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M2 Ecophysiologie et Ethologie

M2S4 Training course in Behavioural Sciences

Time and Activity Budgets and Mating Success of Male Richardson's Ground Squirrels

Summary

My Contribution

During this internship at the University of Lethbridge, AB in Canada, my work consisted in observing behaviours of free-living male Richardson's ground squirrels (*Spermophilus richardsonii*) during the pre-mating, mating and post-mating seasons and live-trapping adult males and adult females, litters and juveniles to obtain data about body mass and body condition, reproductive status and litter size and sex ratio. Additionally, I assisted with a study of burrow systems.

Field work was conducted at a research site located 40 km from the University.

I acquired my behavioural data over an 7-week period from 19 February to 17 April 2008. The time in the fields to trap ground squirrels included the preceding period and continued until mid-June (11 weeks). Field work accounted for about 71 % of my internship time.

Computerized data entry and analysis occurred from early April through early June and accounted for 29 % of my internship time.

Introduction

Review of seasonal variation in male behaviour in ground squirrels

In many species of animals, activity patterns differ between the sexes. Moreover these differences often change with time and reproductive status, and animals express behaviours appropriate for each season (e.g.,mating and non-mating seasons for males; estrus, pregnancy, and lactation for females). Sexual and seasonal variations in time and activity budgets have been studied for several species in the genus Spermophilus.

Because most species of ground squirrels hibernate, often for more than 6 months of the year, all major biological activities occur within a restricted active season. For example, male Richardson's ground squirrels (*Spermophilus richardsonii*) hibernate for 8 months from mid-June to mid-February and are active for the remaining 4 months. During this active period, males adjust their behaviour relative to the energetic demands of mating and pre-hibernatory fattening.

Various studies reveal that in Richardson's (b,j,m,n,q,w,ac), Columbian (*S. columbianus*) (r,s), Arctic (*S. parryii*) (g,ab) and California (*S. beecheyi*) (c) ground squirrels, males mainly forage and establish a territory after they emerge from hibernation and before the mating season starts. Social behaviours between males are agonistic and may result in dominance reversals or establishment of territorial boundaries.

During the mating season, males move more, interact more and feed less, with consequent decrease in weight, than at other times of year. Because the operational sex ratio (number of females in estrus per male per day) is usually male biased in ground squirrels, interactions between males during the mating season are agonistic and often characterized by chases and fights to gain access to females or to maintain territoriality. These aggressive interactions are consequences of mate guarding. In fact, once a female is in estrus, the potential mate keeps other males away from the female and prevents her from finding other males. By preventing females from engaging in extrapair copulation attemps, the male protects his paternity. None-the-less multiple-male mating by females is known in several Sciurid species and can result in multiple paternity of the litter (b,e,h,t). Interactions between males and females vary according to the female's reproductive status and are primarily determined by the female. If the female is not receptive, the interaction is agonistic. But if the female is in estrus (a few hours on one day in the year), the interactions become more cohesive, and may result in copulation either aboveground and underground.

Starting the day after copulation, females become aggressive to males and chase them. Once all females have mated, males engage in fewer social interactions, both with other males and with females, and they primarily spend their time foraging to recover from the mating season and to gain weight before the hibernation. Male Richardson's ground squirrels do not exhibit paternal care. Although infanticide by males has been recorded for some species of ground squirrels (g), it has

never been recorded in Richardson's ground squirrels.

Review of mating behaviour and mating success in male ground squirrels

In Columbian ground squirrels, territoriality increases the fertilization success of a territory owner by facilitating the first mating with females that live on his home range. Richardson's ground squirrels are less territorial than other species of ground squirrels, like Arctic ground squirrels (h), but they occupy home ranges with fluid boundaries that change according to which females are in estrus (k). Aggressive mate guarding in some species of ground squirrels (d,h,i,t,aa) prevents females from engaging in extrapair copulation, thereby increasing male fitness and resulting in high mating success (a). For example, male Arctic ground squirrels actively prevent competitors from acquiring access to his mate by chasing and fighting with individuals that approach the female, and they appear to restrict the movements of the female by chasing her back to the burrow system in which consortship has occured (h). In this species, mate guarding prevents females from susequently mating with other males and thereby reducing sperm competition, also guaranteeing his paternity. However, multiple mating and multiple paternity of the litter are common in Arctic ground squirrels, but the first male to mate sires more of the litter, indicating that sperm precedence occurs. Moreover, for Columbian ground squirrels, in addition to mate guarding, males emited deceptive calls after mating to occup the attention of male rivals or to prolong lordosis of a mated female (i). Finally, for European ground squirrels (*Spermophilus citellus*), in addition to aggressive mate guarding behaviour, males protect their offspring by taking care of the litter burrow and spending time in digging behaviour (d).

Objectives

The objectives of my study were to observe seasonal variations in the time and activity budgets of male Richardson's ground squirrels in relation to mating success. I tested the following predictions by observing individually marked males throughout the active season. (1) Males engage in more agonistic behaviours with other males and fewer neutral behaviours during the mating season than during the premating and postmating season. (2) Proximity to females varies with season, reproductive status of females, kinship to females, and morphological characteristics of males. (3) Characteristics of the interactions (kind, sex and kinship to the other individual) differ with seasons. (4) Characteristics of mating vary with the age and weight of males and females. (5) Males modify their home range during the year.

	Emergence	from hibernation	Estrus	Birth	Emergence
	Males	Females	of females	of litters	of litters
Mean dates	23 February	4 March	7 March	31 March	1 May
First dates	31 January	19 February	26 February	20 March	21 April
Last dates	7 March	15 March	19 March	11 April	11 May
N	25	75	75	74	74
Mean body mass (g)	379,8 ± 51	224 ± 33,8	251,55 ± 40,8		

Table 1: Dates of emergence, mating and weight of Richardson's ground squirrels at the Picture Butte site in 2008.

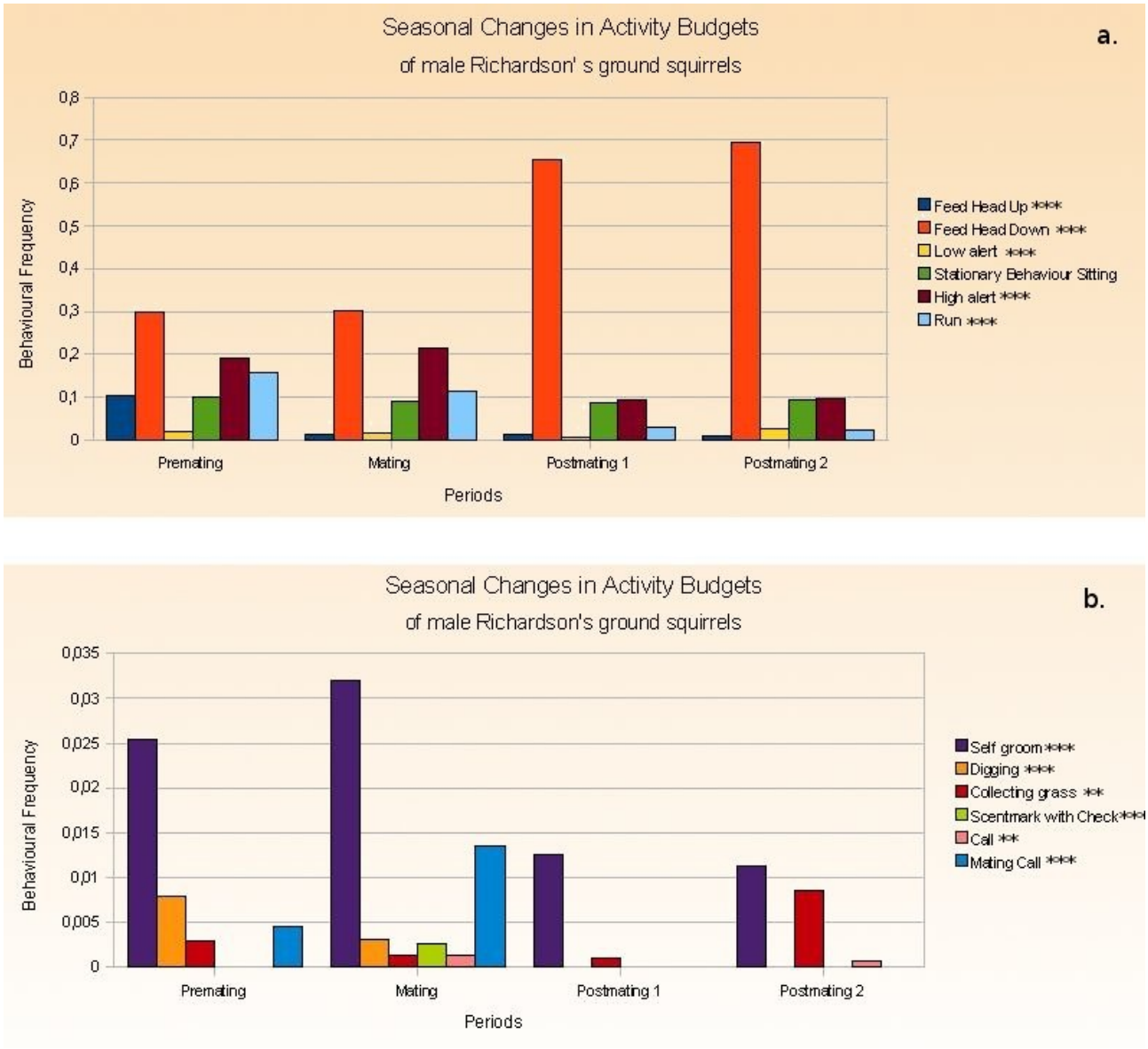


Fig. 1: Seasonal changes in activity budgets of adult male Richardson's ground squirrels in 2008, a) for feeding, running and stationary behaviours, b) for other neutral behaviours. Data are presented as mean values for 10 males in the Premating season, 13 in the Mating season, 11 in Postmating 1, and 7 in Postmating 2. Stars represent the level of statistical significance (*** means highly significantly p-value < 0,009). For most of observed behaviours, we found a statistically significant seasonal effect, except for some agonistic and recognitive behaviours ().

Methods

Biology of Richardson's ground squirrels

Richardson's ground squirrels (*Spermophilus richardsonii*) are semi-fossorial diurnally active mammals, that sleep and hibernate underground but forage and interact above ground in the grassland of south western Canada and adjacent states in the USA. Adults measure around 30 cm and weigh from 200 to 600 g depending on age, sex, and season. Both sexes of Richardson's ground sqiurrels are reproductively mature on emergence from their first hibernation, when they are 11 months old and referred to as yearling. Although the population sex ratio is strongly female biased (male:female = 1:4), the operational sex ratio is male biased (3:1). Females often live for 3-4 years and occasionally to 6 years, but males rarely live to 3 years. Richardson's ground squirrels are gregarious, but each animal has its own home range.

Richardson's ground squirrels are seasonal breeders, with mating restricted from to a 2- to 3-week period in March (Table 1). Each female comes into estrus 3-4 days after emergence from hibernation and usually mates in the late afternoon on only one day during the mating season. Pregnancy lasts 23 days, and litters first appear above ground when the young are 29 days old. Adult males immerge in mid-June, followed by adult females in July, juvenile females in August and juvenile males in October. My observational study began in mid-February when most adult males had emerged from hibernation and ended in mid-April when all females had birth to litters.

Study Area and Capture Techniques

From February to June 2008, I observed a population of Richardson's ground squirrels, that has been investigated continuously by Dr. G. Michener since 1987. The site is located 5 km east and 1 km south of Picture Butte, in southwestern Alberta, Canada. In March 2008, the population was composed of 25 adult males and 119 adult females. The observable portion of the study area measures 2 ha and is bordered by a road, cultivated fields, and residences. All animals have been trapped and ear tagged previously. With few exceptions (N = 3 males), male squirrels were of known age and known maternal genealogy, so the coefficient of relatedness was known for most of the observed males and in relation to adjacent females. Commencing in early February, the site was checked daily for emergence of animals. Newly emerged squirrels were immediately captured in Tomahawk un-baited live traps (19*19*48 cm) and their identity was checked from the numbered ear tags. For observational purposes, each animal was given a unique dye mark on the fur with human hair dye. On first capture and each capture thereafter, animals were weighed to the nearest 5 g, examined for their reproductive status (e.g. colour of scrotal skin and location of testes in males),

and investigated for wounds and scars. Each male in the observable portion of the study area was weighed and examined at least once per month.

Behavioural Observations

Behavioural observations were conducted to obtain time and activity budgets. Observations were conducted from observational booths using 7*42 binoculars. During scan sampling, behaviour and location of each male were noted every 10 min for 2-4 hours of observation on 5 days per week for a total of 142 hours of observation on 48 days between 19 February and 17 April. Observation hours covered all daylight hours, with 40% of observations conducted before noon and 60% after noon.

In addition to scan samples, during the late afternoon in the mating season, focal-individual sampling, of 5 min on 7 days per week, for males (in randomised order) was used to follow males continuously to determine which females they mated with, and interrupted by a scan sampling every 10 min to see the mate situation of each male, for a total of 43 hours of observation on 15 days between 29 February and 14 March. Estrous status of females was known from other studies being conducted simultaneously on the site.

Copulation sometimes occurs above ground, but more commonly occurs underground. Underground mating was inferred using behavioural criteria and focusing our attention on males and estrus females (h): male approaches and touches noses with a female; one individual (usually the female) enters a burrow, followed immediately by the second individual; the pair remained out of sight for at least 2 min, after which one animal emerges from the burrow, followed shortly by the second animal; and one, or usually both, individuals groom their genitalia. Mating was usually confirmed the next day by examination of the female's external genitalia and microscopic inspection of her vaginal lavage to detect sperm and characteristic changes in the identity of cells in the vagina. Using these behavioural criteria, I determined the number of matings per male per observed days, based on observed mating events, 12 of which I observed myself, 42 by four other observers and 21 suspected.

For each observational method, the following information was recorded:
date, weather conditions, time of observation, location of the observed animal to the nearest 1 m (ascertained from a 10m x 10m grid on the study site), proximity to females within a 20-m radius to the nearest 1 m and identity of those females, and behaviour (w): Feed (with head up, with head down); Self-groom; Move (Run; Go underground; Come aboveground); Burrow maintenance (Digging; Collecting grass); Scentmark with cheek; Alert (low alert = on all four legs, close to the ground and watching; high alert = on hind legs, watching attentively); Sitting; Social interactions (Recognitive: nose to nose, nose to body; Agonistic: threat, attack, attacked, fight, chase, chased; Avoidance; Copulation). I identified the individuals involved in interactions and which initiated and

		Period				
		Premating	**Mating**	**Postmating 1**	**Postmating 2**	
		(19 Feb- 28 Feb)	(29 Feb- 15 Mar)	(16 Mar- 30 Mar)	(31 Mar-17 Apr)	
		N= 10 males	N = 13 males	N= 11 males	N= 7 males	**P-value**
Activity Budgets (%)						
Feeding	Feed Head Up	10,53 ± 1,33	1,26 ± 0,23	1,41 ± 0,39	0,99 ± 0,37	0,000
	Feed Head Down	29,87 ± 1,93	30,19 ± 0,93	65,49 ± 1,51	69,47 ± 1,68	0,000
Staionary Behaviour	Low Alert	1,98 ± 0,58	1,62 ± 0,24	0,78 ± 0,27	0,28 ± 0,60	0,003
	Sitting	10,09 ± 1,28	9,06 ± 0,58	8,76 ± 0,92	9,30 ± 1,07	0,069
	High Alert	19,08 ± 1,61	21,36 ± 0,72	9,42 ± 0,92	9,74 ± 1,07	0,000
Move	Run	15,66 ± 1,38	11,54 ± 0,57	3,19 ± 0,47	2,43 ± 0,46	0,000
	Go Underground	0,20 ± 0,19	0,97 ± 0,15	0,59 ± 0,22	0,50 ± 0,23	0,000
	Come Aboveground	0,00 ± 0,00	0,66 ± 0,12	0,44 ± 0,19	0,21 ± 0,12	0,000
Self Groom		2,54 ± 0,67	3,20 ± 0,35	1,26 ± 0,35	1,14 ± 0,38	0,000
Burrow Maintenance	Digging	0,79 ± 0,34	0,32 ± 0,10	0 ,00 ± 0,05	0,00 ± 0,00	0,004
	Collecting Grass	0,30 ± 0,22	0,13 ± 0,07	0,11 ± 0,07	0,85 ± 0,34	0,023
Scentmark with Cheek		0,00 ± 0,00	0,26 ± 0,08	0,00 ± 0,00	0,00 ± 0,00	0,000
Recognitive Interaction	Nose to Nose	0,30 ± 0,21	2,38 ± 0,27	0,25 ± 0,10	0,11 ± 0,11	0,000
	Nose to Body	0,10 ± 0,09	0,16 ± 0,08	0,00 ± 0,00	0,00 ± 0,00	0,171
Agonistic Interaction	Threat	0,18 ± 0,10	0,32 ± 0,10	0,19 ± 0,10	0,19 ± 0,11	0,480
	Attack	0,00 ± 0,00	0,05 ± 0,03	0,00 ± 0,00	0,00 ± 0,00	0,417
	Attacked	0,00 ± 0,00	0,19 ± 0,00	0,17 ± 0,00	0,00 ± 0,00	0,060
	Fight	1,53 ± 0,51	1,25 ± 0,21	0,60 ± 0,22	0,27 ± 0,12	0,001
	Chase	2,09 ± 0,59	4,60 ± 0,41	0,66 ± 0,22	0,14 ± 0,11	0,000
	Chased	1,65 ± 0,50	6,17 ± 0,48	5,99 ± 0,74	1,95 ± 0,48	0,000
Avoidance Interaction	Avoidance	0,48 ± 0,20	1,88 ± 0,21	0,60 ± 0,18	0,21 0,09	0,000
Cohesive Interaction	Mating	0,00 ± 0,00	0,23 ± 0,07	0,00 ± 0,00	0,00 ± 0,00	0,012
Call	Call	0,00 ± 0,00	0,14 ± 0,05	0,00 ± 0,00	0,07 ± 0,00	0,029
	Mating Call	0,45 ± 0,00	1,36 ± 0,16	0,00 ± 0,00	0,00 ± 0,00	0,000
Use of Space	Home Range (m²)	909 ± 376	2263 ± 257	894 ± 158		0,001
	Core Area (m²)	226 ± 101	514 ± 106	147 ± 27		0,016
Body Mass (g)		379,8 ± 51	392,5 ± 40,2	356,11 ± 17,5	406,2 ± 37	0,023

Table 2: Activity budgets, use of space and body mass for adult male Richardson's ground squirrels in relation to the period in 2008. P-values were obtained with the Kruskal-Wallis-test. Data are presented as mean ± SD.

which terminated the interaction. In addition, I noted if a male was alarm calling or mate calling while engaged in other behaviours, such as when Alert and I noted whether the male was flicking his tail vertically or horizontally while engaged in other behaviours such as nose to nose.

Data Analysis

Time budgets, the proportion of time spent in each behaviour, were compared between seasons (pre-mating, mating and post-mating period) in Anova. I considered the feeding, moving, alerting, sitting patterns and maintenance of the burrow like neutral behaviours, in opposition to the social interactions which were not personnal care behaviours.

I divided the observation period into three seasons based on the reproductive status of females. The premating season was defined as the period from emergence of the first male (31 January) to the beginning of the mating season; my observations began on 19 February, at which time 9 of 25 males had emerged. I considered the beginning of mating season to be 29 February, at which time 18 of 75 females had emerged but only 3 of those had mated). I defined the end of the mating season as 15 March, at which time all females had emerged and 95% of females (71/75) were pregnant. The postmating season began on 16 March, but I sub-divided this into two periods; Postmating 1 ended on 30 March, when about 50% of females had given birth, and Postmating 2 ended on 17 April, the day before the earliest litters emerged above ground.

Because some males disappeared or moved relative to observation area, only five individuals were seen every day during the four periods. The behaviour and the time and activity budgets of these five males were similar to those based on inclusion of all, consequently data from all males were used; 10 males in the premating season, 13 males in the mating season, 11 males in the postmating 1 season and 7 males in the postmating 2 season.

Time budgets, the proportion of time spent in each behaviour, were compared between seasons (pre-mating, mating and post-mating period) using ANOVA. I considered feeding, moving, alerting, sitting and maintenance of the burrow to be neutral personal-care behaviours.

Within the mating system, I used ANOVA and linear regression to compare the activity budget and mating success of individuals according to age, weight during the mating season, number of wounds, core area (defined as the area encompassing 50% of locations) and proximity to females. I also calculated home range as the minimum convex polygon encompassing 95% of locations.

I used minimum convex polygons with 95% of points included to estimate a « home range » for each male and 50% of points to estimate a « core area ».

I used the Minitab 15.0 package for statistical analysis and Biotas 1.03 alpha for home range analysis. Parametric tests were used when data were normally distributed and nonparametric tests when they were not; p-values < 0,05 are considered to indicate significance.

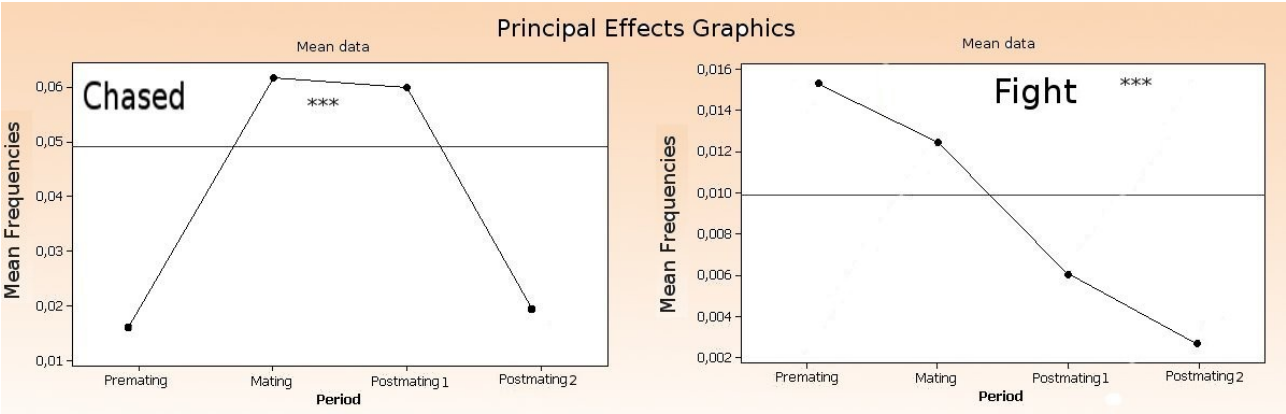


Fig. 2: Principal Effects Graphics for Chased and Fight patterns functions of period in male Richardson's ground squirrels. Horizontal line indicate the mean of total frequency, points indicate the mean of frequency in each period and stars indicate the level of significance (*** means highly significantly p-value < 0,009).

		Period					Sexe other individual			Kind interaction				
		Premating	**Mating**	**Postmating 1**	**Postmating 2**	p-value	**Male**	**Female**	p-value	**Recognitive**	**Agonistic**	**Cohesive**	**Avoidance**	p-value
Social Interaction frequencies														
Recognitive		0,00	0,01	0,00	0,00	0,000	0,00	0,07	0,000	/	/	/	/	/
Agonistic		0,01	0,02	0,01	0,00	0,000	0,12	0,08	0,000	/	/	/	/	/
Cohesive	Mating	0,00	0,23	0,00	0,00	0,012	/	/	/	/	/	/	/	/
Avoidance		0,48	1,88	0,60	0,21	0,000	0,04	0,09	0,000	/	/	/	/	/
Rank	Initiator	1,34	1,38	1,83	1,84	0,000	1,43	1,47	0,297	1,02	1,78	2,00	1,29	0,000
	Terminator	1,37	1,40	1,81	1,84	0,000	1,43	1,49	0,116	1,20	1,56	1,00	1,00	0,000
Kin ratio other idividual		0,0338	0,0313	0,0162	0,0000	0,327	0,0494	0,0144	0,000	0,0144	0,0334	0,0000	0,0179	0,198

Table 3: Social interactions, rank in the interactions and coefficient of relatedness of the other individual depending on season and sex of the other individual for male Richardson's ground squirrels. P-values were obtained with the Kruskal-Wallis' test.

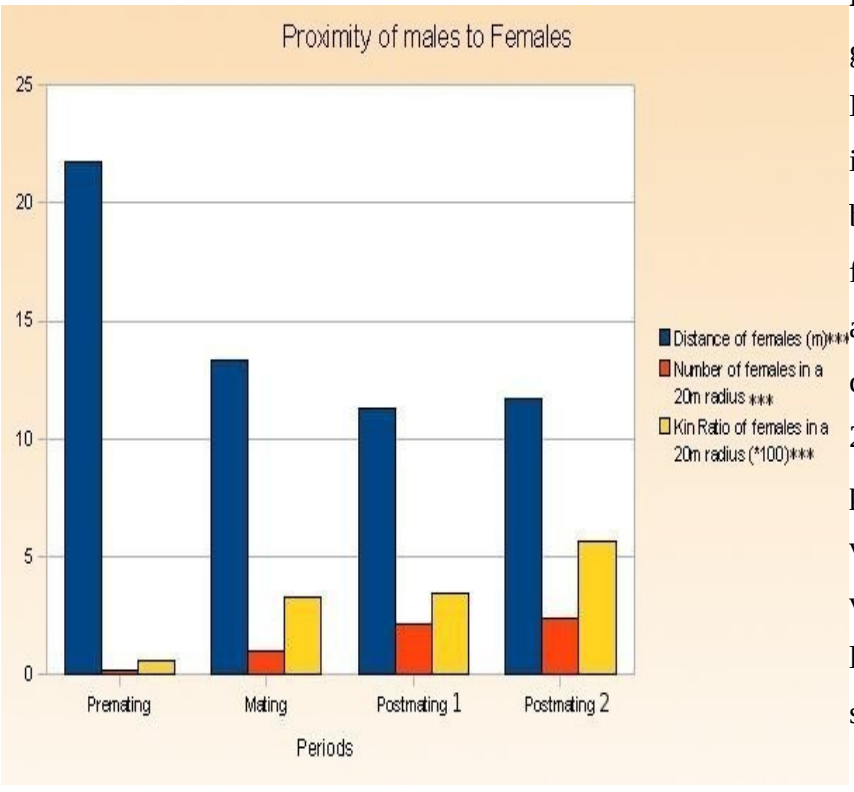


Fig. 3: Proximity of males Richardson's ground squirrels to females in 2008. Blue bars indicate the mean of distance in meters from males to females, red bars indicate the mean number of females in a 20-m radius around males and yellow bars indicate the mean of coefficient of relatedness of females in a 20-m radius around males in each periods. Coefficient of relatedness' values were multiplied by 100 for visibility on the graph. Stars indicate the level of significance (*** means highly significantly p-value < 0,009).

Results

Seasonal Changes in Activity Budgets

Behavioural Patterns

I found an effect of season on the frequency of most of the 22 behavioural activities of male Richardson's ground squirrels (Fig. 1).

Males devoted over two thirds of their time above ground to feeding with the head down during the postmating season, significantly more time (p-value= 0,000) than premating and mating (Table 2). Increased foraging coincided with increased body mass, which significantly increased between the mating season and the postmating (Kruskall-Wallis; p-value=0,000). Time spent high alerting followed an inverse pattern to feeding, with highest values in the mating season and reaching a seasonal low during postmating (p-value= 0,000). During the premating and mating season, males spent significantly more time running and scent marking than postmating (p-value=0,000).

Digging behaviour was restricted to the premating period (p-value=0,004) in all males and was not observed in the postmating period. In contrast, collecting grass was most frequent postmating, especially postmating 2 (p-value=0,023). Finally, time spent grooming was more frequent in the mating season than in either pre- or post-mating (p-value=0,000).

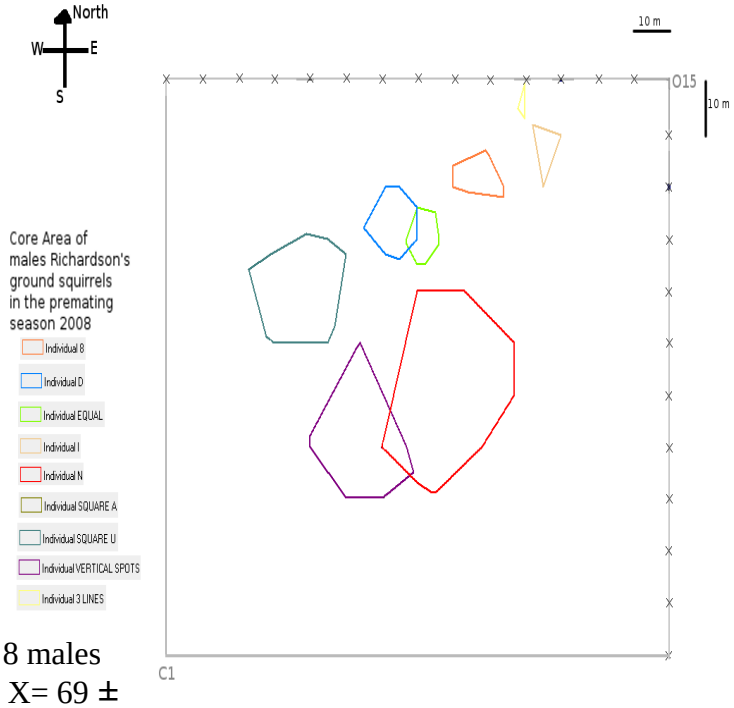
Social activities were considerably less frequent than personal care activities. Social interactions peaked at 17,23 % of above-ground timeduring the mating season, in part because of frequent male-male interactions, especially fighting and chasing (p-value=0,001 and 0,000), and in part because of inter-sexual interactions initiated by either the male or female, especially recognitive, cohesive and avoidance interactions (p-value=0,000; p-value=0,012 and p-value=0,000). Males spent significantly more time fighting in the premating and mating seasons than postmating (p-value=0,001) (Fig. 2), and more time being chased in the mating and postmating seasons than premating (p-value=0,000).

Finally, males spent more time calling in the mating season than in the other periods (p-value= 0,029), especially mate calling (p-value= 0,000).

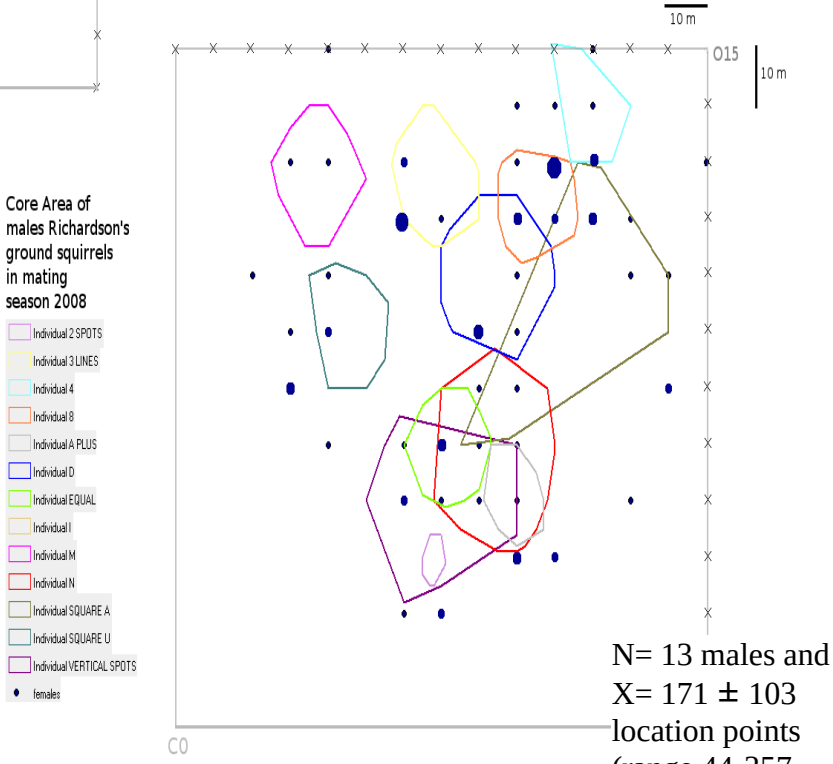
Social Interactions

Interaction rates calculated from all periods revealed similar patterns to those obtained from activity budget data. Here I expand just on selected aspects of social interactions not already reported and which give more detailed information.

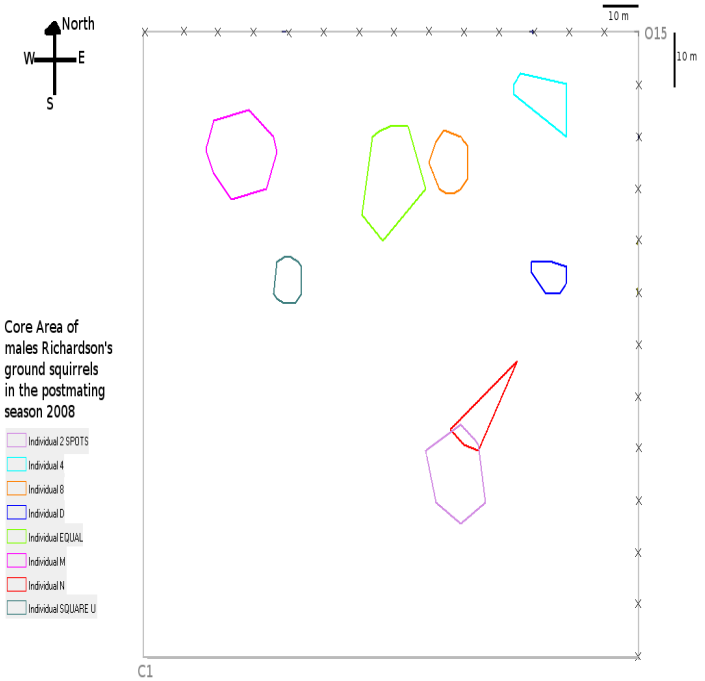
Firstly, I found a significant effect of season on most social behaviours. Male Richardson's



N= 8 males and X= 69 ± 33 location points per males (range 15-115 points)



N= 13 males and X= 171 ± 103 location points (range 44-357 points)



N= 8 males and X= 198 ± 140 datapoints (range 13-376 points)

Fig.4: Core areas of male Richardson's ground squirrels used during the premating, mating and postmating seasons 2008 on the study site near Picture Butte, AB, Canada. I used the minimum convex polygon to estimate these core areas. Points represent the main locations of females when in estrus in 2008 and their sizes indicate the density of females in a same location. Polygons indicate the males' home ranges, with same colour for a same male.

ground squirrels spent significantly more time engaged in recognitive, agonistic, avoidance and cohesive interactions in the mating season (p-value=0,000; p-value=0,000; p-value=0,000; p-value=0,012) than in other periods (Table 3).

Most agonistic interactions involved two males (p-value=0,000), who engaged in chases and fight that resulted in large numbers of wounds on males during the mating season. Some males had as many as 39 wounds, whereas they had no more than five wounds during the other periods. In contrast, interactions with females were primarily recognitive, especially nose to nose and nose to body patterns (p-value=0,000 and p-value=0,030), and avoidance (p-value=0,000). During mating season, we found males interacted more with non-related individuals, especially with non-related females (p-value=0,000), than pre- and post-mating.

To consider the role of the initiator and terminator of interactions, I gave a rank of 1 whenthe focal male initiated or finished the interactions and 2 when other interactant was the initiator or terminator. Males initiated interactions significantly more than females for recognitive interactions (p-value=0,000), whereas females initiated more agonistic interactions than males. Males terminated interactions significantly more for cohesive and avoidance interactions (p-value=0,000), whereas females finished the recognitive and agonistic interactions they started. Finally, males started and finished interactions significantly more in the premating and mating seasons (p-value=0,000) than postmating, whereas females initiated and finished interactions more after than during the mating season.

Proximity of males to females

Although the number of active females above ground was not the same in each periods (Fig. 3), males were closer to females in postmating than in the other two periods (p-value=0,000). However males were significantly closer to females in the mating season (d=13 m) than in the premating season (d=22 m). Also, the number of females in a 20-m radius around males was higher postmating, especially postmating 2 (p-value=0,000).

Because males changed the location of their home range with season (Fig.4), the identity of females in a 20-m radius varied with the periods, too. The coefficient of relatedness of these females was higher in the postmating 2 period than in other periods (p-value=0,000).

Seasonal Changes in Use of Space

The size of the home range used by male Richardson's ground squirrels changed with season. Before the mating season, when most females were still in hibernation, males mostly fed and their home ranges were small (909 ± 376 m^2; n= 8) (Table 2). Home ranges occupied by males during the mating season were significantly bigger (p-value=0,001) than in the premating season at

		Mating Success	p-value
Behaviours	Feed	0,6279 – 0,419feed	0,000
	High alert	0,5116 + 0,2362alert	0,000
	Run		0,467
	Fight		0,716
	Chase	0,5557 + 0,1358chase	0,070
	Chased		0,246
	Recognitive interactions		0,753
	Agonistic interactions		0,997
Distance to females		0,5765 – 0,001070d	0,462
Number of females in a 20m radius		0,5382 + 0,0238n	0,068
Individual caracteristics	Age	6,115 + 0,0385age	0,967
	Weight (g)	8,596 – 0,00619weight	0,760
	Wounds	5,147 + 0,08799wounds	0,153
	Home range (m²)	2,734 + 0,001517hr	0,072
	Core area (m²)	5,377 + 0,001537ca	0,485

Table 4 : Linear Regression for some mostly observed behaviours, proximity of males to females and individual characteristics on the mating success of males Richardson's ground squirrels (N= 13 males). For the study of the effects of the behaviours and the proximity to females, we used the daily mating success of males, and we used the total mating success for the individual characteristics, wich were calculated during the mating season. P-values were obtained with the linear regression.

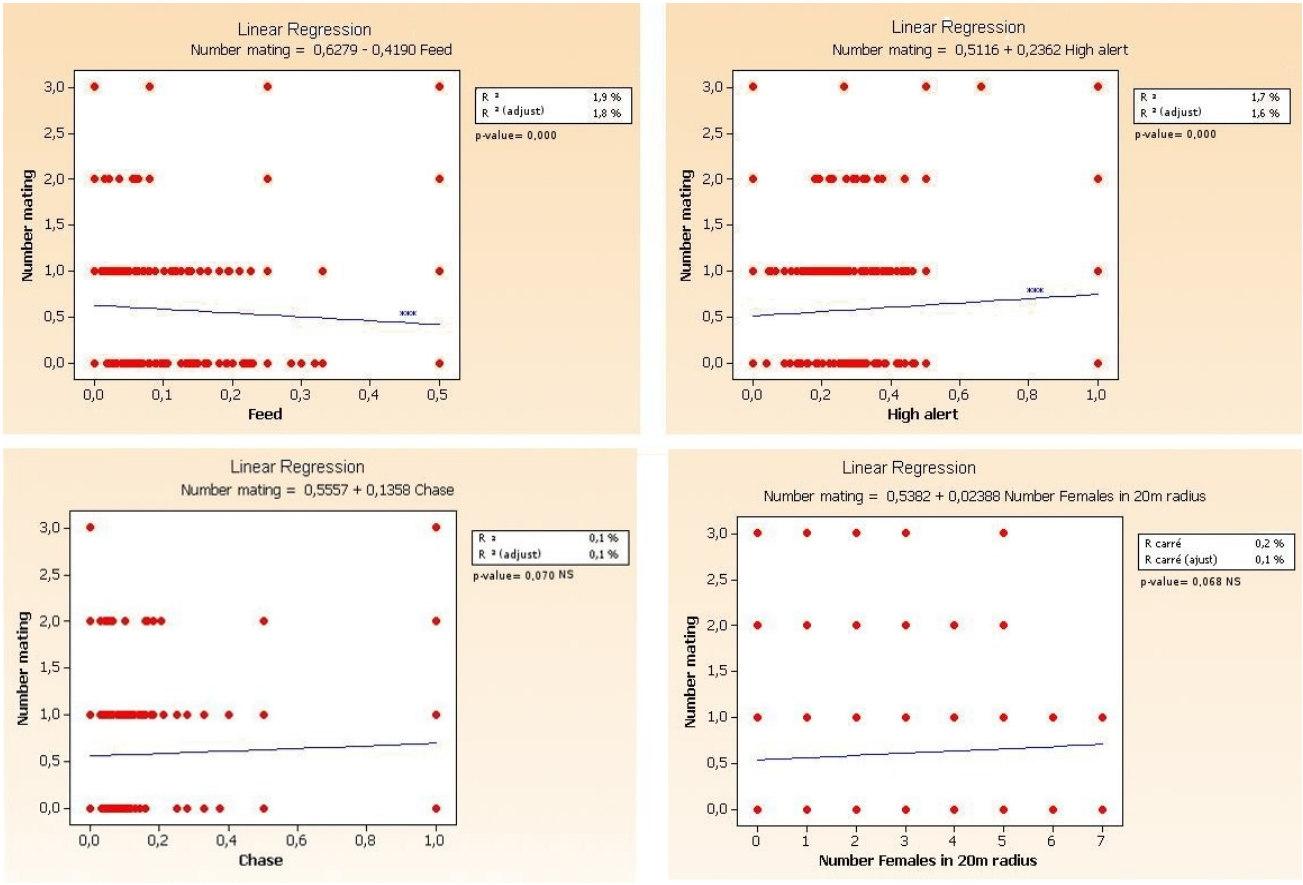


Fig.5: Linear Regression for some significantly behavioural effect (Fighting, Alerting, Chasing patterns and Number of females in a 20-m radius around a male) on the daily mating success of males Richardson's ground squirrels. The linear regression straight are represented by the blue lines. For each studied behaviour, the statistical package gives the regression equation, R^2 (proportion of variance of the observed response, which is explain by the factors) and R^2 adjusted and the p-value, which indicates the significance of the behaviour.

about 2263 m² (n=13; SD = 257). Finally, once all the females were mated, home ranges significantly declined to about 894 m² (n = 8; SD = 158) in the post-mating season.

In addition to seasonal changes in size of the home range, male Richardson's ground squirrels changed the location of their home ranges, too (Fig.4), in response to which females were in estrus each day and their kinship to those females (Kruskal-Wallis: p-value= 0,000). In the mating season, males spent more time close to non-related females, and moved during the postmating period to be significantly closer to related females (p-value=0,000). During the premating and postmating periods, each male occupied a distinct area that overlapped minimally with other males. During the mating season, the home ranges were larger, they overlapped extensively with each other.

Characteristics of Mating Success

Behavioural Effects

Using 75 females with complete and suspected mating data, the number of mates per males was calculated daily and summed for the entire mating season (Table 6).

Mating success of males who spent less time eating was significantly higher than males who were eating more often (p-value=0,000) (Table 4). Additionaly, males that spent more time alert had higher mating success than other males (p-value=0,000). Other behaviours did not significantly affect the daily mating success of males. Nevertheless, because mate searching means competition between adult males, I found that males who spent more time chasing other males had somewhat higher mating success than chased males (p-value=0,070) (Fig.5).
Finally, males in proximity to more females had a higher mating success than other males (Fig.5), as did those that had bigger home ranges.

Effects of Age

Yearling males were significantly more alert (p-value=0,000), and engaged in more recognitive and agonistic interactions than older males (p-value=0,007 and p-value=0,043). Additionally, yearling males were in proximity to significantly more females than older males, and they were more likely to be close kin of those females (p-value=0,000), even though their home ranges were not larger than those of older males during the mating season. In contrast, I found that older males fed and ran significantly more than youger males (p-value=0,000) during the mating season (Table 5).

Although behaviour had an effect on mating success, and age had an effect on behaviour, age of male Richardson's ground squirrels did not significantly affect their mating success.

		Age	p-value	Weight (g)	p-value
Distance to females		12,8 + 0,585a	0,000		0,942
Number of females in a 20m radius		1,67 – 0,210a	0,000	3,04 – 0,00423w	0,000
Kin ratio of females in a 20m radius		0,06238 – 0,01706a	0,000	0,00501 + 0,000084w	0,035
Behaviours	Feed	0,3806 + 0,04060a	0,000	1,239 – 0,002026w	0,000
	High alert	0,1987 – 0,02203a	0,000	-0,1628 + 0,000836w	0,000
	Run	0,06482 + 0,01613a	0,000		0,170
	Fight		0,480		0,833
	Chase		0,544	-0,07132 + 0,000251w	0,000
	Chased		0,107		0,674
	Recognitive interactions	0,01011 – 0,002103a	0,007	-0,02736 + 0,000087w	0,000
	Agonistic interactions	0,01722 – 0,00145a	0,043	-0,000007 + 0,000038w	0,004
Individual characteristics	Wounds	7,327 + 3,192age	0,481	67,73 – 0,1430weight	0,135
	Mating success	6,115 + 0,0385age	0,967	8,596 – 0,00619weight	0,760
	Home range (m²)	1199 + 165,3age	0,462	512 + 2,381weight	0,590
	Core area (m²)	276,4 + 27,41age	0,682	23,7 + 0,755weight	0,566

Table 5: Principal effects of age and weight of male Richardson's ground squirrels on frequent behaviours (Feed, High alert, Run, Chase, Recognitive interactions and Agonistic interactions), the proximity of males to females (Distance to females, Number and coefficient of relatedness of females in a 20-m radius around a male) and on individual characteristics. P-values were obtained with the linear regression.

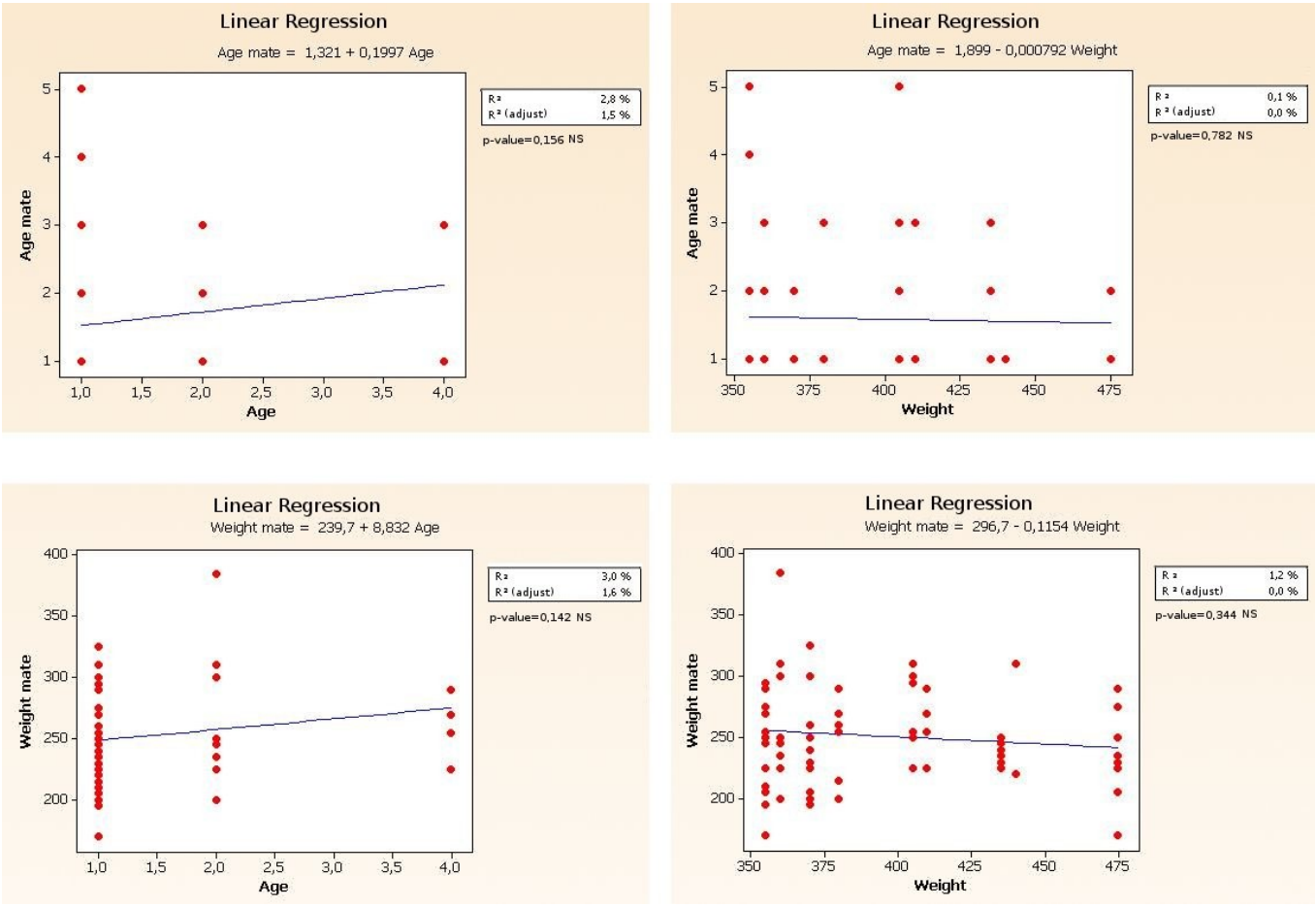


Fig.6: Correlation between the ages and weights of male Richardson's ground squirrels (12 males) and the ages and weights of their mates (75 females). The linear regression is represented by the blue lines. For each studied couple, the statistical package gives the regression equation, R^2 (proportion of variance of the observed response, which is explain by the factors) and R^2 adjusted and the p-value, which indicates the significance of the behaviour.

Effects of Body mass

Using males' weight during the mating season, I found light-weight males fed significantly more than heavier males (p-value=0,000) during the mating season (Table 5). Heavy males (body mass > 425g) were more often in high alert than lighter males (p-value=0,000) and they chased significantly more often (p-value=0,000) than other males. Heavier males had more recognitive and agonistic interactions than lighter males (p-value=0,000 and p-value=0,004). Finally, lighter males had significantly more females in the 20-m radius around them (p-value=0,000) than heavier males, whereas heavier males had more related females around them (p-value=0,035) than lighter males.
However, weight did not affect mating success of males Richardson's ground squirrels.

Which males mate with which females

Except for a suspected mating between a male and his cousin, no males mated with close genetic kin even though 9 males were known to have at least one living littermate sister, non-littermate sister, or mother.
Older males usually mated with older females and heavier females (p-value= 0,156 and p-value= 0,142), even though yearling females were lighter than older females the day of their estrus (Kruskall-Wallis; p-value=0,000). In contrast, lighter males underlying mated with heavier females and older females (p-value= 0,844 and p-value= 0,782) (Fig.6).

Discussion

For male Richardson's ground squirrels, the patterns of daily behaviours changed with season, adapted to feeding or mating needs, in agreement with the observations of Michener and McLean (k) on Richardson's ground squirrels (Table 2).

During the premating season, when females were starting to emerge from hibernation, males spent most of their time (40%) eating and they gained weight immediately after hibernation, whereas they lost weight during the mating season, when they expended a lot of energy. Because of the setting up and containmenting of their home range and their defence against other males, most of the remaining time in the premating season was divided between alerting and running patterns (30% and 15%) associated with interacting with males.

In the mating season, when all the females were emerged and in estrus, males spent less time feeding (30%) and running (11%), but more time in social interactions. Firstly, they investigated females with recognitive behaviours (2,5%), particularly nose to nose or nose to body sniffing with enables males to identify the females and determine their reproductive status. Because all males moved from their original home range, they mostly interacted with non-related individuals in the

Individual	Age	Weight	Date mating	Name of the mate	Age of the mate	Weight of the mate	Mating event
N	2	360	26/02/08	Lollipop	2	300	Sure
N	2	360	26/02/08	Arrow	1	385	Sure
Vertical Spots	1	440	26/02/08	Spot Lazy T	1	310	Sure
N	2	360	01/03/08	3 Spots	2	385	Sure
N	2	360	02/03/08	Angle	3	225	Suspected
A plus	1	435	02/03/08	Angle	3	225	Sure
A plus	1	435	02/03/08	Trough	1	240	Sure
8	1	355	03/03/08	11	2	275	Suspected
8	1	355	03/03/08	Trident	1	245	Sure
N	2	360	03/03/08	1	1	235	Suspected
Equal	1	370	03/03/08	H	2	325	Sure
D	1	475	03/03/08	11	2	275	Sure
Square U	4	410	03/03/08	Grass	1	255	Sure
M	1	380	04/03/08	Ppdr	1	270	Suspected
Square U	4	410	04/03/08	Ppdr	1	270	Suspected
Vertical Spots	1	440	04/03/08	Sq root	1	220	Sure
A plus	1	435	04/03/08	S	2	235	Sure
Equal	1	370	04/03/08	Infinity	1	250	Sure
3 lines	1	405	04/03/08	Cresent	3	310	Suspected
D	1	475	04/03/08	N	1	250	Suspected
3 lines	1	405	04/03/08	N	1	250	Suspected
Equal	1	370	05/03/08	Because	1	260	Sure
A plus	1	435	05/03/08	V	1	230	Sure
N	2	360	06/03/08	G	1	245	Suspected
3 lines	1	405	06/03/08	3	2	300	Sure
D	1	475	06/03/08	Y	1	225	Sure
A plus	1	435	06/03/08	G	1	245	Sure
D	1	475	06/03/08	Peace	1	230	Sure
A plus	1	435	07/03/08	Equal	2	250	Sure
8	1	355	07/03/08	Rectangle	5	295	Suspected
3 lines	1	405	07/03/08	F	1	255	Suspected
3 lines	1	405	07/03/08	Rectangle	5	295	Sure
Square U	4	410	07/03/08	C	3	225	Sure
8	1	355	07/03/08	S	1	270	Sure
3 lines	1	405	07/03/08	C	3	225	Suspected
D	1	475	07/03/08	Lazy S	1	235	Suspected
M	1	380	07/03/08	F	1	255	Sure
N	2	360	07/03/08	W	3	310	Sure
N	2	360	07/03/08	Lazy S	1	235	Sure
Equal	1	370	08/03/08	Staple	1	250	Sure
N	2	360	08/03/08	Staple	1	250	Suspected
3 lines	1	405	08/03/08	1	1	250	Sure
Square U	4	410	08/03/08	2 T	3	290	Suspected
8	1	355	08/03/08	Circle	1	245	Sure
M	1	380	08/03/08	2 T	3	290	Suspected
Equal	1	370	08/03/08	Vertical divide	2	300	Suspected
Square U	4	410	08/03/08	A	3	270	Suspected
Square A	1	355	08/03/08	Sigma	1	225	Sure
D	1	475	09/03/08	K	1	205	Suspected
Equal	1	370	09/03/08	E	1	240	Sure
3 lines	1	405	09/03/08	4	1	225	Sure
M	1	380	09/03/08	T		260	Sure
Equal	1	370	10/03/08	Heart	1	195	Sure
Equal	1	370	10/03/08	Dagger	1	205	Sure
M	1	380	10/03/08	Z	1	200	Sure
2 Spots	1	370	11/03/08	Small b	1	225	Suspected
M	1	380	11/03/08	One minus	1	215	Sure
Square A	1	355	11/03/08	Unhappy	1	210	Sure
4	1	355	11/03/08	Double divide	1	250	Suspected
4	1	355	11/03/08	Target	2	275	Sure
D	1	475	12/03/08	M	2	290	Sure
Square A	1	355	12/03/08	M	2	290	Suspected
Square A	1	355	12/03/08	Fast A	1	170	Suspected
D	1	475	12/03/08	Fast A	1	170	Suspected
2 Spots	1	370	12/03/08	Wing	2	250	Suspected
N	2	360	13/03/08	Wishbone	1	200	Sure
8	1	355	13/03/08	Bowtie	1	195	Suspected
8	1	355	13/03/08	Square U	1	205	Sure
Square A	1	355	14/03/08	6	2	270	Sure
4	1	355	15/03/08	2 Spots	1	205	Sure
Square A	1	355	16/03/08	10	1	255	Sure
Square A	1	355	17/03/08	13	4	290	Sure
2 Spots	1	370	19/03/08	Diamond	1	230	Sure
Equal	1	370	19/03/08	Wishbone	1	200	Suspected

Individual	Age	Weight	Number of mates
N	2	360	10
Vertical Spots	1	440	2
A plus	1	435	6
8	1	355	7
D	1	475	8
Equal	1	370	9
Square U	4	410	5
3 lines	1	405	8
2 Spots	1	370	3
4	1	355	3
M	1	380	6
Square A	1	355	7

Table 6: List of mating events each day and the total for each male, associated with the age and weight of males during the mating season and the age and weight of females during their estrus.

mating season. In this period, the distance between males and females decreased significantly and males were mostly surrounded by about one or two estrus females each day. But mating period was especially characterised by the increase in agonistic interactions between males, whose fighting (1,25%) and chasing (10%) to gain access to females, resulted in wounding and loss of weight. Finally, during the mating season, males increased time in high alert (21%) , scentmarking (0,2%) and calling (1,5%), which are characteristics of mate guarding behaviour. In fact, before mating, males marked their territories to prevent other males entering their home range, and once males had mated, they were mate calling to indicate they had mated and alerting to watch their mates and prevent other males mating with them.

During the postmating season, once all the females were mated, males primarily spent their time eating (70%) with very little time moving (3%). Consequently, social interactions were rare, except for being chased patterns by pregnant and lactating females, who becomed intolerant against adult males and defended their home range and litters burrow against all neighboring adults, so including males. But because this pattern was really lower than in mating season (2%), males were often surrounded by two or three females, some of whom were related to them. These changes in feeding and running budgets resulted in a quick and significant weight gain by all males, from <375 g in mid-March during the mating season to >450 g by early May.

As with many species of mammals, male Richardson's ground squirrels had a home range they defended more or less according to season and their reproductive and energetic needs. Before and after the mating season, the home ranges of males were quite small (about 900 m^2) and limited for their foraging needs. During the mating season, because the daily number of females in estrus was lower than the number of sexually mature males, home range area was significantly larger (about 2000 m^2) to increase their proximity to females and to be closest of the females who were in estrus each day. In addition to changes in home-range size, males also changed the location of their home range. After the mating season, most males resided in a home range which overlapped the ranges of related females, whereas they were never close to related females during the mating season. This use of space was especially noticeable in a yearling male, who was in a defined core area in the premating season, close to his female kin, who moved during the mating season and then came back close to his family after the mating season (Fig.4).

Social interactions were most frequent during the mating season (Table 3), with intra-sexual agonistic interactions, and inter-sexual recognitive interactions. During the mating season, males initiated interactions with females to know their identity and reproductive status, information essential to mating success. After the mating season, because the females defended their home range and litter burrows, inter-sexual interactions were primarily initiated by pregnant and lactating females and were agonistic in nature.

One component of competitive mate searching is acquiring advance information about females' reproductive status and location, which then is used to assign priorities for seeking a particular female at competitively profitable times in the future (t). To have the highest mating success, males increase the frequencies of their social and recognitive interactions and alertness, but decreased the frequencies of their personal care. First, I observed that males who had the highest daily mating success spent less time eating than the other (Table 4). In contrary, they spent more time having social interactions. To have the highest mating success, males spent more time recognizing their future mates, knowing their reproductive status in sniffing or doing nose to nose contacts, and maintaining the closest proximity with the females who were in estrus, so decreasing the time spent in their personal care. Moreover these intersexual interactions, males spent more time having intrasexual interactions, especially agonistic interactions with the other males. In fact, to guard their mates, the most successful males spent more time chasing their contestants than the other males. Finally, they spent significantly more time watching attentively around their home range, preventing other males to approach their mates and preventing their mates to mate with other males. These differences in the behavioural patterns were characteristic of the trade-off concept, whereby males spent more energy in mate guarding and guaranteed their paternity or kept and gained energy and improved their own survival.

In addition to these behavioural effects, oldest males had a higher mating success than the youngest males and usually mated with oldest females, thus lightest males had a higher mating success than the heaviest and usually mated with heaviest females (Table 5). But the paternity of litters of Richardson's ground squirrels will be confirmed from electrophoretic data, which will give the real mating success for each observed male and could confirm or invalidate our first analysis of mating success.

In opposition to male European ground squirrels (d) , we found a considerable collecting grass behaviour in all males during the postmating period, but without digging behaviour. These data could indicated that collecting grass pattern represented paternal effort, but the abscence of digging at litter burrows invalidated this prediction. Moreover, the collecting grass behaviour was underlying more observed when the weather was cloudy, windy and cold or with snow (p-value=0,317), indicated probably that burrow maintenance pattern in males Richardson's ground squirrels was just a personal care.

Finally, in addition to the knowledge about the variations in the male behaviours according to the seasons, I can now appreciate that the daily behaviours during the mating season have an effect on the mating success of each male Richardson's ground squirrels. By feeding less and interacting more, they optimised their chance to mate, notably with the oldest females for the old males and with the heaviest females for the light-weight males.

Acknowledgements

I thank Dr. G. Michener and the University of Lethbridge for receiving me for this internship. I thank N. Magyara and C. Ovens for their friendship, their help and for driving me to the study site. I thank the Jarman family for their hospitality. And finally, I thank all the Richardson's ground squirrels for their voluntary participation in my research and giving me my data.

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Time and Activity Budgets and Mating Success of male Richardson's ground squirrels

Key words: Richardson's ground squirrels, Seasonal Changes, Activity Budgets, Use of Space, Mating Behaviour, Mating Success

Abstract

Richardson's ground squirrels (*Spermophilus richardsonii*) are obligate hibernators, that adjust their behaviours according to the feeding, mating or hibernating needs. Activity budgets, use of space and social interactions of adult males were studied in relation to season and mating success. Before the mating season, males spent the most of their time eating and etablishing their home ranges. During the mating season, they increased their home range to be closer to estrus females, spending more time in social interactions, which were agonistic between males and recognitive with females, and less time eating. Moreover, higher mating success was observed in males that spent less time eating, more time interacting with females, chasing other males and being alert, and surrounded by the highest number of females. After the mating season, adult males spent most of their time feeding to prepare for immergence and they were often chased by pregnant and lactating females. Some males returned to their original home range where their female kin were located.