great for females as males, the absolute number of non-sibling individuals available to females to interact with was less than that of males.

### 2.3.3 Behaviour

Comparisons of activity budgets for 1982 and 1983 revealed significant differences in the percent time spent in locomotion (12.0 ± 0.8, N=69 for 1982;21.6 ± 1.4, N=62 for 1983; Mann-Whitney U-test P<0.0001). There were no other significant differences and data on the other behaviours were pooled for both years.

Feeding was the main activity of juveniles throughout the summer, ranging from 40% of the time budget at emergence to 64% near immergence (Table 2.6). Another 15 to 27% of the time was spent sitting and resting. Comparatively little time was spent in grooming or nest maintenance, at least above ground.

The most common social behaviour amongst juveniles of both sexes was play. The first 10 days above ground juveniles spent approximately 10% of their time in play activity (Figure 2.5a). The time spent in play declined throughout the summer, as time spent in non-social behaviours increased. During the first twenty days after the emergence of the first litter, rates of play were higher for sibling females than for any other dyad (Figure 2.6). Brothers had the lowest rate of sibling play. Non-sibling play occurred infrequently. Both sexes spent similar amounts of time in play or chasing other juveniles (Figure 2.5a,c). However, during the first twenty days above ground, females spend more time being chased by other squirrels than did males (Mann-Whitney U-test, Interval one P=0.003; Interval two P=0.009)(Figure 2.5d). Males spent more time than females in "greeting", significantly so in intervals 2 and 4 (Mann-Whitney U-test; 1-10days P=0.013, 31-40 days P=0.04) (Figure 2.5b). Males engaged in more juvenile "greetings" than did females ($X^2$ contingency table, P=0.006)(Table 2.7). Males "greeted" brothers, sisters, and non-sibling males with approximately the same frequency, whereas females only "greeted" brothers. Females greeted female siblings less often that either sibling or non-sibling males, and never greeted non-sibling females. However the proportion of "greetings" between a juvenile and its mother are three times greater in females than males.

### 2.3.4 Activity and weather conditions

Some of the differences in the use of space and behaviours of 1982 and 1983 may be due to the small sample size of females in 1983, or to the shift in the sex ratio. However, differences in the time spent moving (and the spatial aspects associated with this) may have been the response of the squirrels to differences in the weather. Compared to 1982, 1983 was a much hotter and drier year (Figure 2.7). Such heat tends to reduce the hours of activity of squirrels, as well as possibly altering their behaviours.

## 2.4 Discussion

Overall, juvenile home ranges and distances from the burrow increased over the summer. As well there was an increase in the time spent in feeding and a decrease in the time engaged in social interactions. Activity centres appeared to remain in the area of first emergence, and individuals did not appear to become greatly independent of their mother's home range.

Davis (1982a) found that in Richardson's ground squirrels, differences in movements between sexes were not apparent until the fourth week after emergence. Similar differences between males and females in the Columbian ground squirrel were apparent after the first 10 days above ground. Richardson's ground squirrels not only breed as yearlings (in contrast to Columbians where few yearlings breed) but they spend a longer time above ground in their first summer than do the more montane Columbians. Thus they are less restricted than Columbians in the amount of time in which to prepare for the winter. Davis (1982a) and Michener (1981) found that juvenile Richardson's become independent of their natal burrow. This was especially true of the females who begin to establish their territory as juveniles, and breed the following spring as yearlings. There was little evidence of such behaviour in Columbians, although females remained closer to the natal burrow than did males. Findings by Harris and Murie (1984) indicate that in many cases, females inherit the nest burrows of their mothers when they breed. The greater movements of males may reflect preliminary exploration of their environment in preparation for dispersal (Davis 1982a). These sexual differences in the movement patterns of juveniles seem to correspond with the adult spatial system. However the differences seen between the sexes at such early stages may have more than just spatial influences. Males, at an early stage, begin to move much farther from the natal burrow than do females. The result is that males have larger home ranges, greater shifts in their activity centres (away from their initial activity centre), and overlap a greater number of non-sibling juveniles (as well as other age classes). Females, on the other hand, with shorter travelling distances and smaller home ranges, remain closer to the natal burrow, stay closer to their sisters than to brothers, overlap with fewer non-siblings, and interact more than males with sibling females. Not only do females have the opportunity for greater exposure to their sisters, but also to their mothers and to other close neighbours (who are possibly related). If non-littermate sisters have settled on nearby areas, they may be able to identify their juvenile sisters through their spatial and social proximity to their mother (Sherman, 1980).

Richardson's ground squirrels (Davis 1982b), Arctic ground squirrels and Belding's ground squirrels (Holmes and Sherman 1982) have all been found, experimentally to recognize siblings. Holmes and Sherman (1982) suggest association with relatives, as well as phenotypic matching, are important in the ontogeny of sibling recognition. Other species have been found to only discriminate siblings on the basis of familiarity (Porter et al 1979; Porter et al 1981; Kareem and Barnard 1982). In Columbian ground squirrels, siblings raised for the first 30 days isolated from non-sibling juveniles, may learn to recognize each other by association. Porter (1981) found that not only was association important for recognition in spiny mice, but that this recognition was maintained by frequent reinforcement (i.e. during frequent meetings). By remaining in close proximity, juvenile females may reinforce their recognition. In males, who usually disperse as yearlings, it would be less advantageous to maximize their familiarity with siblings, as they will be unlikely to associate with kin as adults. The even spread of "greeting" behaviour across both sibling and non-sibling juveniles may indicate that either males are less familiar with the individuals around them and/or that they are less exclusive about whom they interact with than females.

The higher rate of play between female siblings in the first two weeks after emergence can be interpreted in a number of ways. Play might function to reinforce bonds between individuals, to assess abilities, as exercise, or even as competition (Bekoff 1978, 1984; Fagen 1981; Smith 1982). If sisters live to be yearlings or even two year olds, there may be competition for the natal burrow of their mothers. Such competition might be settled by these early interactions. Even though two year old sisters are rare (King 1984), the possibility for such competition still exists. Two pairs of sibling sisters were still alive on my study area as two year olds.

Although generalities in the spatial and behavioural patterns of juveniles may be drawn, the variability in the space use and behaviour between years and individuals warrants caution. Immediate and future effects of the weather on the behavioural and spatial patterns must be considered. The hot, dry summer of 1983 was characterized by restricted movements by both sexes, but especially males, as well as an increase in locomotion. This most likely was due to squirrels remaining closer to the burrow, and moving to and from the burrow more often, in order to avoid the heat. The long term effects of these weather changes, especially on males, is unknown. It may be that such effects reduce the amount of experience that juvenile males obtain in their first summer. In a species like the Columbian ground squirrel, which can live in a variety of habitats, with variable environments, the effects of weather on animal behaviour on just one study area indicate that any generalizations about social development should be interpreted cautiously.

In conclusion, sex differences in use of space and social behaviour, develop relatively early in Columbian ground squirrels. Such differences could influence the responses that individuals make in immediate and future social contacts. Females have more opportunity than do males to become familiar with their kin, as well as to reinforce associations with their sisters. Males, by greater exploration of the area around them, and by interacting with more non-sibling individuals, may become better prepared for their future dispersal and settlement among strangers elsewhere.

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**Table 2.1.** Density of Columbian ground squirrels on study area by age class and sex (1982-1983).

| Age | 1982 |  | 1983 |  | Both Years |
|---|---|---|---|---|---|
|  | Number of Squirrels | Density (indiv./ha) | Number of Squirrels | Density (indiv./ha) | Average Density |
| Adults: |  |  |  |  |  |
| male | 12 | 6.0 | 12 | 6.0 | 6.0 |
| female | 35 | 17.5 | 37 | 18.5 | 18.0 |
| Yearlings: |  |  |  |  |  |
| male | 13 | 6.5 | 12 | 6.0 | 6.3 |
| female | 14 | 7.0 | 18 | 9.0 | 8.0 |
| Juveniles: |  |  |  |  |  |
| males | 31 | 15.5 | 49 | 24.5 | 20.0 |
| females | 41 | 20.5 | 37 | 18.5 | 19.5 |

**Table 2.2.** Total home range estimates ($m^2$) for male and female juveniles (1982-1983).

| Year | Males | N | Females | N |
|---|---|---|---|---|
| 1982 | 742.7±68.8 | 20 | 441.5±55.9 | 29 |
| 1983 | 537.9±69.7 | 26 | 396.4±110.5 | 19 |

2-way ANOVA, N=94, no difference between years (F=2.72, P>0.1); difference between sexes(F=8.86, P=0.004).

Table 2.3. Distance (metres) from the first 10-day activity centre, of later activity centres (over 10-day intervals from emergence), for juveniles.

| Sex | Days from emergence (N) | | | | P[1] |
|---|---|---|---|---|---|
| | 11-20 | 21-30 | 31-40 | 41-50 | |
| Females | 5.5±0.6 (28) | 7.2±1.2 (27) | 8.3±1.4 (27) | 8.7±1.3 (21) | 0.003 |
| Males | 6.9±0.6 (40) | 9.2±0.9 (37) | 11.2±1.0 (37) | 13.0±2.0 (32) | |

[1] 3-way ANOVA, F=6.67, N=252; P<0.0001 between all intervals; no difference between years.

**Table 2.4.** Average distances (metres) between juvenile siblings during individual scans.

| Year | Brothers | N | Brother-Sister | N | Sisters | N | P[1] |
|---|---|---|---|---|---|---|---|
| 1982 | 12.1±0.5 | 509 | 11.3±0.4 | 1130 | 10.2±0.5 | 665 | <0.25 |
| 1983 | 11.9±0.4 | 1356 | 12.3±0.6 | 597 | 4.5±0.7 | 62 | |

[1](2-way ANOVA; F=1.324 N=4319, log transformed)

**Table 2.5.** Number of non-siblings overlapped within the home ranges of male and female juveniles.

| | Number of Non-siblings overlapped (Mean ±S.E.) | | | |
|---|---|---|---|---|
| | Males | N | Females | N |
| Males | 4.4±0.3 | 45 | 3.0±0.3 | 45 |
| Females | 3.1±0.4 | 36 | 2.6±0.4 | 36 |

**Table 2.6.** Percent of total time spent in different behaviours by male and female juveniles (1982-1983).

| Sex | Days after Emergence | N | Sit/Rest | Feed | Groom | Dig | Social Interaction |
|---|---|---|---|---|---|---|---|
| Males | 1-10 | 23 | 26.8±2.8 | 41.9±2.7 | 1.5±0.4 | 0.4±0.4 | 14.7±1.7 |
| | 11-20 | 32 | 15.9±1.5 | 48.1±2.3 | 4.4±1.0 | 0.5±0.3 | 13.6±1.1 |
| | 21-30 | 24 | 19.0±2.2 | 50.3±3.0 | 4.8±0.9 | 1.2±0.4 | 6.2±0.8 |
| | 31-40 | 24 | 15.7±1.2 | 58.8±2.6 | 3.6±1.0 | 1.0±0.6 | 4.8±0.8 |
| | 41-50 | 22 | 17.6±1.9 | 64.7±2.7 | 3.1±0.6 | 0.1±0.1 | 1.9±0.5 |
| Females | 1-10 | 15 | 21.2±2.7 | 49.5±4.6 | 1.1±0.5 | 0.0±0.0 | 13.6±2.7 |
| | 11-20 | 21 | 17.0±1.7 | 46.0±2.5 | 4.4±1.1 | 0.1±0.1 | 13.8±1.3 |
| | 21-30 | 22 | 17.8±2.5 | 47.2±2.9 | 6.0±1.5 | 2.6±1.2 | 7.8±1.1 |
| | 31-40 | 21 | 16.6±1.1 | 60.8±2.7 | 3.2±0.7 | 0.1±0.1 | 2.8±0.7 |
| | 41-50 | 14 | 21.7±2.3 | 64.6±2.3 | 3.5±0.9 | 0.0±0.0 | 1.2±0.5 |

**Table 2.7.** Percentage of "greetings" initiated by juvenile males and females with siblings, non-siblings and their mother.

| Recipients | Initiators (Frequency)[1] (Mean ± S.E.) Males | Initiators (Frequency)[1] (Mean ± S.E.) females |
|---|---|---|
| Non-siblings: | | |
| Males | 22.2±3.4 (13) | 16.2±1.8 (6) |
| Females | 11.1±1.4 (6) | 0.0±0.0 (0) |
| Siblings: | | |
| Males | 20.4±11.3 (13) | 51.5±5.4 (20) |
| Females | 38.9±12.5 (20) | 10.8±1.2 (4) |
| Mother: | 7.4±0.9 (4) | 21.6±2.4 (8) |

[1] Based on %"greeting" per individual

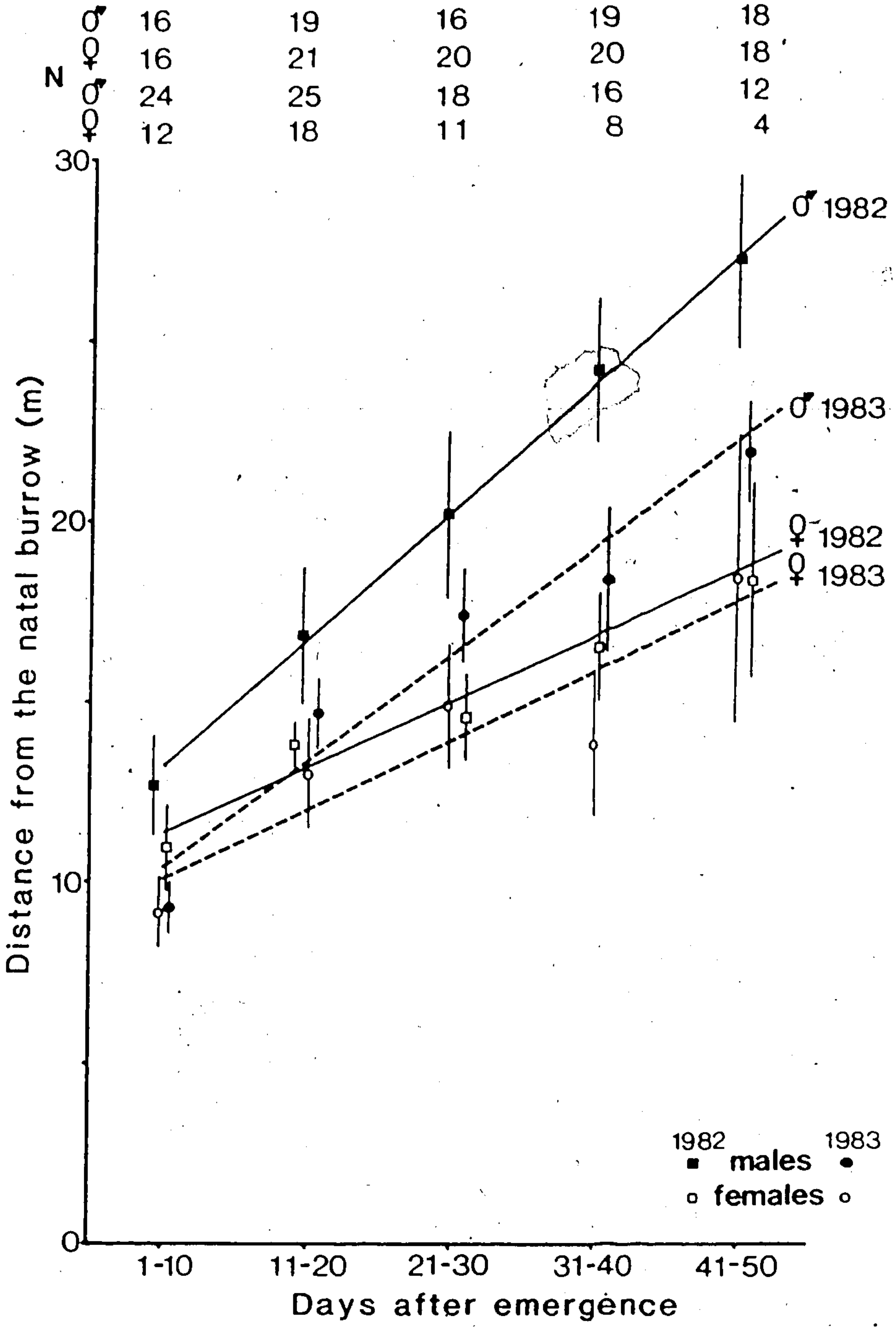

**Figure 2.1.** Movements from the natal burrow for juvenile males and females (1982 and 1983). N=number of individuals. Regressions equations: 1982, Males Y=0.357X+11.4 Females Y=0.182X+10.43; 1983. Males Y=0.30X+8.93 Females Y=0.195+9.14.

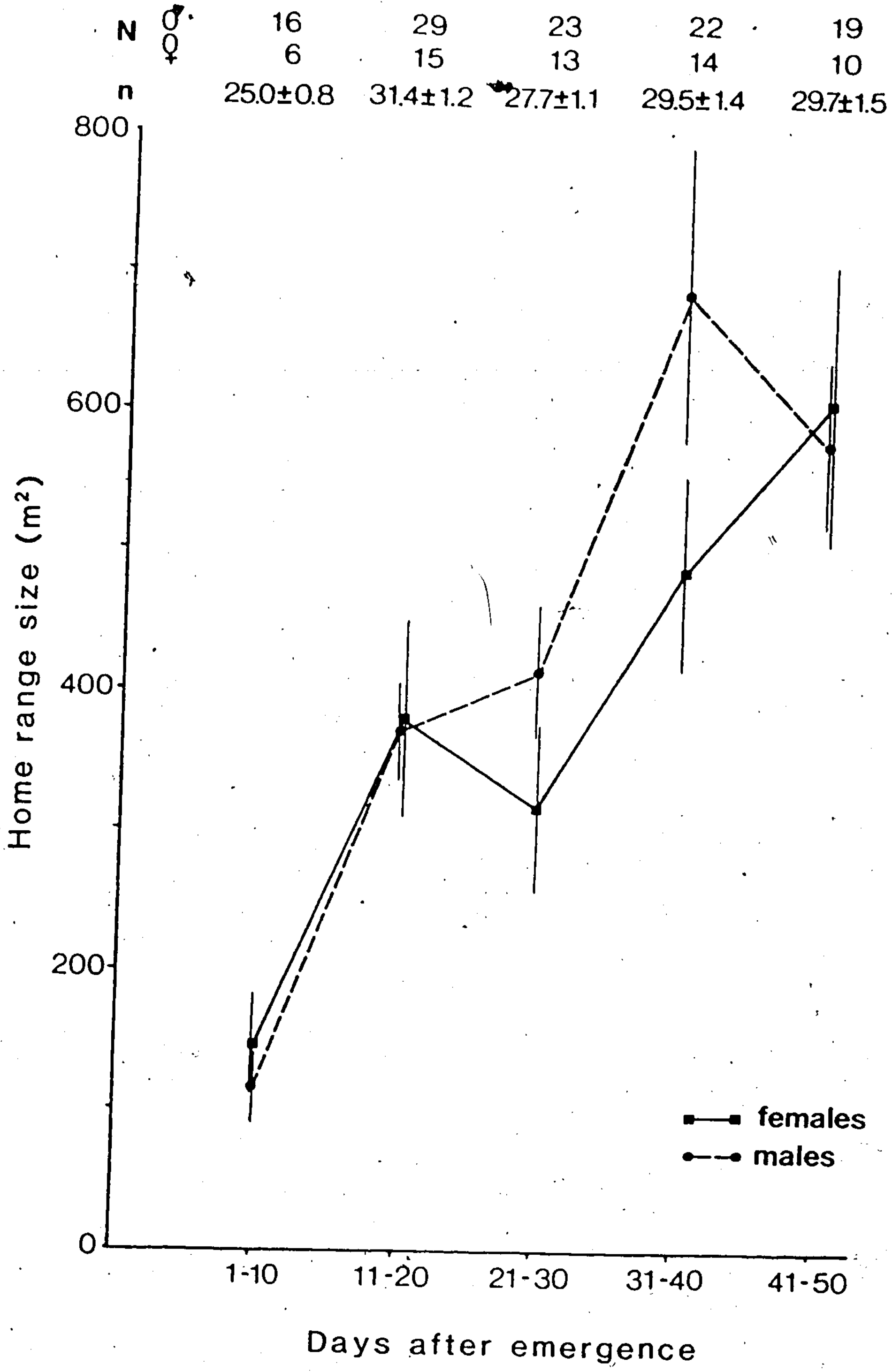

Figure 2.2. Juvenile home ranges (mean ± S.E.) over 10 day intervals after emergence, 1982 and 1983 pooled. N = number of individuals; n = number of observations/individual (mean ± S.E.).

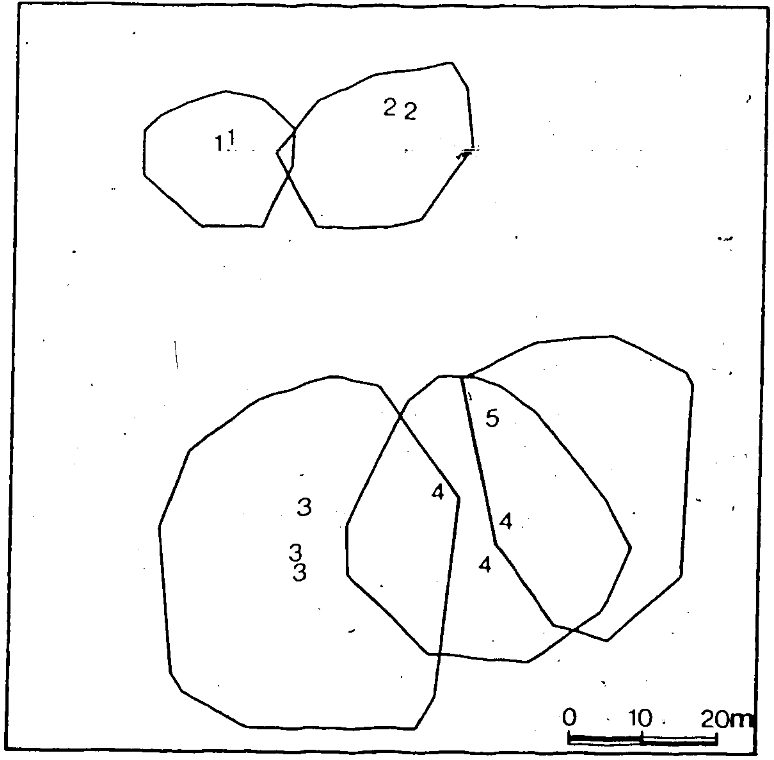

Figure 2.3. Representative example of the activity centres of 5 litters, within their mother's home range. Members of the same litter are represented by the same number. All juveniles, in both years, had activity centres within their mother's home range.

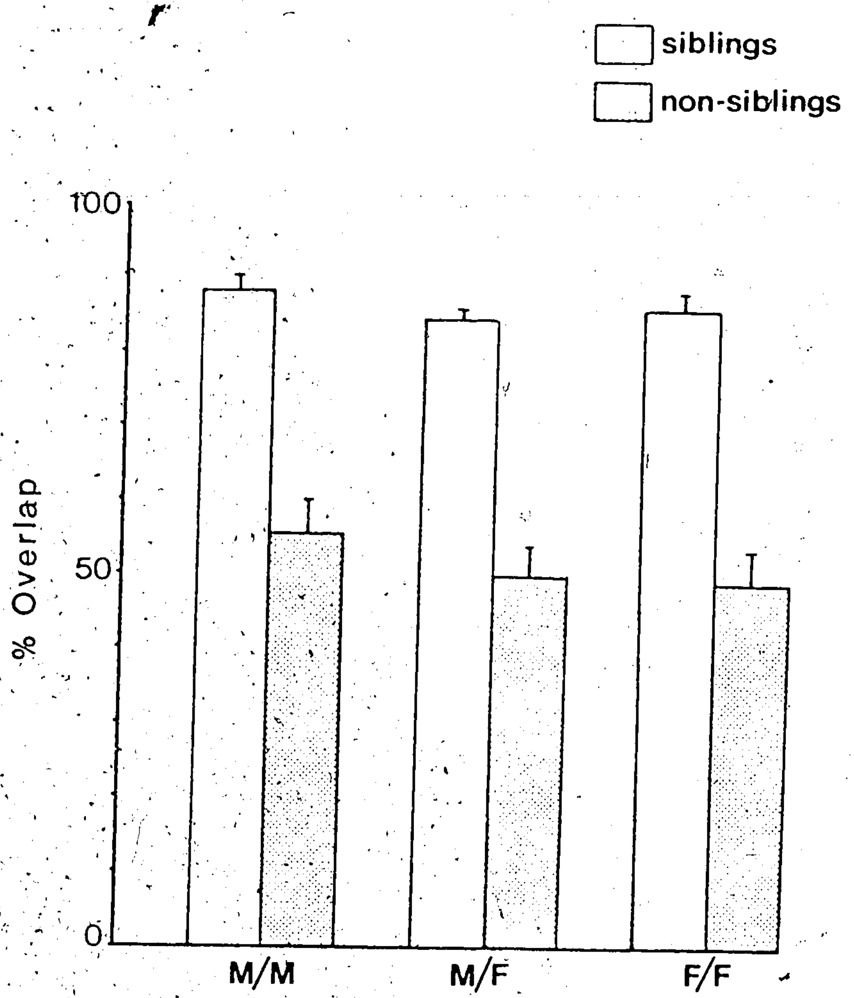

Figure 2.4. Percentage of overlap of home ranges between nearest male-male, male-female and female-female sibling and non-sibling dyads. (Mann-Whitney U-test, P<0.0001 for all comparisons between siblings and non-siblings).

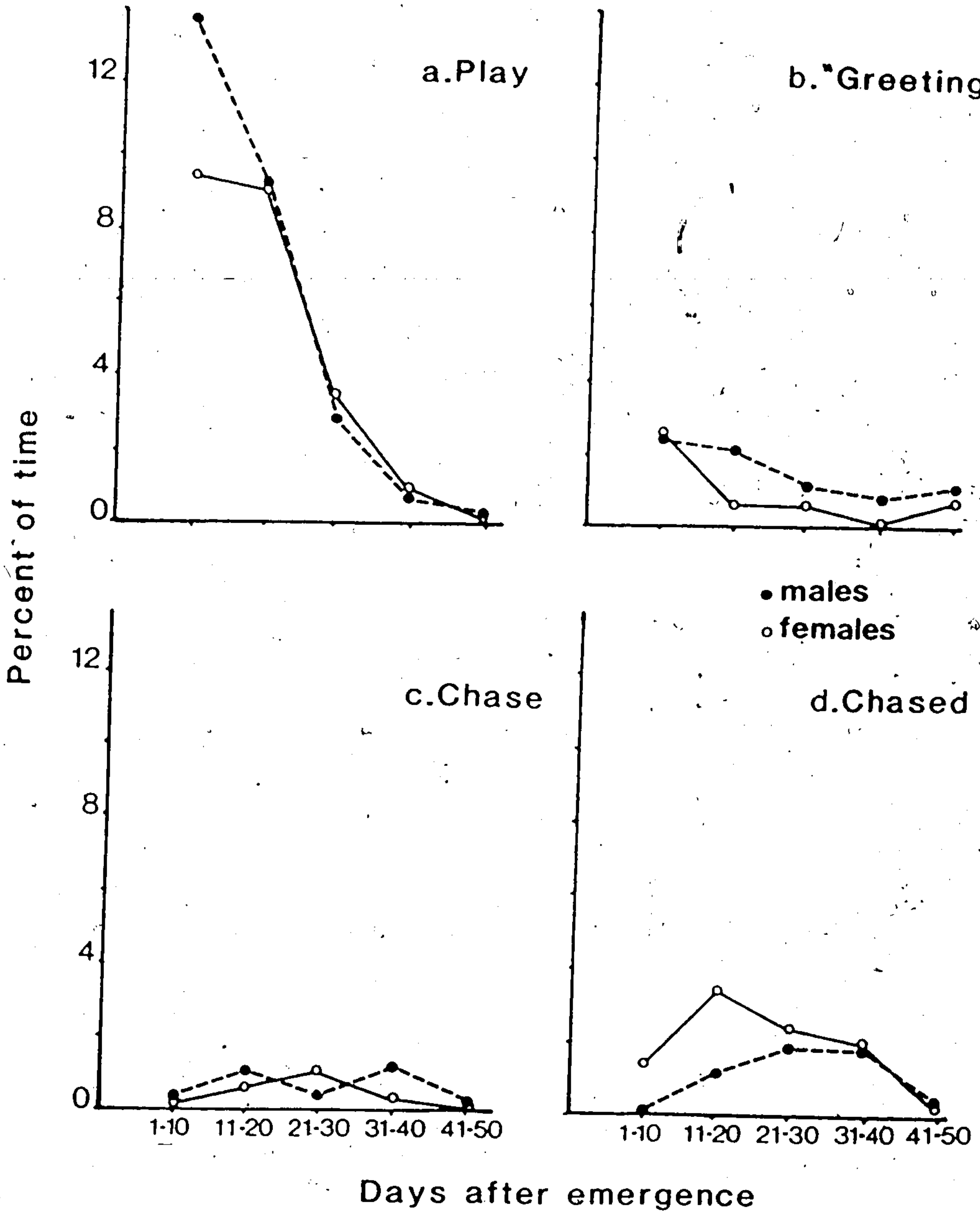

Figure 2.5. Percent of total time spent in each of four social behaviours by juveniles, over 10 day intervals after emergence.

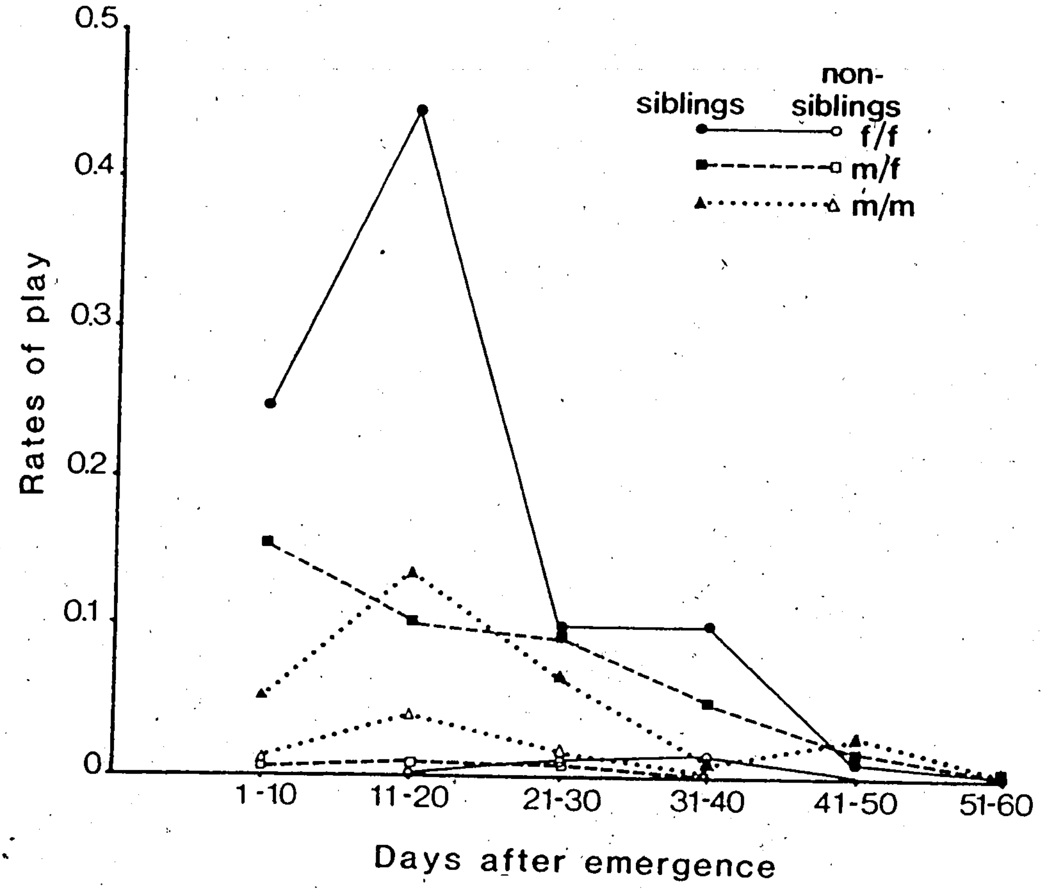

Figure 2.6. Average rates of play in juveniles (1982 and 1983 pooled) for intrasexual and intersexual groups, in sibling and non-sibling dyads. Rates are calculated for each pair as the number of interactions/mutual scans/%overlap.

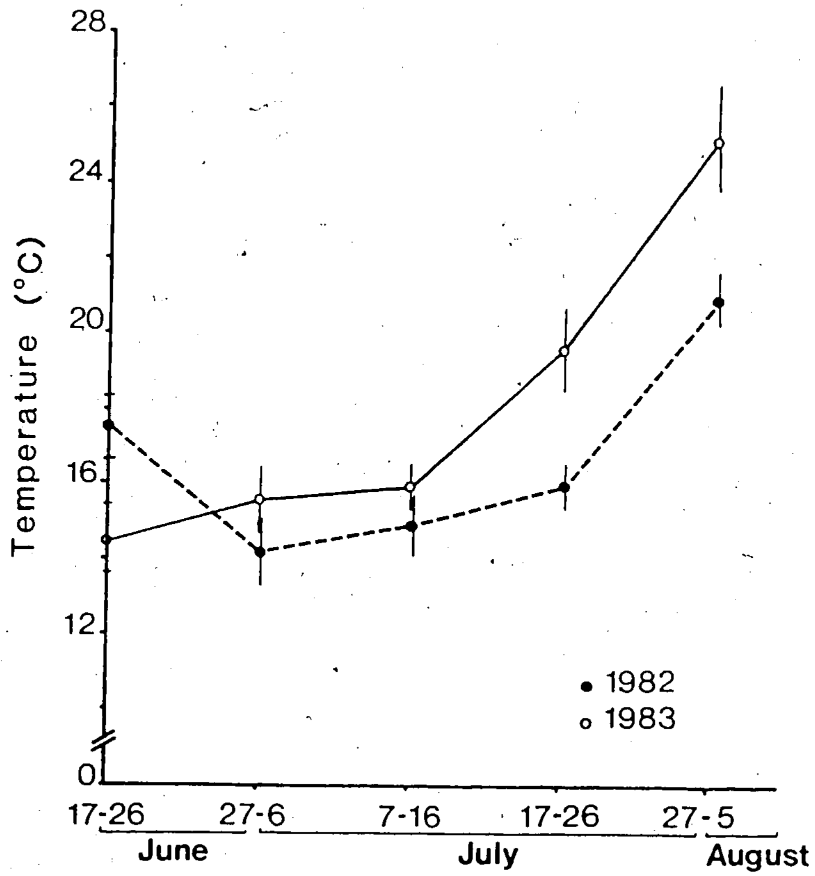

Figure 2.7. Average high daily temperature over five 10 day intervals of the summer (corresponding to the 10 day intervals used in behavioural analyses). Only the fourth and fifth periods were significantly different (Mann-Whitney U-test, P =0.02 and P =0.03 respectively).

# 3. Social Play in the Columbian ground squirrel

## 3.1 Introduction

The development of an individual's behaviour can be modified by early social interactions (Bekoff 1972). In mammals and some birds a great deal of this early socialization involves play. Although play seems energetically costly, it presumably has arisen by natural selection (Fagen 1981) and therefore influences the inclusive fitness of animals. The study of play has been hindered by controversy over the definition of play and by unclear hypotheses. Reviews of the various definitions of play can be found in Fagen (1981) and Bekoff (1978, 1985). Play is often defined as lacking immediate purpose or in some other functional context. However, as the function of play is uncertain, it should not be included in its definition (Grier 1984). Perhaps a more appropriate approach is to describe the common characteristics or defining criteria that help identify playful behaviour from non-playful behaviour. Bekoff (1985) lists five defining characteristics of play, including: activities from a variety of contexts linked together sequentially; the presence of play signals; the absence or rarity of certain behaviours such as threat and submission; role reversals and self-handicapping; and detectable changes in an individuals motor activities and differences in sequencing compared to non-play situations. Definitions such as this help to clarify what play is, as opposed to what play does, which seems more appropriate for studies examining the benefits of play.

Fagen (1981) listed six overlapping hypotheses of the benefits of play to young animals: play develops physical strength, endurance and skill; regulates developmental rates; yields specific experiential information; develops cognitive skills necessary for behavioural adaptability, flexibility, inventiveness, or versatility; develops behavioural tactics used in intraspecific competition; and establishes or strengthens social cohesion in a dyad or group.

Most researchers of play agree that through the locomotor responses of play, muscle and neural coordination improve (Bekoff 1984; Fagen 1981, 1982; Smith 1982; Poirier 1982).

However, Fagen (1981, 1982) and Vandenberg (1982) point out that exercise and practice (of specific behaviours) fail as sole explanations of social play. Also gentle play (considered a poor exercise) and differences noted in mixed age, sex or kinship groups are not explained (Vandenberg 1982).

The way in which play might regulate developmental rates is, at this point, unclear. However, like exercise, the benefits that accrue to the individual if play does affect development, would not explain differences in play due to age, sex or relationship.

The learning of specific information essentially covers everything not included by the other hypotheses. The benefits of social play involved could be learning the identity of kin (Wilson and Kleiman 1974) or the assessment of the abilities of others relative to one's own abilities (Fagen 1974, 1981). Differences in mixed age, sex and kinship play would be expected if this was a benefit.

Developing flexibility (increasing the ability to handle future, novel or unexpected events) suggests that individuals who play would increase their experiences prior to dispersal. Individuals would not be expected to prefer particular individuals in play, on the basis of sex or relatedness, but to increase their experiences by playing with anyone.

The idea of play as a damaging behavioural tactic has been suggested as a form of aggressive competition (Fagen 1981). Geist (1978) suggested that soliciting play in an amicable fashion, and then attacking one's opponent and causing harm, would be one method of reducing future competition. Thus individuals would be expected to elicit attacks on future competitors. In many species these competitors would be individuals of the same sex thus sexual differences could be expected. In species in which kinship plays a role in structuring social relationships, animals would be unlikely to harm relatives.

The last major hypothesis, that of social bonding or cohesion, suggests that play is a form of reinforcing, in an amicable fashion, the interactions between individuals. Bekoff (1977,1978,1982,1984) suggested that individuals who play more may defer dispersal (exactly the opposite to the flexibility hypothesis). The social bonding hypothesis predicts that individuals may discriminate with whom they play, if kinship is important, by reinforcing associations with kin.

Thus the exercise (and practice), as well as the regulation of developmental rates and flexibility hypotheses predict nothing about asymmetries in play between different sex, age or kinship groups. However, the assessment of abilities, aggressive competition and social bonding hypotheses do allow predictions to be made with regard to these asymmetries.

In the Columbian ground squirrel, *Spermophilus columbianus*, individuals are usually non-reproductive in their first two summers (as juveniles and as yearlings)(Festa-Bianchet 1982). It is in these age classes that play is common in the activity budget. Play makes up 62% of all juvenile and 30% of all yearling social interactions (Waterman, unpubl. data). Although the importance of other interactions should not be overlooked, the predominance of play in the social repertoire suggests that it is likely important in socialization.

Michener (1982) has described the social system of the Columbian ground squirrel as that of female kin clusters with male territoriality. Males are essentially territorial in the spring, during the breeding season (Murie and Harris 1978). Females become more aggressive and appear to be territorial after breeding until the juveniles (young of the year) emerge (Festa-Bianchet 1982). Litters remain relatively intact and isolated from other litters for the first thirty days after birth (Murie and Harris 1982). As yearlings, male Columbian ground squirrels usually disperse from the natal area, whereas females usually remain on the area (Boag and Murie 1981b; Festa-Bianchet and King 1984; D. Hackett pers. comm.), often inheriting their natal site from their mother (Harris and Murie 1984). During their lifetime, females have much greater site fidelity than do males (Murie and Harris 1984).

In Columbians, future competitors would most likely be individuals of the same sex. If the benefit of play were assessment of others, squirrels would be expected to prefer individuals of the same sex. Differences in littermate and non-littermate play could also be explained; as litters are isolated, siblings may already know the abilities of each other and may thus play differently with unknown individuals.

Aggressive competition would also predict differences in play. Squirrels would be expected to prefer partners of the same sex (possible future competitors). As well, it would be unlikely that they would harm siblings, so differential treatment of siblings and non-siblings could be expected.

If social bonding were a major benefit of play, females would be expected to play with individuals of the same sex, and if kinship is important, to prefer to play with relatives. Males would be unlikely to reinforce bonds with either sex in particular, as it is unlikely that they will remain on the area. However, if play is the "bond" that delays dispersal of males until mid-summer, decreases in play may initiate dispersal. However, no preferences in sex or relatedness would be expected in males.

The aim of this study was to describe the structure and sequences of juvenile and yearling play and examine any differences in different age, sex or kinship groups, as they relate to the relevance of the aforementioned hypotheses.

## 3.2 Methods

The study site was located 15 km southwest of Longview, Alberta, Canada, in the foothills of the Rocky Mountains (50°33'N, 114°33'W; elevation 1295m). The 2 ha area was grazed regularly by horses and dairy cows, resulting in relatively good visibility for observing squirrels throughout the summer.

All squirrels on or adjacent to the study area were captured using National live traps (15x15x50cm) baited with peanut butter. Individuals were marked for identification using numbered metal ear tags in each ear (National Band and Tag Co., Monel #1) and dye marks on the body using hair dye (Lady Clairol Nice N'Easy blue-black). In addition coloured plastic strips were attached to one eartag of each juvenile and yearling to aid in identification. All squirrels were weighed (±5g) with a Pesola spring balance, examined for sex and reproductive status, and released at the place of capture. As 1982 was the first year of the study, the approximate ages (ie. either as a yearling or an adult) were estimated by weight based on Boag and Murie (1981a). However, only known aged yearlings from 1983 and 1984 were used in analysis of yearling behaviour. In order to mark litters before they could intermix, juveniles were trapped within 3 days of first emergence using wire mesh traps placed over the burrow. Coloured surveyors flags were used to mark the coordinates of a 10x10m grid. Squirrels were observed with 10x50 and 20x60 binoculars, or a 20x60 spotting scope from either a 3m or a 2.5m observation stand. Observations were made from 1 June to 17 August in 1982, 5 May to 11 August in 1983, and 1 May to 1 June in 1984. In total, 620 hours of behavioural observations were made.

All play interactions were recorded in detail on a cassette tape, and later transcribed. The identity of all interactors, location, time, and the duration and sequence of behaviours were recorded. All behavioural units were derived from Steiner (1971), Betts (1976) and Davis (1982), and the operational definitions are described in Table 3.1. In order unt for variation in duration of bouts, all behavioural component frequencies for e were divided by the total time of the bout, resulting in a rate per second of occurrence of each component.

Data were not normally distributed so were analyzed using non-parametric statistics (Siegel 1956; Conover 1980). The 0.05 probability level of a Type I error was considered significant. However in cases where many univariate tests were used, the significance value of 0.05 was divided by the number of tests used in each analysis (Snedecor and Cochran 1980). In these cases, 21 tests were run per analysis, thus 0.0024 was used as the significance level. This reduced the chance of Type I errors, but increased the chances of Type II error.

## 3.3 Results

A total of 950 play bouts were observed during the study years. Play was seen in yearlings from 5 May to 16 June in 1983 and from 1 May to the 1 June in 1984. Play of juveniles was recorded from 19 June to 13 August in 1982, and from 13 June to 28 July in 1983.

Most bouts occurred during the morning, especially later in the summer when activity was restricted, possibly due to hot weather (see paper 1). On the first day juveniles emerged from the natal burrow, they were reasonably coordinated and play did not appear to differ from play later in the season. In juveniles, rates of play declined towards the end of the summer (see paper 1). Play ceases in yearlings around the time of emergence of the juveniles, and approximately when yearlings disperse (Boag and Murie 1981b; Festa-Bianchet and King 1984; and D. Hackett pers. comm.).

In 1983, 7 of 18 yearling females raised young and in 1984, 5 of 8 yearling females lactated. Females who had yearling sisters either bred or their sister bred. No breeding female yearling was ever seen playing with another yearling. As a result, no female yearling sibling play was recorded in either study year.

### 3.3.1 Duration of play

The average duration of yearling play bouts was longer than that of juveniles (Mann-Whitney U-test, $P = 0.04$)(Table 3.2). Within yearlings, male-male, male-female and female-female durations were significantly different (Kruskal-Wallis, $P < 0.0001$). Multiple comparisons (Conover 1980) between the durations of all three groups revealed significant differences ($P < 0.0001$). Males had the longest play durations, followed by females and finally male-female play (Table 3.2). Sibling and non-sibling play durations were only significantly different in male-male interactions, in which durations of sibling play bouts were over twice that of non-sibling play (Table 3.2). Male-female play bouts were of similar length regardless of the relatedness of individuals.

Within juveniles, there were no significant differences in the average duration of bouts for male-male, male-female and female-female dyads (Kruskal-Wallis, $P = 0.76$). Although there was a trend for siblings to play longer, only in male-male play was this significant (similar to yearlings) (Table 3.2).

In order to compare changes over time, comparisons were made of play early and late in the season. In yearlings, early and late play was determined by dividing in half the total number of days on which play was recorded. For 1984, as play was not followed until dispersal of yearlings, the same dates were used as in 1983. With juveniles, early and late play was determined in the same manner. No changes in the average duration of a play bout were seen in any sex, age or sibling-non-sibling comparisons of early and late interactions.

### 3.3.2 Components of Play

In both yearlings and juveniles, the behaviours which initiated most play bouts were "wrestling" (28%), "approach" (19%), and "greeting" (15.5%).

Yearling play appeared to be much more aggressive than juvenile play. Differences in the components of juvenile and yearling play are listed in Table 3.3 (see Appendix II for detailed descriptive statistics of all behavioural components). Yearlings had higher mean rates in all these components than did juveniles, except for "side jumps", in which juveniles were higher. "Chases", "run away", "into burrow" are all behaviours that move individuals apart. "Fighting" was also much higher in yearling play.

Differences in the frequency of components between intra- and intersexual play in yearlings were only seen in the occurrence of "bites" and "pounces" (Kruskal-Wallis, $P=0.001$ for "bites" and $P=0.001$ for "pounces"). Multiple comparisons revealed significant differences between all groups ($P<0.05$). Female-female play had the highest occurrence (recall this was only non-sibling dyads) of "bites" and "pounces", followed by males and then male-female play. In yearlings, male-male sibling play had higher frequencies per bout of components that involved contact (such as "pounce", "wrestles", "bite", "box"), whereas non-sibling play had a higher frequency of "running away" (Table 3.4). No significant differences were found in any male-female sibling and non-sibling play bouts.

In juveniles no significant differences (Kruskal-Wallis, $P>0.0024$ for all tests) were found between intra- and intersexual components of play. When the mean rate of components were compared between sibling and non-sibling dyads in the three groups, (male-male, male-female and female-female) no differences were found in intersexual play. In females, "arch back", "fights" and "tail bush" were more frequent in non-sibling play than that of siblings (Table 3.4). In males, only "tail bushes" were more frequent in non-sibling play. However sibling play had higher frequencies of "pounces", "wrestles", "bites", "push away" and "box", similar to the differences noted in male-male yearling comparisons.

As with duration, comparisons were made between early and late play bouts. No differences were found between early and late play components in yearlings regardless of the sexes or relationships of the dyads (Mann-Whitney U-test, $P>0.0024$ for all tests). Changes in the frequency of a few components were seen in juveniles (Table 3.5). In male-male and male-female dyads, there were changes in components in non-sibling interactions, with an increase in "arch back" in male-female play, and a decrease in "push away" in male-male play. In females, changes in "chases" and "wrestling" occurred between early and late sibling play.

Nowicki and Armitage (1979) suggested that "flips" in play wrestling may be an indication of a dominance struggle between individuals. They defined "flips" as an exchange of whomever was on top during a "wrestle". The number of times a "flip" occurred during a bout where wrestling occurred was calculated. This frequency was then divided by the duration of the bout to reduce durational biases (Nowicki and Armitage did not do this).

Yearlings, on average, had higher rates of "flips" in bouts with wrestling than did juveniles (Mann-Whitney U-test, $P=0.006$). Comparison of intrasexual bouts of juveniles and yearlings showed similar differences (Mann-Whitney U-test, $P=0.014$ for males and $P=0.008$ for females)(Table 3.6). However, intersexual comparisons between the age groups were not significant (Mann-Whitney U-test, $P=0.055$) with the trend being lower rates of "flips" in yearling male-female play than in juveniles.

The average rate of "flipping" was not different between juvenile male-male, male-female and female-female dyads (Table 3.6). Differences were found in yearlings. Multiple comparisons indicated significant differences between intra- and inter-sexual rates of "flipping" (male-male vs male-female $P<0.01$; female-female vs male-female $P<0.025$). Rates of "flips" were similar between intrasexual play bouts (male-male vs female-female $P>0.05$). Intrasexual yearling play had higher frequencies of "flipping" per bout than did intersexual play, and overall yearlings "flipped" more than juveniles. However a trend to decrease "flipping" was noted in yearling intersexual play.

### 3.3.3 Sequential Analysis

A total 9450 transitions in juveniles and 9183 transitions in yearlings were recorded, which was greater than the 4410 ($10R^2$) recommended by Fagen and Young (1978) (where R is the repertoire size, here 21 behavioural components). Fagen and Young (1978) point out that transition analysis only indicates significant correlations and often misses the importance of rare behaviours. However the major facilitating (transitions that occurred more often than expected) and inhibited (transitions that occurred less often than expected) sequences can be determined. Expected matrices and rejection criteria were determined using the methodology of Fagen and Young (1978). Only the most significant facilitating and inhibiting behaviours were chosen, as they are the most likely to precede or not to precede a behaviour.

Juvenile play appears to be sequentially very similar to that of yearlings (Figures 3.1 and 3.2). The most significantly facilitating transitions fell into four groups, regardless of the sex or ages of the interactors. These groups comprised of approach-widthdrawal behaviours, contact behaviours, agonistic behaviours and a fourth group of "box"-"pause". The approach-withdrawal group involved predominately behaviours in which individuals were either moving towards ("follow", "rush", "approach", "chase") or away from ("side jump", "into burrow", "break off", "run away" and "chased") each other. In yearlings, "arch back" was also in this group. The second group, contact behaviours, was almost identical for both age classes, except for the "no reaction" of yearlings following "pounces". This group included behaviours where animals were touching each other, such as "biting", "pushing away", "wrestle" and "belly-up". The third group was comprised of behaviours that in adults are considered agonistic (Betts 1976), such as "tail bush" and "fight" in both ages, with the addition of "arch back" in juveniles. Interestingly, the components of this third group are the same behaviours as those found to occur more frequently in juvenile female-female non-sibling play. The last group is made up of "boxing" and pauses, in which both behaviours facilitate the occurrence of the other.

In both juveniles and yearlings, four behaviours were most likely to inhibit or decrease the occurrence of all other behaviours (Figure 3.3 and 3.4). These behaviours were "wrestle", "chase", "greeting" and "push away", two being contact behaviours and the other two approach-withdrawal.

## 3.4 Discussion

### 3.4.1 Structure of Play

The play of the Columbian ground squirrel had many of the characteristics listed by Bekoff (1985). "Greeting", "approach" and "wrestling" were the more common initiating behaviours of a play bout. Nowicki and Armitage (1979) suggested that greeting in the yellow-bellied marmot was possibly a play signal. In the Columbian ground squirrel, wrestling tended to be the initial behaviour in a play sequence when individuals were already near each other, whereas "greeting" and "approaching" were antecedent to play as animals neared each other from a greater distance. More subtle cues, not easily observed, were most likely also involved. Another characteristic that appeared to occur in Columbian ground squirrel play was that of role reversals, in which there were frequent exchanges of positions in wrestling, and changes in the individuals chasing in play bouts. Lastly, the transitions in play sequences were relatively consistent between juveniles and yearlings. Similar findings by Chalmers and Lock-Haydon (1981), and Nowicki and Armitage (1979) indicate that play is not simply a random activity. In juvenile Columbian ground squirrels, a breakdown of these transitions resulted in four groups, two of which accounted for the component differences found in intrasexual sibling and non-sibling play.

Age, sex and relatedness did appear to have some influence on social play in the Columbian ground squirrel. Overall yearlings had longer play bouts with more aggressive components than did juveniles. Although there were significant changes between juvenile and yearling play, little change over time in the structure of play occurred within the age classes. Sex differences in play were more pronounced in yearling play. Sex differences in play have been noted in other animals including: cats (Caro 1981); ferrets and many South American canids (Biben 1982); bighorn sheep (Berger 1980); yellow-bellied marmots (Nowicki and Armitage 1979); and many primates (Poirier and Smith 1974; see Fedigan 1982 for review). Early observations of kittens 4 to 12 weeks of age did not demonstrate sexual differences (West 1974); however work with older animals (16 weeks) did reveal the development of sexual differences in play (Caro, 1981). In Columbian ground squirrels, analysis of intra- and intersexual play, on the level of siblings and non-siblings pairs, indicated that sexual differences occurred in intrasexual play. In both juveniles and yearlings, no differences between sibling or non-sibling play were seen in intersexual play. Males had higher rates of contact behaviours with their sibling brothers than with non-sibling males. In juvenile female play, females tended to escalate non-sibling bouts into "fights", "arch back" and "tail bushes" (components associated with adult aggressiveness (see Betts 1976)). Little comparative data is available on sibling and non-sibling play. Poirier (1982) states that in his studies of primate play, individuals preferred kin as play partners. Wilson (1982) found differences in the social interactions between sibling and non-sibling voles, but these animals did not appear to play.

### 3.4.2 Benefits of play

Precise evaluation of the benefits of play were not addressed in this study. All the benefits that have been suggested are not really testable hypotheses because they are overlapping, lack clear predictions, and can be interpreted in a number of ways. Social bonding, assessment and aggressive competition all suggest benefits most likely not to be immediate in the Columbian ground squirrel. Competition for food would be unlikely in the Columbian ground squirrel (Murie and Harris 1978), and since juveniles and yearlings sleep together (D. Hackett, pers. comm.), competition for burrows would also be unlikely. Also, the future advantages would be with individuals of the same sex. The occurrence of intersexual play indicates exercise, practice or flexibility may be important benefits of play. No discrimination between siblings and non-siblings occurred in intersexual play because other benefits appear unlikely to accrue. As well, the rate of flipping decreased between juveniles and yearlings in intersexual play. It would be unlikely that males and females would reinforce association (ie. bonding) in lieu of male dispersal. As well, adult females must compete with other females in the future, and would gain little by learning to assess males or provoking aggressive interactions with males.

However, the differences noted in intrasexual play between siblings and non-siblings suggests that more than just exercise and practice is involved in the play of the Columbian ground squirrel. Also, as the behavioural components of adult interactions are similar in both sexes (Betts 1976), sex differences in play would not be predicted by the exercise or practice hypothesis. The flexibility hypothesis would predict play to increase prior to dispersal of males, increasing their exposure to novel experiences. However, the criteria for evaluating this benefit are rather vague. In the Columbian ground squirrel the increased frequency and duration of yearling play compared to juveniles supports the prediction of increased play prior to dispersal. Yet, in the short term, within the play season of yearlings, play declined in frequency prior to dispersal (Festa-Bianchet and King 1984; Waterman unpubl. data). The absolute frequency of play may not be the appropriate criteria in which to determine if flexibility is a benefit. Some aspects of the quality of play or perhaps certain thresholds of play experience (not necessary just quantity) may be involved. However, even if flexibility is a benefit, the differences noted in mixed sex and sibling/non-sibling play are still not explained.

The social bonding, assessment, and aggressive competition hypotheses all predict sex and sibling/non-sibling differences in play. The social bonding hypothesis would predict that females, who will most likely remain on the natal area, will play to reinforce associations with sisters. The high rates of sister play (paper 1), as well as the aggressiveness of non-sibling female play, suggests that females may prefer sisters as play partners over brothers and non-siblings, and hence implicate a role for social bonding. It is difficult to see a benefit to males, who disperse, in reinforcing associations with other individuals on their natal area. Bekoff (1977) discusses the possibility that individuals delay dispersal if they play frequently (and thus reinforce "bonds"). A decrease in play frequency just prior to dispersal (Festa-Bianchet and King 1984) fits the idea of the social bonding hypothesis that "bonds" had deteriorated and this initiated dispersal. However, whether such a delay is beneficial is questionable. Also, similar to the flexibility hypothesis, the appropriate aspects or criteria of play with which to evaluate this hypothesis are vague.

Future competitors for juvenile Columbian ground squirrels would be individuals of the same sex. Thus the difference seen in rates of flips and in treatment of siblings versus non-siblings in inter- and intrasexual play would be expected if assessment was a benefit of play. Also assessment may be more important at the yearling age when animals are nearing reproductive maturity. Increased intraand intersexual differences in yearling play components, as well as increases in "flips" and aggressiveness in yearling play support this idea. If individuals already know their siblings abilities, higher rates of play with non-siblings would be expected. Males had higher rates of play with non-siblings (Paper 1) than did females. However, in male-male play, confrontation with non-siblings was perhaps avoided by decreasing contact during play. If males were assessing non-siblings, they would not be expected to reduce contact with them. Juvenile females did not decrease contact, and non-sibling bouts had higher rates of agonistic components. Therefore assessment could be a benefit of non-sibling play among females.

Play as a damaging tactic used in aggressive competition seems unlikely. No minor or major injuries were seen in any play bout. However the increased agonistic behaviour of non-sibling, female juveniles may be an indication of a more subtle aggressive competition, perhaps involving the establishment of dominance. As females have more restricted movement patterns than males, it may be that females are just more aggressive in non-sibling play because the other individual is unknown. Males with wider movement patterns, have more opportunity from quite early in the summer to interact with non-siblings (paper 1). However, this does not explain the lack of discrimination between siblings and non-siblings in intersexual play. The differences in contact behaviours between males in sibling and non-sibling play may be a way in which escalations (like those in females) are avoided by males. Little evidence was seen for such aggressive competition in juvenile males. However, the increase of aggressive components in yearling play may indicate an increased competition in this age class.

In conclusion, the play of Columbian ground squirrels had a relatively consistent structure. The differences between intra- and intersexual treatment of siblings and non-siblings suggests that more than just exercise and increased behavioural flexibility are involved. The social bonding and assessment hypotheses are plausible in this social system, but the importance of such benefits are very likely to differ for different sex and age classes.

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Table 3.1. Operational definitions of the behavioural components of play.

| | |
|---|---|
| **Approach** | -walking towards another animal. |
| **Arch back** | -upward convex bending of the spine, hindlegs vertically extended. |
| **Belly-up** | -lying on back with all four legs spread and raised upwards; mouth is held open. |
| **Bite** | -bringing teeth into contact with another animal and closing them. |
| **Box** | -two animals facing each other, rearing up on hindlegs with forepaws extended, and striking one another with forepaws. |
| **Break off** | -stopping or diverting attention from the play bout (for >5 seconds) without either animal leaving the vicinity. |
| **Chase** | -running after a moving animal. |
| **Fight** | -similar to wrestling but with escalated biting, kicking (with hindlimbs) and usually vocalization by one or both animals. |
| **Follow** | -walking pursuit of another animal. |
| **"Greeting"** | -head extended towards other animal, often with a slight lowering of forebody, mouth is open, head rotated and mutual contact of naso-oral areas. |
| **Into burrow** | -moving either slowly or quickly into a burrow entrance. |
| **Mount** | -jumping onto other animal's lower back and grasping it with forelimbs. |
| **No reaction** | -although in contact with or near other animal, no response to behaviour of other animal is perceivable. |
| **Pause** | -brief stop (<5 seconds) in play; animals still directing attention to each other. |
| **Pounce** | -jumping or leaping onto another animal. |
| **Push away** | -kicking using each hindleg (simultaneously or successively). |
| **Run away** | -hurriedly running from another animal without pursuit. |
| **Rush** | -running towards another, with the other animal not moving away. |
| **Side jump** | -animal sitting with four paws on the ground, leaps laterally, usually in a direction away from the other animal. |
| **Tail bush** | -piloerection of the tail. |
| **Wrestle** | -grasping or clinging to each other, two animals perform whole-body rolling, with no vocalization. |

**Table 3.2.** Average durations of play bouts (s) by sex, age and relatedness.

| Age | Sex | Relatedness | Duration (s) (Mean±S.E.) | N[1] | n[2] | P[3] |
|---|---|---|---|---|---|---|
| Juveniles: | Males | siblings | 44.13±4.97 | 171 | 27 | <0.05 |
| | | non-siblings | 29.67±5.57 | 84 | 43 | |
| | Male/female | siblings | 41.60±5.79 | 142 | 24 | >0.05 |
| | | non-siblings | 29.67±4.23 | 73 | 36 | |
| | Females | siblings | 27.24±6.18 | 97 | 23 | >0.05 |
| | | non-siblings | 15.57±1.96 | 11 | 8 | |
| | Overall | | 35.80±2.45 | 578 | 161 | |
| Yearlings: | Males | siblings | 94.23±12.71 | 81 | 5 | <0.0001 |
| | | non-siblings | 39.29±4.66 | 186 | 16 | |
| | Male/female | siblings | 28.05±3.88 | 36 | 2 | 0.21 |
| | | non-siblings | 25.92±6.50 | 34 | 13 | |
| | Females | non-siblings | 49.88±6.79 | 35 | 4 | |
| | Overall | | 65.11±9.38 | 372 | 40 | |

[1] Total number of play bouts
[2] Total number of pairs of interactors (dyads)
[3] Mann-Whitney U-test

**Table 3.3.** Frequency of occurrence of seven components in play bouts of juveniles and yearlings. Only these components occurred at significantly different frequencies in juvenile and yearling play (Mann-Whitney U-test, $P \leq 0.0024$).

| | Occurrence/sec. (Mean±S.E.) | | |
|---|---|---|---|
| Behaviour | Juveniles | Yearlings | P[1] |
| Chases | 0.029±0.003 | 0.045±0.005 | <0.0001 |
| Run away | 0.022±0.003 | 0.026±0.003 | 0.0008 |
| Belly up | 0.004±0.001 | 0.007±0.001 | 0.0024 |
| Into Burrow | 0.006±0.001 | 0.019±0.003 | <0.0001 |
| Box | 0.017±0.002 | 0.035±0.004 | <0.0001 |
| Side jump | 0.046±0.003 | 0.024±0.003 | <0.0001 |
| Fight | 0.001±0.001 | 0.017±0.005 | <0.0001 |

[1] Mann-Whitney U-test

Table 3.4. Components that occurred at significantly different rates (frequency/sec) in sibling (S) and non-sibling (NS) play.

| | Male/male | | Male/female | Female/female | |
|---|---|---|---|---|---|
| Juveniles | Pounce | | Non-significant | Arch back | |
| | Wrestle | | | Fight | S < NS |
| | Bite | S > NS | | Tail bush | |
| | [illegible]ay | | | | |
| | [illegible]ox | | | | |
| | [illegible]ush | S < NS | | | |
| | N[1] = 255<br>n[2] = 70 | | N = 215<br>n = 60 | N = 108<br>n = 31 | |
| Yearlings | Pounce | | Non-significant | No female-female sibling play | |
| | Wrestle | | | | |
| | Bite | | | | |
| | Push away | S > NS | | | |
| | Box | | | | |
| | Belly up | | | | |
| | Pause | | | | |
| | Run away | S < NS | | | |
| | N = 267<br>n = 21 | | N = 70<br>n = 15 | | |

[1] Total number of play bouts

[2] Total number of pairs of interactors (dyads)

**Table 3.5.** Components that changed significantly (Mann-Whitney U-test, $P \leq 0.0024$) in early and late juvenile play.

| | Relatedness | Behaviour | Rate (frequency/sec)<br>(mean ± S.E.(N[1]))<br>Early | <br><br>Late |
|---|---|---|---|---|
| Males | non-siblings | push away | 0.013 ± 0.005<br>(37) | 0.001 ± 0.001<br>(47) |
| Male/female | non-siblings | arch back | 0.000 ± 0.000<br>(48) | 0.021 ± 0.008<br>(25) |
| Females | siblings | chased | 0.018 ± 0.005<br>(67) | 0.000 ± 0.000<br>(30) |
| | | wrestle | 0.043 ± 0.007<br>(67) | 0.113 ± 0.021<br>(30) |

[1] Total number of play bouts

**Table 3.6.** Average flips per second in wrestling sequences of play.

| | | Flips/second | | |
|---|---|---|---|---|
| | | (mean ± S.E.) | N[1] | P[2] |
| Juveniles: | overall | 0.007 ± 0.001 | (319) | |
| | Males | 0.008 ± 0.002 | (116) | |
| | Male/female | 0.006 ± 0.001 | (145) | 0.457 |
| | Females | 0.005 ± 0.003 | (58) | |
| Yearlings: | overall | 0.010 ± 0.001 | (263) | |
| | Males | 0.011 ± 0.001 | (201) | |
| | Male/female | 0.002 ± 0.001 | (34) | 0.01 |
| | Females | 0.009 ± 0.003 | (28) | |

[1] Total number of wrestling sequences
[2] Kruskal-Wallis

Figure 3.1. Transitions that occurred more often than expected (facilitated) in juvenile play sequences.

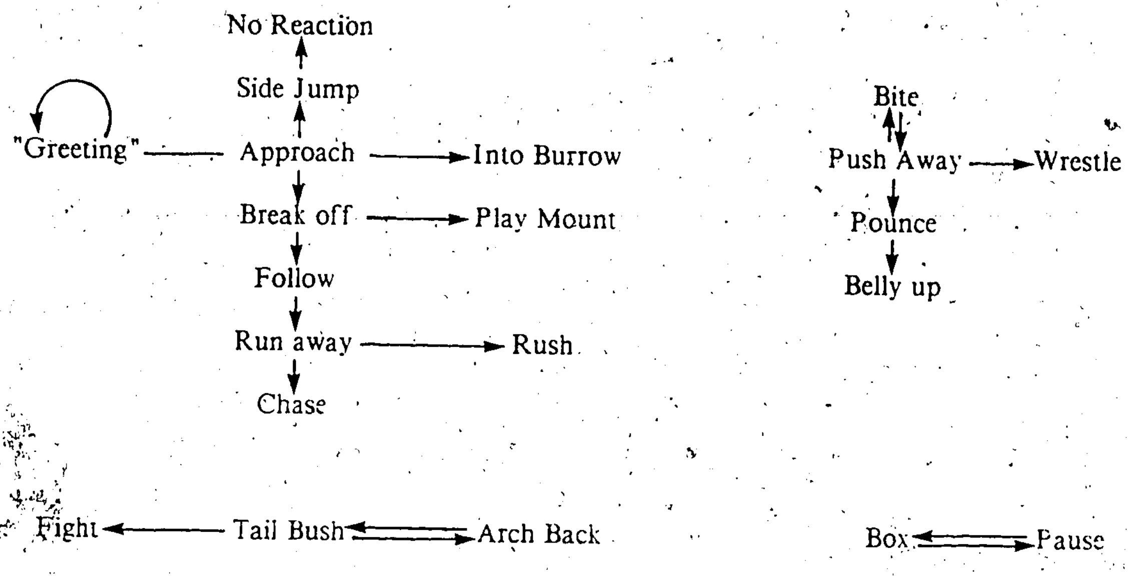


Figure 3.2. Transitions that occurred more often than expected (facilitated) in yearling play sequences.

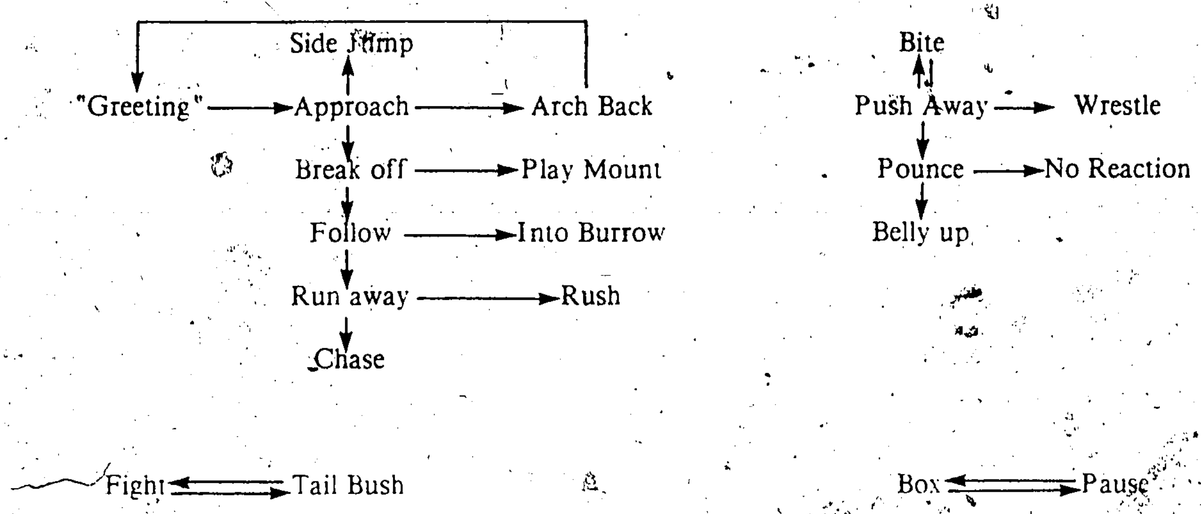


**Figure 3.3.**The four most significantly inhibiting behaviours and the transitions that they inhibited (occurred less often than expected), in juvenile play sequences.

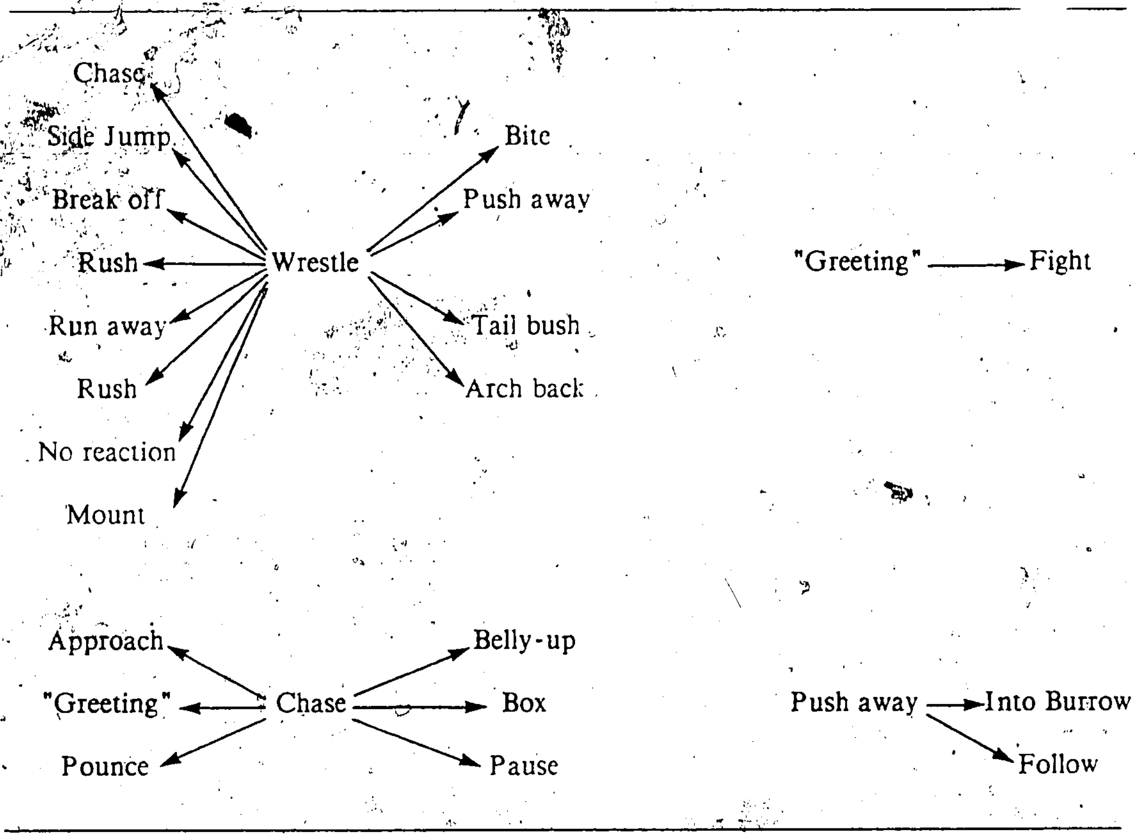
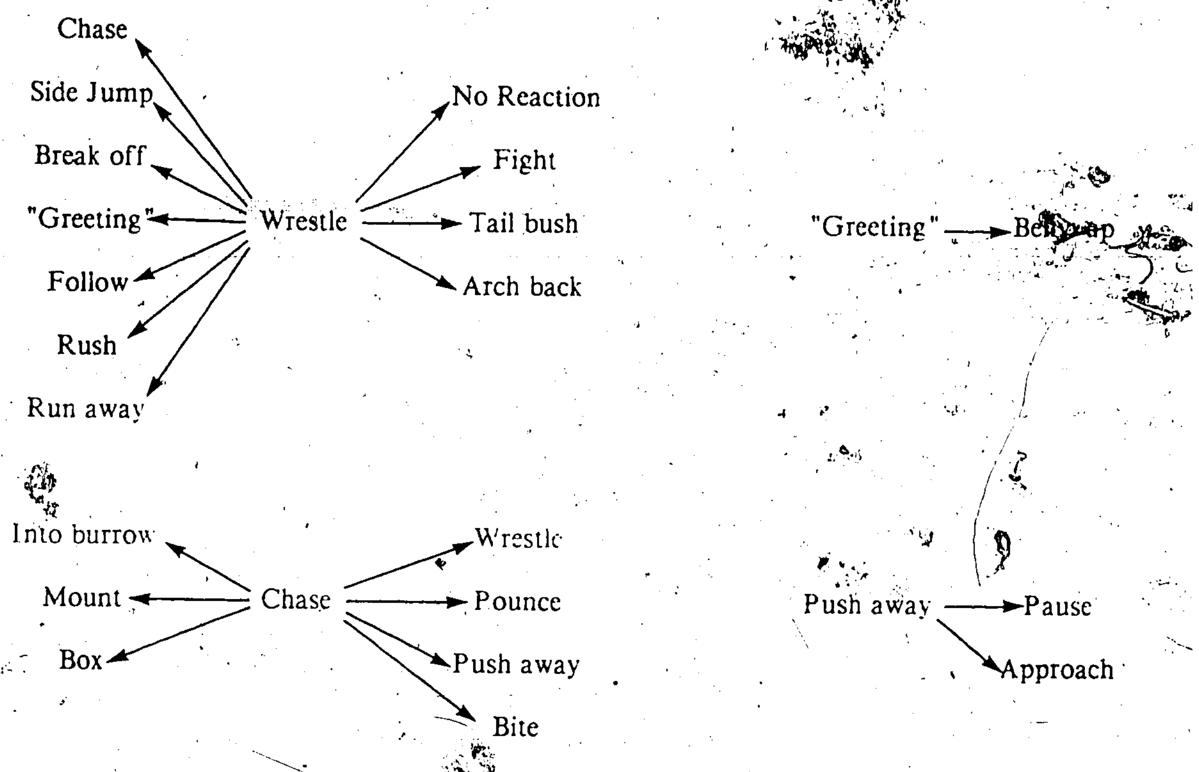


Figure 3.4.The four most significantly inhibiting behaviours and the transitions that they inhibited (occurred less often than expected), in yearling play sequences.



## 4. Concluding discussion

Sexual differences in use of space and behaviour occur within the second week after emergence in juvenile Columbian ground squirrels, *Spermophilus columbianus*. Juvenile males are more likely to gain greater exposure to conspecifics than are females, owing to their greater movement patterns. Females remain closer to their natal burrows, possibly increasing their associations with close relatives. These sexual differences in movement correspond to later situations where males most likely will disperse as yearlings and females most likely will remain on the natal area, often inheriting the natal burrow from their mother (Harris and Murie 1984; Murie and Harris 1984).

Opportunities for play are influenced by these movement patterns. Females remained closest to the natal burrow and to their sisters, and had the highest rate of play with their sisters. As well, play with non-sibling females was characterized by more aggressive components. This could be a consequence of competition, or to being less familiar with non-siblings because of restricted movements. Males overlapped with more non-siblings and thus had more opportunity for greater exposure to non-siblings than did females. Perhaps as a results of this greater exposure, males appeared to avoid the escalations in aggressive components seen in female play. However, intersexual play between non-siblings was not characterized by either escalations in aggressive components or a decrease in contact components as was seen in female-female and male-male play. It may be that the benefits (or costs) of intra- and intersexual play differ.

Yearling play was more aggressive than juvenile play. Increases in aggressive play over time have been noted in wolves and beagles (Bekoff 1974), Steller's sea lions (Gentry 1974), rhesus macaques, Nilgiri langurs, (Poirier and Smith 1974), squirrel monkeys (Baldwin and Baldwin 1974) and vervet monkeys (Lee 1983). Steiner (1971) reported yearling *S. columbianus* play became more aggressive prior to dispersal. In my study, there did not appear to be an increase in aggressiveness in the play of yearling Columbian ground squirrels in late spring. Rates of aggression towards yearlings by adults on my study area were lower than those of similar studies (Festa-Bianchet 1982; D. Hackett pers. comm.; Waterman unpubl. data). It is possible that aggressive play between yearlings was also lower than that reported by Steiner (1971). Thus environmental factors, such as habitat and elevation, may affect play. Berger (1980) found that in bighorn sheep, the environment can affect play greatly, and Nowicki and Armitage (1979) came to similar conclusions for yellow-bellied marmots.

Socialization in the Columbian ground squirrel appears to be different in male and females, with males having more opportunity to interact with other squirrels than females. Much of this socialization involves play. Play in *S. columbianus* may benefit females by reinforcing associations with close female kin, by facilitating learning the abilities of possible future competitors and/or by subtle aggression with possible future competitors. In males, who are unlikely to remain on the natal area for breeding, play may be a means of increasing their exposure to novel situations and/or to learn how to assess other individuals.

The variation in the use of space in juveniles in 1982 and 1983, as well as the lack of increased aggression in late yearling play, suggests that the environment may affect the development of young ground squirrels. The varying degrees of sociality, as well as varying life history characteristics, of ground dwelling sciurids suggests that comparisons between species may suggest possible explanations of the constraints influencing social integration and social play. Observations of species which vary in ages of maturity, litter sizes, survivorship and other characteristics may reveal differences in play which may help to determine its evolutionary significance.

## 4.1 Literature cited

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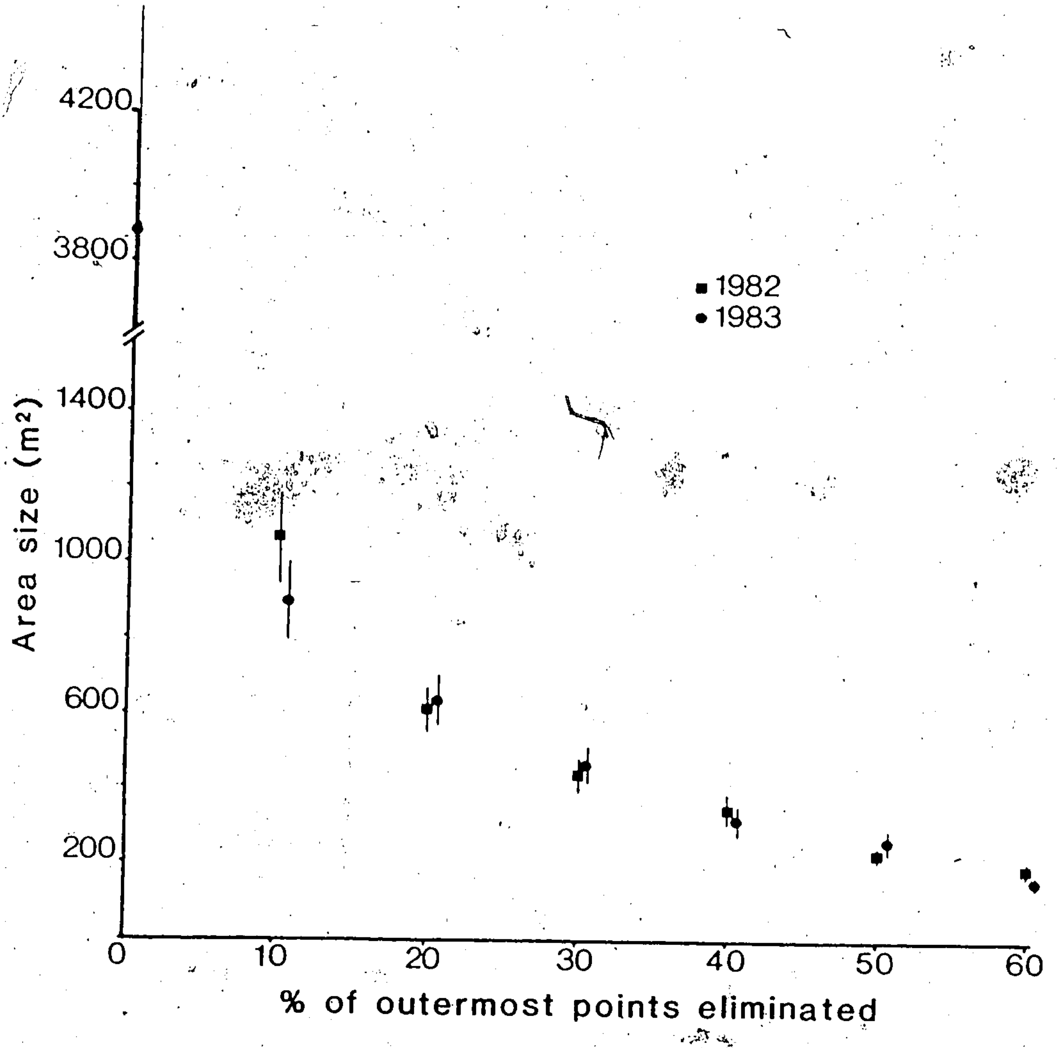
# 5. Appendix I. Home range estimation



Appendix 5.1. Size of juvenile ranges after incremental elimination of outermost points.

## 6. Appendix II. Mean rates of behavioural components

**Appendix 6.1** Mean (±SE) rates of 21 behavioural components in juvenile and yearling play for 1983.

| Behaviour | Rate per second (Mean±SE) | | P[1] |
|---|---|---|---|
| | Juveniles | Yearlings | |
| Arch back | 0.008±0.002 | 0.003±0.001 | 0.4023 |
| Pounce | 0.009±0.002 | 0.016±0.002 | 0.0042 |
| Rush | 0.002±0.001 | 0.001±0.001 | 0.5598 |
| Chase | 0.029±0.003 | 0.045±0.005 | <0.0001 |
| Wrestle | 0.116±0.006 | 0.102±0.009 | 0.1274 |
| Bite | 0.006±0.001 | 0.007±0.001 | 0.4302 |
| Push away | 0.010±0.001 | 0.009±0.001 | 0.2922 |
| Mount | 0.003±0.001 | 0.005±0.001 | 0.0455 |
| Approach | 0.033±0.004 | 0.031±0.004 | 0.2663 |
| Follow | 0.000±0.000 | 0.002±0.001 | 0.0185 |
| Run away | 0.022±0.003 | 0.026±0.003 | 0.0008 |
| Belly-up | 0.004±0.001 | 0.007±0.001 | 0.0024 |
| Greeting | 0.032±0.004 | 0.047±0.006 | 0.0034 |
| No reaction | 0.074±0.005 | 0.076±0.004 | 0.3730 |
| Into burrow | 0.006±0.001 | 0.019±0.003 | <0.0001 |
| Box | 0.017±0.002 | 0.035±0.004 | <0.0001 |
| Break off | 0.006±0.001 | 0.013±0.003 | 0.0503 |
| Side jump | 0.046±0.003 | 0.024±0.003 | <0.0001 |
| Fight | 0.001±0.001 | 0.017±0.005 | <0.0001 |
| Tail bush | 0.009±0.002 | 0.005±0.001 | 0.9129 |
| Pause | 0.008±0.001 | 0.013±0.002 | 0.0885 |

[1] Mann-Whitney U-test

**Appendix 6.2** Mean (±SE) rates of 21 behavioural components in male-male juvenile sibling and non-sibling play (1982-1983).

| Behaviour | Rate per second (Mean±SE) | | P[1] |
|---|---|---|---|
| | Siblings | Non-siblings | |
| Arch back | 0.001±0.001 | 0.010±0.004 | 0.0200 |
| Pounce | 0.023±0.004 | 0.006±0.002 | <0.0001 |
| Rush | 0.002±0.001 | 0.001±0.001 | 0.0489 |
| Chase | 0.044±0.006 | 0.075±0.013 | 0.1696 |
| Wrestle | 0.099±0.008 | 0.051±0.009 | <0.0001 |
| Bite | 0.022±0.004 | 0.006±0.003 | <0.0001 |
| Push away | 0.022±0.006 | 0.006±0.002 | 0.0001 |
| Mount | 0.020±0.009 | 0.004±0.003 | 0.0035 |
| Approach | 0.032±0.004 | 0.042±0.007 | 0.4805 |
| Follow | 0.001±0.000 | 0.000±0.000 | 0.0269 |
| Run away | 0.022±0.004 | 0.042±0.008 | 0.1070 |
| Belly-up | 0.003±0.001 | 0.003±0.0[illegible] | 0.8866 |
| Greeting | 0.039±0.006 | 0.045±0.00[illegible] | 0.9755 |
| No reaction | 0.097±0.015 | 0.064±0.064 | 0.0070 |
| Into burrow | 0.007±0.001 | 0.006±0.003 | 0.0189 |
| Box | 0.024±0.008 | 0.004±0.002 | 0.0002 |
| Break off | 0.027±0.008 | 0.018±0.007 | 0.0966 |
| Side jump | 0.036±0.007 | 0.038±0.006 | 0.8627 |
| Fight | 0.008±0.007 | 0.010±0.004 | 0.0100 |
| Tail bush | 0.002±0.001 | 0.018±0.006 | <0.0001 |
| Pause | 0.003±0.001 | 0.002±0.001 | 0.2193 |

[1] Mann-Whitney U-test

**Appendix 6.3** Mean (±SE) rates of 21 behavioural components in male-female juvenile sibling and non-sibling play (1982-1983).

| Behaviour | Rate per second (Mean±SE) | | |
|---|---|---|---|
| | Siblings | Non-siblings | P[1] |
| Arch back | 0.001±0.001 | 0.007±0.003 | 0.0160 |
| Pounce | 0.016±0.003 | 0.007±0.002 | 0.4091 |
| Rush | 0.003±0.001 | 0.002±0.001 | 0.3464 |
| Chase | 0.037±0.006 | 0.043±0.008 | 0.0334 |
| Wrestle | 0.072±0.007 | 0.061±0.011 | 0.5929 |
| Bite | 0.018±0.002 | 0.008±0.003 | 0.0190 |
| Push away | 0.019±0.004 | 0.007±0.003 | 0.0040 |
| Mount | 0.014±0.003 | 0.003±0.001 | 0.1858 |
| Approach | 0.026±0.003 | 0.046±0.010 | 0.8118 |
| Follow | 0.002±0.001 | 0.001±0.001 | 0.1455 |
| Run away | 0.019±0.004 | 0.028±0.006 | 0.8600 |
| Belly-up | 0.001±0.001 | 0.002±0.001 | 0.6058 |
| Greeting | 0.032±0.005 | 0.032±0.007 | 0.9283 |
| No reaction | 0.069±0.005 | 0.071±0.010 | 0.9496 |
| Into burrow | 0.009±0.003 | 0.002±0.001 | 0.1224 |
| Box | 0.020±0.004 | 0.013±0.005 | 0.1530 |
| Break off | 0.027±0.004 | 0.011±0.003 | 0.0490 |
| Side jump | 0.022±0.003 | 0.029±0.006 | 0.9761 |
| Fight | 0.002±0.001 | 0.001±0.001 | 0.2107 |
| Tail bush | 0.001±0.000 | 0.007±0.004 | 0.1232 |
| Pause | 0.005±0.002 | 0.005±0.002 | 0.1767 |

[1] Mann-Whitney U-test.

**Appendix 6.4** Mean (±SE) rates of 21 behavioural components in female-female juvenile sibling and non-sibling play (1982-1983).

| Behaviour | Rate per second (Mean±SE) | | P[1] |
|---|---|---|---|
| | Siblings | Non-siblings | |
| Arch back | 0.000±0.000 | 0.016±0.011 | 0.0010 |
| Pounce | 0.013±0.004 | 0.004±0.003 | 0.3227 |
| Rush | 0.002±0.001 | 0.012±0.010 | 0.2414 |
| Chase | 0.038±0.007 | 0.024±0.018 | 0.5011 |
| Wrestle | 0.064±0.009 | 0.039±0.026 | 0.1096 |
| Bite | 0.030±0.005 | 0.000±0.000 | 0.0076 |
| Push away | 0.013±0.003 | 0.004±0.004 | 0.2036 |
| Mount | 0.006±0.002 | 0.000±0.000 | 0.1802 |
| Approach | 0.030±0.005 | 0.035±0.017 | 0.8161 |
| Follow | 0.001±0.000 | 0.000±0.000 | 0.6323 |
| Run away | 0.014±0.003 | 0.042±0.022 | 0.2288 |
| Belly-up | 0.001±0.001 | 0.000±0.000 | 0.4430 |
| Greeting | 0.044±0.009 | 0.035±0.024 | 0.3189 |
| No reaction | 0.081±0.007 | 0.041±0.019 | 0.0421 |
| Into burrow | 0.002±0.001 | 0.009±0.009 | 0.7627 |
| Box | 0.021±0.005 | 0.000±0.000 | 0.0654 |
| Break off | 0.033±0.007 | 0.013±0.009 | 0.0646 |
| Side jump | 0.024±0.004 | 0.002±0.018 | 0.5853 |
| Fight | 0.000±0.000 | 0.013±0.009 | 0.0010 |
| Tail bush | 0.000±0.000 | 0.016±0.011 | 0.0000 |
| Pause | 0.001±0.001 | 0.000±0.000 | 0.6323 |

[1] Mann-Whitney U-test

**Appendix 6.5** Mean (±SE) rates of 21 behavioural components in male-male yearling sibling and non-sibling play (1983-1984).

| Behaviour | Rate per second (Mean±SE) | | P[1] |
|---|---|---|---|
| | Siblings | Non-siblings | |
| Arch back | 0.003±0.001 | 0.009±0.002 | 0.1507 |
| Pounce | 0.021±0.003 | 0.010±0.002 | <0.0001 |
| Rush | 0.002±0.002 | 0.000±0.000 | 0.1460 |
| Chase | 0.057±0.008 | 0.101±0.008 | 0.0082 |
| Wrestle | 0.137±0.011 | 0.093±0.007 | <0.0001 |
| Bite | 0.013±0.011 | 0.093±0.007 | 0.0001 |
| Push away | 0.018±0.003 | 0.010±0.002 | <0.0001 |
| Mount | 0.004±0.001 | 0.007±0.002 | 0.4489 |
| Approach | 0.017±0.003 | 0.034±0.003 | 0.0221 |
| Follow | 0.001±0.000 | 0.002±0.001 | 0.4926 |
| Run away | 0.013±0.004 | 0.038±0.004 | 0.0002 |
| Belly-up | 0.010±0.002 | 0.005±0.001 | 0.0006 |
| Greeting | 0.026±0.006 | 0.054±0.005 | 0.0040 |
| No reaction | 0.054±0.005 | 0.076±0.005 | 0.0157 |
| Into burrow | 0.021±0.003 | 0.018±0.002 | 0.0334 |
| Box | 0.043±0.006 | 0.029±0.005 | 0.0009 |
| Break off | 0.005±0.002 | 0.007±0.002 | 0.9329 |
| Side jump | 0.030±0.004 | 0.033±0.003 | 0.7591 |
| Fight | 0.007±0.003 | 0.010±0.003 | 0.5009 |
| Tail bush | 0.002±0.001 | 0.009±0.002 | 0.2450 |
| Pause | 0.018±0.003 | 0.009±0.002 | <0.0001 |

[1] Mann-Whitney U-test

**Appendix 6.6** Mean (±SE) rates of 21 behavioural components in male-female yearling sibling and non-sibling play (1983-1984).

| Behaviour | Rate per second (Mean±SE) |  |  |
|---|---|---|---|
|  | Siblings | Non-siblings | P[1] |
| Arch back | 0.003±0.003 | 0.002±0.002 | 0.5467 |
| Pounce | 0.011±0.004 | 0.006±0.004 | 0.0750 |
| Rush | 0.003±0.002 | 0.002±0.002 | 0.3425 |
| Chase | 0.079±0.018 | 0.071±0.016 | 0.4890 |
| Wrestle | 0.087±0.016 | 0.087±0.016 | 0.8645 |
| Bite | 0.004±0.002 | 0.000±0.000 | 0.0470 |
| Push away | 0.010±0.004 | 0.008±0.004 | 0.7950 |
| Mount | 0.002±0.001 | 0.009±0.005 | 0.1830 |
| Approach | 0.031±0.007 | 0.050±0.011 | 0.4388 |
| Follow | 0.004±0.003 | 0.004±0.002 | 0.7349 |
| Run away | 0.021±0.006 | 0.027±0.009 | 0.8801 |
| Belly-up | 0.007±0.003 | 0.004±0.002 | 0.5494 |
| Greeting | 0.068±0.016 | 0.044±0.012 | 0.3456 |
| No reaction | 0.081±0.013 | 0.068±0.013 | 0.4962 |
| Into burrow | 0.023±0.008 | 0.008±0.003 | 0.3506 |
| Box | 0.040±0.011 | 0.024±0.008 | 0.2582 |
| Break off | 0.021±0.007 | 0.011±0.009 | 0.0832 |
| Side jump | 0.017±0.004 | 0.025±0.008 | 0.8336 |
| Fight | 0.017±0.010 | 0.043±0.017 | 0.2425 |
| Tail bush | 0.005±0.005 | 0.000±0.000 | 0.5692 |
| Pause | 0.005±0.003 | 0.022±0.009 | 0.2072 |

[1] Mann-Whitney U-test

**Appendix 6.7** Mean (±SE) rates of 21 behavioural components in male-male juvenile sibling play (1982-1983) for early and late bouts.

| | Rate per second (Mean±SE) | | |
|---|---|---|---|
| Behaviour | Early | Late | P[1] |
| Arch back | 0.000±0.000 | 0.000±0.002 | 0.6127 |
| Pounce | 0.028±0.006 | 0.013±0.003 | 0.0873 |
| Rush | 0.003±0.001 | 0.001±0.001 | 0.2683 |
| Chase | 0.042±0.006 | 0.048±0.013 | 0.7785 |
| Wrestle | 0.101±0.010 | 0.093±0.012 | 0.9238 |
| Bite | 0.026±0.006 | 0.015±0.003 | 0.4117 |
| Push away | 0.025±0.009 | 0.016±0.004 | 0.3500 |
| Mount | 0.024±0.013 | 0.012±0.004 | 0.3283 |
| Approach | 0.030±0.006 | 0.036±0.005 | 0.0215 |
| Follow | 0.001±0.000 | 0.000±0.000 | 0.1537 |
| Run away | 0.018±0.005 | 0.032±0.007 | 0.1119 |
| Belly-up | 0.002±0.001 | 0.003±0.002 | 0.9952 |
| Greeting | 0.035±0.007 | 0.048±0.010 | 0.1988 |
| No reaction | 0.098±0.022 | 0.097±0.011 | 0.1319 |
| Into burrow | 0.008±0.002 | 0.005±0.002 | 0.6821 |
| Box | 0.029±0.011 | 0.014±0.004 | 0.1829 |
| Break off | 0.034±0.012 | 0.012±0.003 | 0.2780 |
| Side jump | 0.039±0.010 | 0.030±0.005 | 0.9456 |
| Fight | 0.011±0.010 | 0.000±0.000 | 0.1827 |
| Tail bush | 0.001±0.000 | 0.005±0.002 | 0.0445 |
| Pause | 0.003±0.003 | 0.003±0.002 | 0.3124 |

[1] Mann-Whitney U-test

**Appendix 6.8** Mean (±SE) rates of 21 behavioural components in male-male juvenile non-sibling play (1983-1984) for early and late bouts.

| | Rate per second (Mean±SE) | | |
|---|---|---|---|
| Behaviour | Early | Late | P[1] |
| Arch back | 0.000±0.000 | 0.018±0.007 | 0.0088 |
| Pounce | 0.008±0.003 | 0.004±0.003 | 0.0220 |
| Rush | 0.000±0.000 | 0.001±0.001 | 0.3749 |
| Chase | 0.071±0.019 | 0.078±0.017 | 0.9181 |
| Wrestle | 0.073±0.016 | 0.034±0.010 | 0.9238 |
| Bite | 0.012±0.006 | 0.001±0.001 | 0.0037 |
| Push away | 0.013±0.005 | 0.001±0.001 | 0.0010 |
| Mount | 0.007±0.005 | 0.002±0.001 | 0.1452 |
| Approach | 0.039±0.013 | 0.043±0.007 | 0.3163 |
| Follow | 0.000±0.000 | 0.000±0.000 | [illegible]597 |
| Run away | 0.040±0.014 | 0.044±0.009 | [illegible]27 |
| Belly-up | 0.003±0.002 | 0.003±0.002 | [illegible]291 |
| Greeting | 0.050±0.016 | 0.041±0.010 | [illegible].36[illegible] |
| No reaction | 0.077±0.016 | 0.054±0.010 | 0.1846 |
| Into burrow | 0.002±0.001 | [illegible]09±0.005 | 0.8322 |
| Box | 0.005±0.003 | [illegible]03±0.002 | 0.2671 |
| Break off | 0.020±0.013 | 0.016±0.006 | 0.3343 |
| Side jump | 0.035±0.010 | 0.040±0.008 | 0.9456 |
| Fight | 0.008±0.004 | 0.011±0.006 | 0.7636 |
| Tail bush | 0.008±0.005 | 0.027±0.010 | 0.1367 |
| Pause | 0.004±0.002 | 0.000±0.000 | 0.0217 |

[1] Mann-Whitney U-test

**Appendix 6.9** Mean (±SE) rates of 21 behavioural components in male-female juvenile sibling play (1982-1983) for early and late bouts.

| Behaviour | Rate per second (Mean±SE) | | $P^1$ |
|---|---|---|---|
| | Early | Late | |
| Arch back | 0.001±0.001 | 0.000±0.000 | 0.3271 |
| Pounce | 0.015±0.003 | 0.021±0.007 | 0.7462 |
| Rush | 0.003±0.001 | 0.005±0.003 | 0.7286 |
| Chase | 0.033±0.004 | 0.051±0.016 | 0.1994 |
| Wrestle | 0.075±0.008 | 0.061±0.015 | 0.4713 |
| Bite | 0.018±0.003 | 0.017±0.006 | 0.7337 |
| Push away | 0.021±0.004 | 0.011±0.005 | 0.1801 |
| Mount | 0.015±0.004 | 0.007±0.005 | 0.3124 |
| Approach | 0.020±0.003 | 0.052±0.012 | 0.0091 |
| Follow | 0.003±0.001 | 0.000±0.000 | 0.0575 |
| Run away | 0.012±0.003 | 0.050±0.015 | 0.0056 |
| Belly-up | 0.002±0.001 | 0.001±0.001 | 0.8042 |
| Greeting | 0.028±0.004 | 0.047±0.014 | 0.4348 |
| No reaction | 0.061±0.005 | 0.102±0.017 | 0.0307 |
| Into burrow | 0.009±0.003 | 0.009±0.006 | 0.2965 |
| Box | 0.022±0.005 | 0.013±0.006 | 0.3371 |
| Break off | 0.027±0.004 | 0.024±0.010 | 0.4157 |
| Side jump | 0.019±0.003 | 0.033±0.009 | 0.2234 |
| Fight | 0.002±0.001 | 0.004±0.004 | 0.9416 |
| Tail bush | 0.001±0.001 | 0.000±0.000 | 0.3980 |
| Pause | 0.006±0.002 | 0.003±0.003 | 0.2915 |

[1] Mann-Whitney U-test

**Appendix 6.9** Mean (±SE) rates of 21 behavioural components in male-female juvenile non-sibling play (1982-1983) for early and late bouts.

| Behaviour | Rate per second (Mean ± SE) |  | P[1] |
|---|---|---|---|
|  | Early | Late |  |
| Arch back | 0.000 ± 0.000 | 0.021 ± 0.008 | 0.0001 |
| Pounce | 0.011 ± 0.004 | 0.001 ± 0.001 | 0.0892 |
| Rush | 0.002 ± 0.002 | 0.002 ± 0.001 | 0.4978 |
| Chase | 0.034 ± 0.008 | 0.061 ± 0.017 | 0.3501 |
| Wrestle | 0.07[illegible] ± 0.01[illegible] | 0.034 ± 0.013 | 0.0579 |
| Bite | [illegible] ± 0.004 | 0.003 ± 0.002 | 0.1711 |
| Push away | 0.010 ± 0.004 | 0.004 ± 0.002 | 0.4074 |
| Mount | 0.000 ± 0.000 | 0.008 ± 0.004 | 0.0229 |
| Approach | 0.045 ± 0.014 | 0.047 ± 0.012 | 0.0091 |
| Follow | 0.000 ± 0.000 | 0.002 ± 0.002 | 0.2174 |
| Run away | 0.020 ± 0.006 | 0.043 ± 0.012 | 0.0466 |
| Belly-up | 0.001 ± 0.001 | 0.002 ± 0.002 | 0.3930 |
| Greeting | 0.029 ± 0.008 | 0.039 ± 0.012 | 0.5150 |
| No reaction | 0.083 ± 0.014 | 0.048 ± 0.010 | 0.1233 |
| Into burrow | 0.003 ± 0.001 | 0.001 ± 0.001 | 0.4573 |
| Box | 0.020 ± 0.007 | 0.000 ± 0.000 | 0.0069 |
| Break off | 0.010 ± 0.003 | 0.013 ± 0.006 | 0.8261 |
| Side jump | 0.034 ± 0.009 | 0.019 ± 0.007 | 0.1403 |
| Fight | 0.002 ± 0.002 | 0.000 ± 0.000 | 0.4705 |
| Tail bush | 0.003 ± 0.002 | 0.014 ± 0.010 | 0.3796 |
| Pause | [illegible] ± 0.002 | 0.005 ± 0.004 | 0.9611 |

[1] Mann-Whitney U-test

**Appendix 6.10** Mean (±SE) rates of 21 behavioural components in female-female juvenile sibling play (1982-1983) for early and late bouts.

| Behaviour | Rate per second (Mean ± SE) | | P[1] |
|---|---|---|---|
| | Early | Late | |
| Arch back | 0.000 ± 0.000 | 0.000 ± 0.000 | 0.5034 |
| Pounce | 0.017 ± 0.006 | 0.005 ± 0.003 | 0.1291 |
| Rush | 0.002 ± 0.001 | 0.002 ± 0.001 | 0.6469 |
| Chase | 0.018 ± 0.005 | 0.083 ± 0.019 | 0.0003 |
| Wrestle | 0.043 ± 0.007 | 0.113 ± 0.021 | 0.0004 |
| Bite | 0.035 ± 0.007 | 0.019 ± 0.005 | 0.2076 |
| Push away | 0.013 ± 0.003 | 0.012 ± 0.004 | 0.8822 |
| Mount | 0.007 ± 0.002 | 0.004 ± 0.003 | 0.1639 |
| Approach | 0.028 ± 0.007 | 0.032 ± 0.006 | 0.2703 |
| Follow | 0.001 ± 0.001 | 0.000 ± 0.000 | 0.3415 |
| Run away | 0.010 ± 0.003 | 0.024 ± 0.006 | 0.0335 |
| Belly-up | 0.001 ± 0.001 | 0.001 ± 0.001 | 0.6688 |
| Greeting | 0.045 ± 0.012 | 0.041 ± 0.012 | 0.7834 |
| No reaction | 0.080 ± 0.009 | 0.083 ± 0.013 | 0.6776 |
| Into burrow | 0.003 ± 0.002 | 0.001 ± 0.001 | 0.8482 |
| Box | 0.028 ± 0.007 | 0.006 ± 0.004 | 0.0234 |
| Break off | 0.040 ± 0.009 | 0.018 ± 0.006 | 0.0190 |
| Side jump | 0.023 ± 0.004 | 0.024 ± 0.008 | 0.6684 |
| Fight | 0.000 ± 0.000 | 0.000 ± 0.000 | 0.5034 |
| Tail bush | 0.000 ± 0.000 | 0.000 ± 0.000 | 1.0000 |
| Pause | 0.001 ± 0.001 | 0.001 ± 0.001 | 0.5682 |

[1] Mann-Whitney U-test

**Appendix 6.11** Mean (±SE) rates of 21 behavioural components in female-female juvenile non-sibling play (1982-1983) for early and late bouts.

| Behaviour | Rate per second (Mean±SE) | | $P^1$ |
|---|---|---|---|
| | Early | Late | |
| Arch back | 0.015±0.015 | 0.016±0.016 | 0.7792 |
| Pounce | 0.006±0.004 | 0.000±0.000 | 0.2622 |
| Rush | 0.018±0.015 | 0.000±0.000 | 0.2622 |
| Chase | 0.032±0.027 | 0.009±0.009 | 0.9043 |
| Wrestle | 0.061±0.040 | 0.000±0.000 | 0.1493 |
| Bite | 0.000±0.000 | 0.000±0.000 | 1.0000 |
| Push away | 0.006±0.006 | 0.000±0.000 | 0.4497 |
| Mount | 0.000±0.000 | 0.000±0.000 | 1.0000 |
| Approach | 0.028±0.022 | 0.048±0.028 | 0.5114 |
| Follow | 0.000±0.000 | 0.000±0.000 | 1.0000 |
| Run away | 0.060±0.033 | 0.009±0.009 | 0.3537 |
| Belly-up | 0.000±0.000 | 0.000±0.000 | 1.0000 |
| Greeting | 0.000±0.000 | 0.097±0.056 | 0.0497 |
| No reaction | 0.022±0.013 | 0.074±0.047 | [illegible] |
| Into burrow | 0.014±0.014 | 0.000±0.000 | [illegible] |
| Box | 0.000±0.000 | 0.000±0.000 | 1.0000 |
| Break off | 0.006±0.006 | 0.023±0.023 | 0.5751 |
| Side jump | 0.007±0.007 | 0.066±0.047 | 0.1493 |
| Fight | 0.021±0.014 | 0.000±0.000 | 0.2622 |
| Tail bush | 0.015±0.015 | 0.016±0.016 | 0.7792 |
| Pause | 0.000±0.000 | 0.000±0.000 | 1.0000 |

[1] Mann-Whitney U-test

**Appendix 6.12** Mean (±SE) rates of 21 behavioural components in male-male yearling sibling play (1983-1984) for early and late bouts.

| Behaviour | Rate per second (Mean ± SE) |  | P[1] |
|---|---|---|---|
|  | Early | Late |  |
| Arch back | 0.003±0.001 | 0.002±0.002 | 0.6505 |
| Pounce | 0.021±0.003 | 0.011±0.005 | 0.7020 |
| Rush | 0.000±0.000 | 0.000±0.000 | 0.7114 |
| Chase | 0.060±0.008 | 0.045±0.024 | 0.8143 |
| Wrestle | 0.144±0.011 | 0.063±0.029 | 0.0438 |
| Bite | 0.014±0.002 | 0.012±0.006 | 0.6312 |
| Push away | 0.019±0.003 | 0.018±0.007 | 0.5750 |
| Mount | 0.004±0.001 | 0.009±0.005 | 0.0550 |
| Approach | 0.018±0.003 | 0.017±0.010 | 0.8861 |
| Follow | 0.001±0.000 | 0.000±0.000 | 0.4747 |
| Run away | 0.013±0.004 | 0.012±0.010 | 0.7598 |
| Belly-up | 0.010±0.002 | 0.003±0.002 | 0.5772 |
| Greeting | 0.022±0.004 | 0.002±0.002 | 0.1737 |
| No reaction | 0.054±0.006 | 0.056±0.018 | 0.7536 |
| Into burrow | 0.0[illegible]±0.004 | 0.019±0.010 | 0.8317 |
| Box | 0.043±0.006 | 0.061±0.032 | 0.4737 |
| Break off | 0.005±0.005 | 0.000±0.000 | 0.3576 |
| Side jump | 0.031±0.004 | 0.021±0.012 | 0.4987 |
| Fight | 0.007±0.003 | 0.009±0.009 | 0.5592 |
| Tail bush | 0.002±0.001 | 0.002±0.002 | 0.4650 |
| Pause | 0.017±0.003 | 0.033±0.018 | 0.3334 |

[1] Mann-Whitney U-test

**Appendix 6.13** Mean (±SE) rates of 21 behavioural components in male-male yearling non-sibling play (1983-1984) for early and late bouts.

| | Rate per second (Mean±SE) | | |
|---|---|---|---|
| Behaviour | Early | Late | P[1] |
| Arch back | 0.009±0.002 | 0.011±0.011 | 0.7453 |
| Pounce | 0.010±0.002 | 0.009±0.009 | 0.4977 |
| Rush | 0.000±0.000 | 0.000±0.000 | 0.7637 |
| Chase | 0.100±0.008 | 0.122±0.029 | 0.2917 |
| Wrestle | 0.093±0.007 | 0.089±0.047 | 0.6209 |
| Bite | 0.006±0.001 | 0.000±0.000 | 0.2268 |
| Push away | 0.010±0.002 | 0.012±0.009 | 0.8429 |
| Mount | 0.007±0.002 | 0.009±0.009 | 0.8442 |
| Approach | 0.035±0.003 | 0.027±0.019 | 0.2525 |
| Follow | 0.002±0.001 | 0.000±0.000 | 0.4700 |
| Run away | 0.037±0.004 | 0.044±0.015 | 0.4271 |
| Belly-up | 0.006±0.001 | 0.000±0.000 | 0.1610 |
| Greeting | 0.052±0.005 | 0.000±0.000 | 0.3035 |
| No reaction | 0.072±0.005 | 0.147±0.026 | 0.0025 |
| Into burrow | 0.018±0.002 | 0.036±0.015 | 0.1792 |
| Box | 0.031±0.005 | 0.000±0.000 | 0.0578 |
| Break off | 0.006±0.002 | 0.019±0.019 | 0.9639 |
| Side jump | 0.032±0.003 | 0.055±0.023 | 0.4456 |
| Fight | 0.010±0.003 | 0.011±0.011 | 0.9246 |
| Tail bush | 0.006±0.001 | 0.006±0.006 | 0.8867 |
| Pause | 0.010±0.002 | 0.000±0.000 | 0.1756 |

[1] Mann-Whitney U-test

**Appendix 6.14** Mean (±SE) rates of 21 behavioural components in male-female yearling sibling play (1983-1984) for early and late bouts.

| Behaviour | Rate per second (Mean±SE) |  |  |
|---|---|---|---|
|  | Early | Late | P[1] |
| Arch back | 0.000±0.000 | 0.036±0.036 | 0.0068 |
| Pounce | 0.008±0.004 | 0.024±0.024 | 0.5769 |
| Rush | 0.005±0.004 | 0.000±0.000 | 0.5940 |
| Chase | 0.100±0.026 | 0.054±0.054 | 0.8657 |
| Wrestle | 0.104±0.023 | 0.090±0.048 | 0.4934 |
| Bite | 0.002±0.002 | 0.000±0.000 | 0.5940 |
| Push away | 0.004±0.003 | 0.000±0.000 | 0.5051 |
| Mount | 0.002±0.002 | 0.000±0.000 | 0.7119 |
| Approach | 0.021±0.007 | 0.036±0.036 | 0.8502 |
| Follow | 0.001±0.001 | 0.000±0.000 | 0.5940 |
| Run away | 0.021±0.006 | 0.078±0.047 | 0.1491 |
| Belly-up | 0.011±0.005 | 0.000±0.000 | 0.3152 |
| Greeting | 0.074±0.018 | 0.048±0.048 | 0.5948 |
| No reaction | 0.073±0.014 | 0.107±0.107 | 0.6708 |
| Into burrow | 0.032±0.013 | 0.036±0.036 | 1.0000 |
| Box | 0.046±0.013 | 0.048±0.048 | 1.0000 |
| Break off | 0.015±0.008 | 0.000±0.000 | 0.9639 |
| Side jump | 0.020±0.005 | 0.036±0.036 | 0.9294 |
| Fight | 0.023±0.016 | 0.000±0.000 | 0.5051 |
| Tail bush | 0.009±0.008 | 0.000±0.000 | 0.5940 |
| Pause | 0.008±0.004 | 0.000±0.000 | 0.4320 |

[1] Mann-Whitney U-test

**Appendix 6.15** Mean (±SE) rates of 21 behavioural components in male-female yearling non-sibling play (1983-1984) for early and late bouts.

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| Behaviour | Rate per second (Mean±SE) | | P[1] |
|---|---|---|---|
| | Early | Late | |
| Arch back | 0.002±0.002 | 0.000±0.000 | 0.7996 |
| Pounce | 0.006±0.005 | 0.000±0.000 | 0.7522 |
| Rush | 0.002±0.002 | 0.000±0.000 | 0.8597 |
| Chase | 0.064±0.015 | 0.000±0.000 | 0.3896 |
| Wrestle | 0.086±0.016 | 0.000±0.000 | 0.3208 |
| Bite | 0.000±0.000 | 0.000±0.000 | 1.0000 |
| Push away | 0.008±0.004 | 0.000±0.000 | 0.6395 |
| Mount | 0.010±0.005 | 0.000±0.000 | 0.6739 |
| Approach | 0.051±0.012 | 0.000±0.000 | 0.3430 |
| Follow | 0.004±0.003 | 0.000±0.000 | 0.7522 |
| Run away | 0.029±0.009 | 0.000±0.000 | 0.4912 |
| Belly-up | 0.005±0.002 | 0.000±0.000 | 0.7111 |
| Greeting | 0.043±0.012 | 0.114±0.114 | 0.1613 |
| No reaction | 0.067±0.013 | 0.000±0.000 | 0.2585 |
| Into burrow | 0.008±0.003 | 0.000±0.000 | 0.6395 |
| Box | 0.021±0.008 | 0.114±0.114 | 0.0506 |
| Break off | 0.012±0.009 | 0.000±0.000 | 0.7111 |
| Side jump | 0.027±0.009 | 0.000±0.000 | 0.4912 |
| Fight | 0.042±0.018 | 0.000±0.000 | 0.6395 |
| Tail bush | 0.000±0.000 | 0.000±0.000 | 0.8597 |
| Pause | 0.023±0.010 | 0.000±0.000 | 0.6072 |

[1] Mann-Whitney U-test

**Appendix 6.16** Mean (±SE) rates of 21 behavioural components in female-female yearling non-sibling play (1983-1984) for early and late bouts.

| Behaviour | Rate per second (Mean±SE) | | P[1] |
|---|---|---|---|
| | Early | Late | |
| Arch back | 0.003±0.002 | 0.000±0.000 | 0.4484 |
| Pounce | 0.030±0.008 | 0.008±0.005 | 0.2346 |
| Rush | 0.000±0.000 | 0.000±0.000 | 0.6698 |
| Chase | 0.052±0.010 | 0.000±0.000 | 0.0130 |
| Wrestle | 0.104±0.015 | 0.136±0.037 | 0.2824 |
| Bite | 0.013±0.003 | 0.003±0.003 | 0.2970 |
| Push away | 0.013±0.003 | 0.018±0.009 | 0.6004 |
| Mount | 0.003±0.001 | 0.000±0.000 | 0.2645 |
| Approach | 0.035±0.008 | 0.028±0.019 | 0.4276 |
| Follow | 0.003±0.002 | 0.000±0.000 | 0.4484 |
| Run away | 0.021±0.005 | 0.021±0.020 | 0.5251 |
| Belly-up | 0.012±0.004 | 0.008±0.005 | 0.8918 |
| Greeting | 0.032±[illegible] | 0.080±0.041 | 0.1621 |
| No reaction | 0.084±[illegible] | 0.025±0.011 | 0.0044 |
| Into burrow | 0.008±0.003 | 0.002±0.002 | 0.5097 |
| Box | 0.016±0.007 | 0.081±0.028 | 0.0180 |
| Break off | 0.016±0.007 | 0.002±0.002 | 0.4468 |
| Side jump | 0.032±0.006 | 0.011±0.007 | 0.1799 |
| Fight | 0.007±0.005 | 0.000±0.000 | 0.6698 |
| Tail bush | 0.000±0.000 | 0.000±0.000 | 0.4484 |
| Pause | 0.006±0.002 | 0.044±0.026 | 0.0689 |

[1] Mann-Whitney U-test