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Time Budgets, Social Interactions and Age/Sex Differences in Eurasian Beavers (*Castor fiber*)

Running Headline
Time Budgets & Social Interactions in Eurasian Beavers by Lisa Wallis.

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Data was collected from May till September 2006 by members of the field team (including - Rita Gonçalves, Magnhild Snaprud, Ruairidh Campbell, Claire Buchanan, Leigh Murray, Karin Widerin and Elisabeth Mølmen). This report uses only the 2006 field data, which was collected by the author and researchers mentioned above. Researchers worked in teams on a nightly basis, and all data collected were shared between all members to allow each individual to carry out their own research topics.'

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ABSTRACT

The Eurasian beaver, *Castor fiber*, is one of the few obligate monogamous cooperatively breeding mammal species known, and very little research on time budgets of males and females and age classes has been carried out. I investigated whether Eurasian beavers would display sex and/or age differences in time budgets and social interactions. Using radiotracking and lodge watching I obtained behavioural data on 13 adults and seven yearlings; comprising 11 males and nine females, and five kits, (unsexed) during 2006 on the Sauar River in southeast Norway. Time budgets and social interactions were compared in territories where kits were present during the study period, and where they were absent, and any effects of colony size were also examined. Finally a comparison of the two observation methods was conducted. The three main behaviours of sex and age groups were swimming, foraging/eating and time spent in the lodge. Social interactions accounted for 1.4, 7.3 and 11.3% (adults, yearlings and kits); 2.6 and 4.0% (male and female) of overall time budgets. I found no sex differences in time budgets or interaction rates. These results suggest that care of offspring by both sexes is essential to the successful rearing of young, leading to reduced behavioural sexual dimorphism. Age had the most significant effect on time budgets and social interactions. Principle activity period, time in the lodge, eat, alert, and static behaviours all varied between adults, yearlings and kits. Yearlings were found to play a large role in care of siblings. Kit presence and colony size had a significant effect on time spent in interactions. The overall rate of interaction decreased with increasing age, reflecting an increasing independence with age. Most interactions observed involved social bonding; supporting the idea that beavers are more social and less aggressive within family groups. Adult animals were considered dominant, and an age class dominance hierarchy exists in this population. A sex class based hierarchy is suggested when examining only afilliative behaviour. Both radio tracking and lodge watching produced similar results in time budgets overall. Lodge watching has the advantage of being able to record data on more than one individual a night, and therefore has greater potential when comparing age and sex groups.

INTRODUCTION

The Rodent family provides an excellent opportunity to study evolutionary paths towards sociality as they occupy a range of social organisations (Armitage 1981 and 1999, and Ebensperger 2001). Cooperative breeding has been documented within the order Rodentia in 35 species from nine of 30 families (Soloman and Getz 1997). Some species are solitary with both sexes dispersing as juveniles, such as woodchucks (Grizzell 1955), Richardson's ground squirrels (Michener 1983), and Patagonian tuco-tucos (Lacey et al 1998). At the other end of the sociality scale lie species such as alpine marmots, black-tailed prairie dogs, and prairie voles, which live in family groups containing a dominant male and female plus offspring from one or more years, (King 1955; Barash 1989).

The genus Castor consists of the North American beaver, *C. Canadensis* and the European beaver *C. fiber*. Beavers are large, nocturnal semi-aquatic herbivorous rodents (Busher 1983; Buech 1995), which display a singular obligate monogamous mating system with parental care (Kleiman 1977; Komers and Brotherton 1997). Beavers live in family groups consisting of a dominant mated pair which breed exclusively, one to four yearlings, and one to four kits. Two-year-old offspring may or may not be present, (Wilsson 1971; Busher 1983). Beavers are cooperative breeders and are extremely territorial. All family members participate in raising the kits of the year directly - through provisioning and babysitting, and indirectly - through vigilance and patrolling behaviour (Brady and Svendsen 1981). They defend their territory by scent marking (Rosell and Nolet 1997; Rosell et al 1998), and aggressive encounters between groups do occur (Rosell and Nolet 1997). In monogamous mammals levels of investment in male parental care are likely to be higher than in other mating systems. Therefore a change in time allocation in regards to time and energy spent on activities and behaviours associated with reproduction and self-maintenance may be expected. Subordinate members of family groups may also display changes in time allocation in cooperative breeding species. Time budget analysis is used to determine how individuals or groups allocate their time to certain behaviours, and whether allocation varies within or between groups (Sharpe and Rosell 2003). Evidence exists for different roles and time budgets for each sex and/or age group of the beaver, (Brady and Svendsen 1981; Busher and Jenkins 1985; Buech 1995; Sharpe and Rosell 2003). Most of these studies have been carried out on N. American beavers, which have a chromosomal difference of eight chromosomes, which may be reflected in a difference in behaviour between the two species. Much of the previous work on beaver time budgets and interactions has been based on anecdotal observations (Hodgdon and Larson 1973; Brady and Svendsen 1981; Hodgdon and Lancia 1983) and has been more descriptive in nature, with little to no quantitative data on social behaviour of beaver populations in N. America and Europe. At present no other studies have addressed the issue of division of labour within age groups, and degree of sociality in the Eurasian beaver. Maintenance of sociality requires a minimum amount of inter-individual communication within a group. Communication is achieved through direct means (encounters), and by indirect means (vocalisations and scent marking). Intragroup interactions may reinforce social cohesion. Family members would therefore be expected to modify their movement patterns to bring about these encounters. When defining social groups and describing social dynamics, all interactions should be examined (whether positive, tolerant or negative in consequence). Macdonald et al 1987 identified a hierarchy of questions to quantify sociality. These questions were formulated to examine cat social dynamics, (but can be applied to any animal society) and involve quantifying proximity, association, interaction rate per unit time, type and quality of interaction, and direction of flow from initiator to recipient for each type of interaction. Interactions include agonistic and non-agonistic behaviours that may determine social position, dominance, and hierarchy relations between individuals within social groups. Dominance hierarchies in beavers have been suggested with conflicting results - Busher 1983, Tevis 1950, Schramm 1968, and Brady and Svendsen 1981, reported an age class hierarchy, while Hodgson and Larson 1973 found a sex and age class hierarchy, using an approach avoidance analysis. They found the adult female to be the central figure in their study colony, and the most dominant member.

By investigating division of labour and sociality within family groups, the present study aims to:

- Test whether the time budgets of adult's yearlings and kits, as well as males and females differed over their principle activity period, to establish whether the evolution of monogamy has resulted in reduced behavioural dimorphism in the adult Eurasian beaver, and also whether yearlings showed alloparenting behaviour.
- Look at colony size and composition to determine whether they affected time budgets and interaction rates.
- Quantify beaver sociality and examine dominance hierarchies within family groups.
- Compare two commonly used observation techniques to establish their relative merits in calculating time budgets.

METHODS

Study Area

We collected data from Eurasian beaver territories along the Sauar River (near Akkerhaugen) in Telemark County, south-eastern Norway, during summer 2006 from 14 May to 24 August. The river flows through a semi-agricultural landscape and mixed woodland, consisting of riparian woodland dominated by grey alder (*Alnus incana*), willow (*Salix sp.*), and bird cherry (*Prunus padus*), birch (*Betula sp*.) and Norway spruce (*Picea abies*), and also some dry deciduous and coniferous forest. (Campbell et al 2005). The Sauar River discharges into Lake Nordsjø and the study was carried out on sequential territories along approximately 15.3 km of the river upstream from the Lake. Beaver densities in the region have stayed relatively stable since the 1970s, after the area was repopulated in the 20s, (Olstad 1937). Predation on beavers was extremely low due to the absence of their main predator, (the wolf, *Canis lupus*) however lynx can be found in the study area but were scarce. Hunting pressures were also low during the study period. There were no beaver dams in the study sites. All rivers were large enough to make damming either difficult or unnecessary.

Study Animals

Between 9 May and 30 August 2006, 22 beavers from seven territories were trapped by Telemark University College staff in Patmos River, from boats using a land-net (Rosell and Hovde 2001). Of these, six were adult males, five were adult females, five were yearling males, two were yearling females, and four were kits.

Licences for the capture, and handling of beavers were granted by the Norwegian Experimental Animal Board and the Norwegian Directorate for Nature Management. Age classes (kit, yearling and adult) were assigned to beavers according to body size and weight, (Rosell and Pedersen 1999; Parker et al 2001). Dominant individuals were assessed according to previous trapping records of weights, evidence of lactation (nipple size) and behavioural observations, (see Sharpe and Rosell 2003; Herr and Rosell 2004). Some territories only contained one adult male and female.

Beavers were quickly transferred into a sack where they remained throughout the procedure; no animals reacted aggressively to their confinement. All individuals were tagged with numbered coloured plastic eartags (3.5cm, Dalton Continental B.V., Lichtenvoorde, The Netherlands), and/or metal/coloured eartags (1.5cm, National Band and Tag Co., Newport, Kentucky, U.S.A). Beavers were sexed by the colour of the anal gland secretion, in males it is yellowish and watery, and in females, gray and extremely sticky, (Rosell and Sun 1999, Rosell and Bjorkoyli 2002), weighted and measured, and implanted with a microchip (1cm, Destron 490, Villaume Ave, St. Paul, Minnesota, USA) to enable identification if tags were lost. The occurrence and number of tail scars were also noted.

The 11 adult beavers from 7 territories in Patmos River were all were fitted with external tail transmitters, (Advanced Telemetry System, Isanti, Minnesota, USA, Model 16M eartag for beaver tail, weight 38g) at the beginning of the study . A small hole (5 mm) was made in the tail using belt pliers (10cm from the base of tail and 3.1 – 2.4cm from the lateral edge). The transmitter was attached with a screw, washer and nut. A freeze spray was applied to numb the area. Beaver’s tails are composed mainly of adipose tissue, so the use of anaesthetic was deemed unnecessary. The technique used has been perfected over a number of years at Telemark, and is the only know reliable method of radio tag attachment in beavers (Rothmeyer 2002). This method is proven to cause little distress and no long term harm. Handling times were kept to a minimum (20 minutes), and all beavers were observed to commence normal activity less than 10 minutes later. Transmitters were removed at the end of the study. We collected data on an additional two adult females, (which were not trapped) in two different territories, increasing the adult sample size to 13. The presence of one other kit increased the total number of kits observed to five, and the overall sample size to 25 (13 adults, 7 yearlings, and 5 kits). Wherever possible both the dominant male and female in each territory was trapped and tagged; this resulted in four territories with both male and female, two territories with the dominant male, and one territory with the dominant female radio tagged.

Beavers are nocturnal, live in lodges and/or underground burrows, and spend much time foraging inland out of sight. Radio tracking was required to relocate the animal and ensure accurate data collection. Exact location fixes of individuals within their territory was not necessary for this study, however radio tracking was carried out as part of a wider study which required these data.

Based on nipple size, weight, recordings of sounds of kits in the lodge, or the provisioning of food into the lodge during July and August, (Wilsson 1971) we assumed all dominant females had given birth during the 2006 field season.

Data Collection

Radio Tracking (RT)

Several two-person teams of recorder and observer/boat driver collected radio-tracking data on Patmos River from 15 May to 24 August 2006. Resulting in an average of 3.1 nights observation (range one to five), equally divided between male and female beavers. Beavers were tracked from boats with an outboard motor. Radio tracking equipment was used to locate animals, (handheld RX-98H tracking receiver with in-built foldable antenna – TVP Positioning AB, Linsberg, Sweden) with a signal range of 353 ± 112m from the boat. We tracked members of a dominant pair on successive nights where possible, to reduce the effects of behaviour and weather conditions; the first to be tracked was determined by flipping a coin.

Beavers generally have only one period of activity per night, (Wilsson 1971; Nolet and Rosell 1994) known as the "principle activity period" (Corp et al 1997). If possible we located the focal animal before it emerged from its daytime resting place, and started recording when the animal commenced its nightly activity. Recording ended when it entered the lodge or burrow for the final time before day at the end of its activity period, (Sharpe and Rosell 2003). Observers waited for twenty to thirty minutes after the beaver entered the lodge in the morning to ensure that the beaver had ended activity for the night. During the short period of darkness in the Norwegian Summer time, we used spotlights to illuminate individuals. The noise and presence of the motorboat, and use of spotlights, appeared to have a minimal effect on the beaver's behaviour (Nolet and Rosell 1994; personal observation). All rivers experienced relatively heavy boat traffic during the day and part of the night, which could have helped to habituate beavers to boat presence. We used binoculars to assist in beaver identification and behavioural observation. Animals often disappeared from view, and radio equipment was used to relocate their positions (Harris et al 1990).

We used continuous focal animal sampling throughout each observation session, and classified behaviour into eight categories, (Altman 1974; Martin and Bateson 1999) Table 1. When the focal animal went out of sight, it was marked as OS, and telemetry equipment was used to locate its position every 15 minutes, until the beaver came into sight again, and continuous behavioural recording was resumed. Data were recorded on a prepared check sheet; including timings of activity change using a stop clock, and ad-lib interactions with other family members when occurred. Behavioural interactions were recorded when two or more individuals were in physical contact, or when a detectable reaction of one beaver to another was noted. Where possible the initiator and receiver were identified, and when unknown the interaction was marked as neutral (Busher 1983). Interactions were divided into nine different categories which are outlined in Table 2.

Behaviour category	Description
In Lodge	Diving into lodge, radio tracking equipment indicates animal is within the lodge, or is out of sight but thought to be in the lodge
Swim/move	All activities which include movement in the water and on land
Eat	Eating food, on the bank, on land or in the water
Forage	Foraging on land or diving for aquatics
Dive	Diving underwater whilst swimming or from land, and resurfacing
Alert	Static in water, on the bank, or on land in a state of alertness, often sniffing the air
Groom	Grooming own fur
Still	Standing, or sitting on the bank or in land, not visibly alert
Interaction	Detectable reaction of an individual to another’s presence or, or direct contact between one or more individuals

Table 1 Categories and description of Eurasian beaver behaviour

Interaction category	Description
Caravanning	Two or more beavers swim in the same direction within 10 m of each other. Sometimes diving for short periods together or splashing in water.
Eat / Forage Int	Beavers eat at the same branch, attempt to secure food (including food begging), or enter on land to forage together (within 10 m)
Recognition	Nosing, or greeting behaviour, nasal to nasal contact
Mutual Groom	Two or more family members groom each other
Social Play	Jumping splashing "frolicking" around other family members
Wrestling	Two animals approach each other in water/on the bank and push their noses/cheeks together often circling one another (like a dance), occasionally using fore legs to swipe at each other. Vocalisations are often heard during wrestling
Vocalisation	Any audible noise produced by animals when in contact with each other
Attempted Int.	Animal approaches another family member, and is ignored
Avoid/Ignore	Focal animal ignores or avoids another approaching beaver, often observed during eating interactions

Table 2 Interaction Categories and description of Eurasian beaver behaviour

Nearest neighbour was recorded when another animal was within 10m of the focal animal, (measured using beaver lengths). Individual family members were identified from unique coloured ear tags. When identification was not possible, the age class status was first used, (adult, yearling, kit) or "unknown" where the age of the animals was not known.

Lodge Watching (LW)

All members of the field team collected data from lodge watches from 3 July to 23 August 2006, producing an average of 3.7 nights of behavioural observation per beaver, (range two to seven), divided between the seven territories. Lodge watching was carried out by one or two individuals from boats situated in the middle of the river. From this position it was possible to view a large part of the territory upstream and downstream from the lodge. Lodge watches were carried out using the same procedure as radio tracking, but rather than following one focal individual, the activity of all individuals (adults, yearlings and kits) within a territory was noted simultaneously using focal subgroup sampling, (Altman, 1974). Where two lodges were utilised, we positioned ourselves so that both were in sight. Boats were equipped with oars and/or motor so that repositioning was possible. The boat was anchored approximately 20 – 30m away from the lodge. When two people were present one recorded information, and the other observed exclusively. If a beaver's location and activity was unknown, this was entered into the data sheet as out of sight, position unknown. Recording started at the beginning of the beaver's principle activity period, and ceased when all members of the territory returned to the lodge after their nightly activity. Once kits were observed, extra night's observations were carried out in that territory. On a number of occasions we followed kits and/or adults to foraging/feeding areas away from the lodge to enable additional data collection. Lodge watches were carried out on all territories where one or more of the adults were radio tracked, producing both radio tracking and lodge watching data for some adult individuals (N=10).

Data Reduction

I chose to use a one minute resolution time to try and reduce bias when observations were not continuous. For example, if during lodge watching, animal A was observed at 2200 eating, then not seen again till 0300, as the length of the activity was not known I reported eating as lasting one minute, and the animal out of sight for the remaining time till it was observed again. We recorded behavioural timings to the nearest minute. At times behaviours occurred in rapid sequence and when this occurred I divided the minute into equal sections depending on the total number of behaviours observed. All behaviours were recorded in sequence, and each separate occurrence of behaviour was noted to obtain true frequencies. Total time spent in each behavioural category was summed, and total active minutes calculated for each individual. The time spent in each category was also calculated as a percentage of the total time spent active per individual per night.

Statistical Methods

Assumptions about continuity, normality and homogeneity were not met due to small sample sizes (Dytham 1999) therefore non parametric tests were used. All statistics were carried out in Minitab version 14.1 (Minitab Inc. 2003) and Past 1.65 (Hammer et al 2001) and all tests were two tailed with a significance level of 0.05.

Comparison of Lodge Watching (LW) and Radio Tracking (RT) Time Budget Data

To test for homogeneity between the two data collection methods, radio tracking and lodge watching, I used a repeated measures design and the Wilcoxon signed-ranks test. I found some differences between the two sets of data, however these difference would not unduly effect overall time budgets in adult beavers, and so the decision to combine both LW and RT data was made. Yearling and kit time budgets were calculated from lodge watch information only.

Principle Activity Period (PAP) and Time Spent in Lodge

The mean principle activity period, (time from emergence from lodge/burrow to completion of nightly activity around dawn, and return to lodge/burrow) was calculated for each beaver, (minute's active per night).

Time in Lodge was calculated and presented separately as the mean percentage of total time spent in the lodge during the principle activity period (or PAP).

I examined differences between the sexes in adults and yearlings, and territories where kits present/absent (excluding kits themselves), using the Mann-Whitney U test. I performed Kruskal-Wallis tests to investigate interactions between PAP and percentage time in lodge, age, and number of adults/yearlings in territory, (excluding kits).

Time Budgets

The Mann-Whitney U Test was carried out to determine any effects of sex and kit presence/absence, (only adult and yearling medians were taken into account). I performed the Kruskal-Wallis test to investigate any differences between percentage time in activity and age, (adult, yearling and kit), and the number of animals in the territory. Territories with two adults were compared with territories with three animals, (two adults and a yearling) and four animals, (two adults and two yearlings).

Interaction Rate (IR) and Duration (ID)

To obtain standardised interaction rates, I used the following calculation –

$$\frac{\text{Total Frequency of Interactions per beaver}}{\text{Total hours spent active (in sight) overall}}$$

Periods of unknown behaviour were discarded, including time in the lodge, as although interactions occur here, once in the lodge, the animal is out of sight of the observer. The IR is a measure of the mean frequency of interactions per active hour per beaver. The interaction duration is a measure of the mean duration (minutes) of interactions per active hour.

I examined differences between the types of interactions using the Kruskal-Wallis test. Most interactions were of short duration (events) and therefore IR was suitable to compare between conditions.

Comparison of Agonistic and social bonding Interaction Rates

Agonistic and amicable interaction rates can provide insights into the extent of sociality in a population. I combined wrestling, avoid and ignore interactions to produce one figure for agonistic interaction rates. Recognition, caravanning, eat/forage interaction, mutual groom and social play interactions were combined to produce a single figure for social bonding interaction rates. I used the Wilcoxon signed-ranks test to determine whether agonistic and social bonding IR different in each age class. I also obtained the sociality Index by subtracting dominance interactions from social Interactions.

Comparison of Interaction Duration (ID) and Nearest Neighbour Duration

Nearest neighbour was recorded when another animal was within 10m of the focal animal, (measured using beaver lengths). Nearest neighbour duration was calculated by –

$$\frac{\text{Total duration nearest neighbour per beaver}}{\text{Total number of hours the animal was “in sight”}}$$

The nearest neighbour duration is a measure of the amount of time the focal beaver was near another beaver per active hour. Interaction duration and nearest neighbour duration are compared by age using Kruskal-Wallis tests, as well as sex using Mann-Whitney U Tests. I used the Wilcoxon signed-ranks test to determine whether interaction and nearest neighbour duration different in each age class.

Interaction Initiation and Receiving Rate

For all interactions where the initiator was known, the mean initiation and receive frequency was calculated for adult males, adult females, yearling males, yearling females, and kits. One way to look at dominance is to analyse dominance in terms of social bonding (De Waal 1986; Macdonald et al 1987; Natoli et al 2001). Kerby and Macdonald 1988 suggested it may be possible to identify the dominant animal as the one receiving the greatest amount of amicable behaviour. I assumed that individuals with high numbers of initiated interactions were subordinate, and individuals with high numbers of received interactions were dominant. The difference between the initiated and received interactions can give an indication to the position of the animal in the hierarchy if one does indeed exist. I used the Wilcoxon signed-ranks test to determine whether initiation and receive rate different in each age class. A social rank hierarchy is suggested on the basis of the amount of affiliative behaviour received.

RESULTS

Comparison of Lodge Watching (LW) and Radio Tracking (RT) Time Budget Data

The percentage time the adult focal animal was in sight during the principle activity period varied greatly in radio tracking and lodge watching sessions, (Median ± IQR % time in sight: RT = 39.97 ± 44.06; LW = 5.40 ± 26.03; Wilcoxon signed-ranks test: T = 49, N = 20, P = 0.028). Therefore I tested for homogeneity between the two data collection methods, using the Wilcoxon signed-ranks test.

Test	**Data collection**	**Median**	**IQR**	**W**	**P**
Interaction	RT	1.50	2.50	18	1.000
	LW	0.00	7.25		
Swim	RT	45.50	12.00	34	0.508
	LW	46.00	51.25		
Eat	RT	36.00	9.50	33	0.574
	LW	27.00	41.50		
Forage	RT	5.50	7.25	29.5	0.838
	LW	6.00	9.50		
Dive	RT	2.50	2.25	45	0.007 *
	LW	0.00	1.00		
Alert	RT	4.00	4.50	41.5	0.002 *
	LW	0.50	3.00		
Groom	RT	1.00	4.00	25.5	0.720
	LW	0.50	1.25		
Still	RT	1.00	3.25	15	0.340
	LW	0.00	1.25		

Table 3 Results from Wilcoxon signed-ranks test. Percentage time spent in each activity compared between radio tracked adult beavers when RT and LW. N=10. *P = 0.005

Radio tracking data differed from lodge watching data in dive and alert behaviours, (Dive: P = 0.007; Alert: P = 0.002). Therefore we can assume that by following the animals when radio tracking we influence their behaviour, and cause them to be more vigilant. These behaviour constitute a very small proportion of beaver behaviour overall. I decided on this basis to pool LW and RT time budget data, enabling the comparison of all age and sex groups.

Principle Activity Period

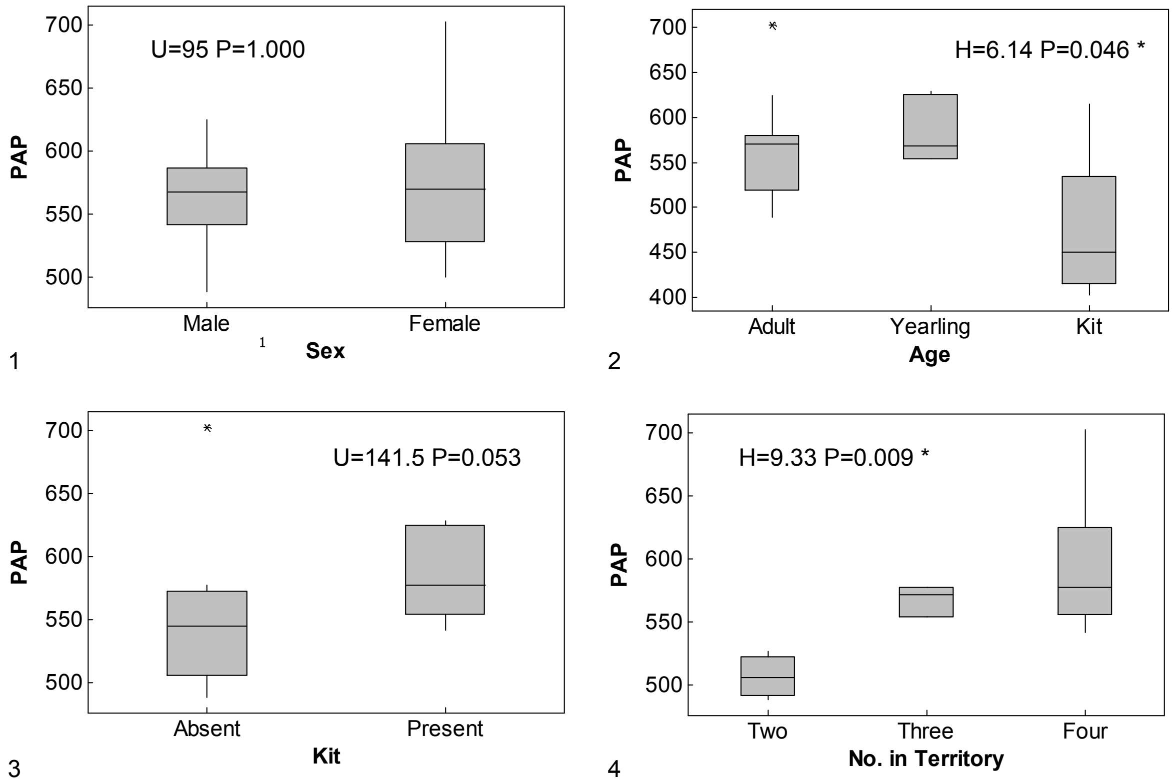

Figure 1 Median (Interquartile range) lengths of PAP (min) (1) Sex - All males and females excluding kits, males (n=11), females (n=9). (2) Age - adult (n=13), yearlings (n=7), kits (n=5). (3) Territories where kits are present/absent, present (n=11), absent (n=9), with kits excluded from the analysis. (4) Number of beavers in territory, two (adults), three (adults and one yearling), and four (adults and two yearlings) all with kits excluded. Two (n=4), three (n=3), four (n=13). * $P < 0.05$.

Males and females did not differ in length of principle activity period, (figure 1.1). Male and female beavers were active over an average 9.5 hours a night. However adults, yearlings, and kits showed significantly different lengths of PAP, (Kruskal Wallis test: $H = 6.14$, $P = 0.046$). Kits showed the shortest period of activity (7 hours and 12 minutes). Differences in length of PAP when kits were present and absent approached statistical significance, (Man Whitney U test: $P = 0.053$). Territories where kits have emerged had longer periods of activity than where kits were still in the lodge (refer to figure 1.3). The number of adults and yearlings present in a territory significantly influences the length of activity, (Kruskal Wallis test: H =

9.33, P = 0.009). When only two animals are present, individuals show a reduced principle activity period, (refer to figure 1.4)

Time Spent in Lodge

Males and females remained in the lodge for equal intervals during the principle activity period, (Figure 2.1) Adults, yearlings and kits showed significantly different percentage time spent in the lodge, (Kruskal Wallis test: H = 8.84, P = 0.012). Kits remained in the lodge for longer periods (25% of activity budget) followed by adults and then yearlings, (refer to Figure 2.2). There is a lot of variation within the kit samples which is due to differing ages of the subjects. As kits got older they stayed out of the lodge for longer periods of time.

Time spent in the lodge by adults and yearlings in territories where kits were present did not differ significantly from territories where kits were absent. The number of animals in the territory did not affect the time spent in the lodge. However considerable variation between individuals could have influenced the results.

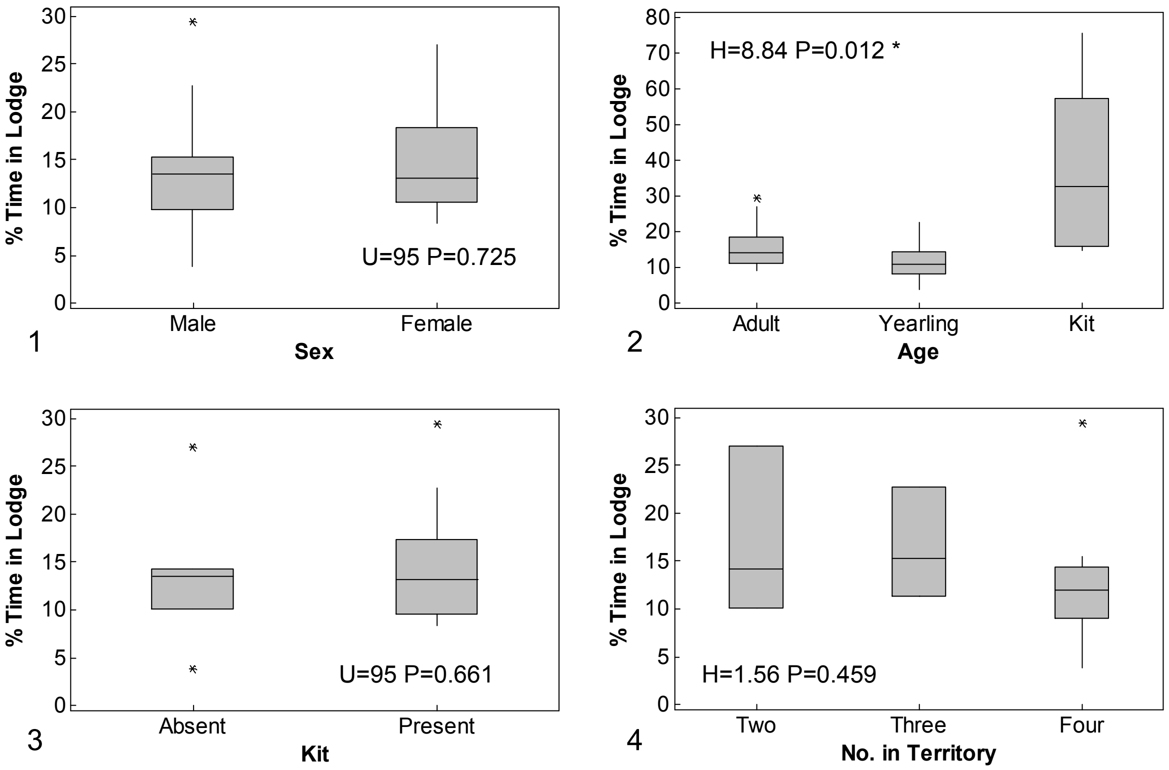

Figure 2 Median (IQR) % time spent in the lodge during PAP (1) Sex - All males and females (excluding kits), males (n=11), females (n=6). (2) Age - adult (n=10), yearlings (n=7), kits (n=5). (3) Territories where kits are present/absent, (present (n=10), absent (n=7), with kits excluded from the analysis. (4) Number of beavers in territory, two (adults), three (adults and one yearling), and four (adults and two yearlings) all with kits excluded. Two (n=3), three (n=3), four (n=11). * P < 0.05.

Time Budgets (Please refer to Table 4)

The dominant behaviours of beavers during the principle activity period were time spent in the lodge, swimming/moving, eating and foraging, accounting for 92.3% of behaviours in males, and 89.8% of behaviours in females. No significant sex differences in time budgets were found (Table 4) Females spent a greater percent of their time budget interacting than males (4.1 and 3.0 %). Males spent longer foraging and in alert behaviours than females, females spent more time in self groom and in static behaviours than males. However these differences were all very minor, (refer to Table 4).

	Sex		Mann-Whitney U Test	Age			Kruskal Wallis Test	Kits		Mann-Whitney U Test	No. Animals in Territory			Kruskal Wallis Test
Behaviour	**Male**	**Female**	**P**	**Adult**	**Yearling**	**Kit**	**P**	**Present**	**Absent**	**P**	**Two**	**Three**	**Four**	**P**
Inter-action	2.979 ± 7.400	4.128 ± 7.180	1.000	1.536 ± 4.046	7.739 ± 9.810	14.635 ± 27.470	0.002 *	7.162 ± 5.430	1.450 ± 4.216	0.025 *	0.257 ± 1.216	5.368 ± 3.630	4.304 ± 7.120	0.019 *
Swim/ Move	47.059 ± 14.290	43.572 ± 14.23	1.000	43.572 ± 17.810	43.704 ± 9.080	47.512 ± 27.770	0.997	41.101 ± 13.200	47.059 ± 18.060	0.820	50.469 ± 26.63	41.101 ± 9.91	43.704 ± 14.070	0.790
Eat	38.596 ± 9.940	33.452 ± 8.910	0.820	33.452 ± 9.81	34.945 ± 14.820	19.361 ± 11.980	0.010 *	33.452 ± 12.100	37.904 ± 10.110	0.761	31.644 ± 20.450	32.874 ± 10.390	37.904 ± 11.140	0.676
Forage	6.599 ± 6.220	2.964 ± 8.430	0.402	6.798 ± 6.97	4.120 ± 6.60	6.766 ± 5.80	0.425	6.599 ± 5.120	2.964 ± 10.420	0.303	10.417 ± 13.800	9.239 ± 5.340	3.832 ± 6.807	0.286
Dive	2.145 ± 1.446	1.294 ± 2.281	0.569	2.076 ± 1.837	1.681 ± 2.631	2.277 ± 2.344	0.892	1.358 ± 1.765	2.076 ± 2.047	0.425	2.858 ± 3.027	2.145 ± 2.656	1.681 ± 1.604	0.403
Alert	1.961 ± 5.302	1.630 ± 3.643	0.447	2.716 ± 4.137	1.350 ± 4.620	0.000 ± 0.591	0.017 *	2.716 ± 3.785	1.754 ± 4.572	0.543	1.022 ± 3.125	4.649 ± 5.450	1.961 ± 4.544	0.518
Groom	0.569 ± 2.541	2.091 ± 4.660	0.341	2.091 ± 3.573	0.284 ± 0.569	0.915 ± 2.229	0.064	0.596 ± 2.254	0.644 ± 7.050	0.542	5.322 ± 10.230	0.596 ± 1.132	0.579 ± 2.820	0.470
Still/sit	1.200 ± 3.697	1.493 ± 7.510	0.594	2.445 ± 7.510	0.710 ± 1.269	5.729 ± 7.500	0.045 *	1.200 ± 2.189	2.445 ± 8.420	0.704	0.347 ± 6.170	1.493 ± 0.648	2.445 ± 7.130	0.676

Table 4 Median and IQR percentage time spent on behaviour categories between sex - all males and females (excluding kits), males (n=11), females (n=6), adults, yearlings and kits, adults (n=13) yearlings (n=7) kits (n=5), kits present and when absent, present (n=11) absent (n=9) with kits excluded from the analysis, and territories with two (adults), three (adults and one yearling), and four (adults and two yearlings) two (n=4), three (n=3), four (n=13). Collated total number of nights observed; all males=61; all females=43; adults=75; yearlings=29; kits=18; present=75; absent=29; two =13; three=31; four=60.* $P < 0.05$

The most influential effect on time budgets was age. Time spent in the lodge, swimming/moving, eating and foraging, accounted for 89.0% of behaviours in adults, 88.9% of behaviours yearlings, and 81.8% of behaviours in kits. Percentage time spent in Interaction was significantly different in the three age groups (Kruskal Wallis test: H = 12.62, P = 0.002, Table 4). Percentage time spent in interactions decreased with increasing age, with kits spending approximately eight times more time in interactions than adults, (adults 1.4%, yearlings 7.3%, and kits 11.3%).

Time spent eating also varied significantly across age groups, (Kruskal Wallis test: H = 9.17, P = 0.010, Table 4). Kits spent less time eating than adults or yearlings.

Age also affected percentage time alert, (Kruskal Wallis test: H = 8.08, P = 0.018 Table 4). Percentage time alert shows a positive correlation with increasing age. Adults were most vigilant, followed by yearlings, with kits showing little to no time alert.

The percentage time spent static varied significantly across the age groups, (Kruskal Wallis test: H = 6.19, P = 0.045, Table 4) with yearlings spending less time in this behaviour than adults or kits.

Percentage time spent grooming approached statistical significance across age groups, (Kruskal Wallis test: H = 6.19, P = 0.045, Table 4). Adults spent more time in self grooming than either yearlings or kits. Yearling spent less time foraging than adults, but more time eating.

Kit presence/absence had a significant effect on time spent in interactions, (Mann-Whitney U test: U = 145.5, P = 0.025, Table 4). Territories with kits showed a greater percentage time spent interacting. Territories where kits were absent spent more time in swimming, grooming, and static behaviours than territories with kits.

The number of animals in the territory significantly affected the percentage of time spent interacting, (Kruskal Wallis test: H = 5.44, P = 0.019, Table 4). Territories which contained only two adults displayed less time in interactions, than territories with three or four individuals.

Adult males and females showed very little behavioural differences in time budgets. Adult males spend more time foraging than all others apart from kits, and also displayed the most time in alert behaviours. I was not able to compare male and female yearlings statistically due to small sample size in the females. From the results yearling females spend more time interacting and grooming than males, and yearling males spend more time eating and foraging.

Interaction Rate (IR)

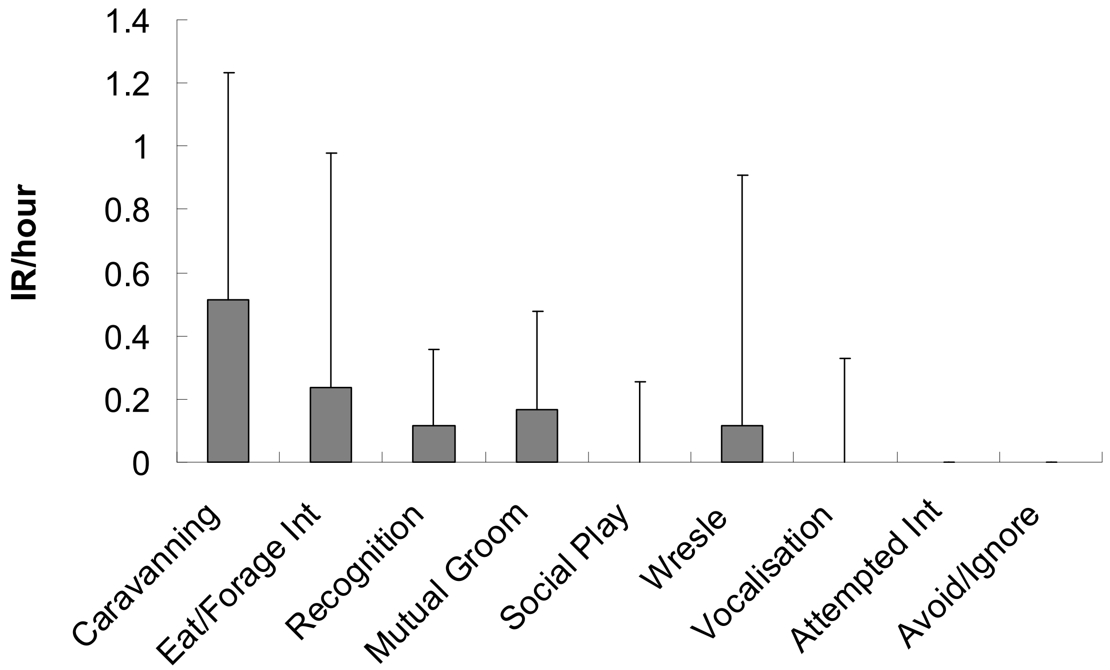

Figure 3 Median (IQR) Interaction Rate in the nine interaction categories for all individuals (N = 25).

When comparing interaction rate between the nine behavioural categories (Figure 3), I found that the most commonly occurring interaction was caravanning, followed by eating/foraging interactions, mutual groom, recognition and wrestle. The nine behavioural category medians are significantly different from each other, confirming that some behaviours are performed more than others (Kruskal Wallis: H = 43.15, P = 0.000). The overall median interaction rate per hour was 1.920 (N=25). The median interaction duration was 4.312 minutes per hour (N=25). Eating/foraging interactions were of the longest duration followed by caravanning, mutual groom and wrestling.

Comparison of Agonistic and social bonding Interaction Rates

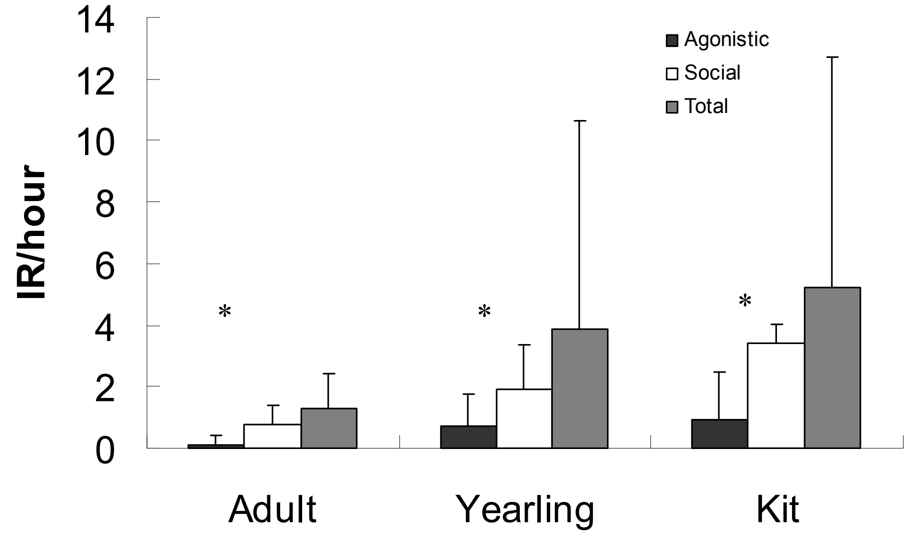

Figure 4 Median (IQR) Rates of sociable, agonistic, and all interactions for three age classes of beaver. Adult (n=13), yearlings (n=7), kits (n=5). Collated total number of nights observed; All =122. * P < 0.05

Agonistic interaction rate differed significantly from social bonding interaction rate in all three age classes, (Adult IR: Wilcoxon signed-ranks test: T = 45, P = 0.007; Yearling IR: Wilcoxon signed-ranks test: T = 21, P = 0.028; Kit IR: Wilcoxon signed-ranks test: T = 15, P = 0.043). The ratio of amicable to agonistic interactions between family members for this population of beavers was 4.6.

Interaction Duration and Nearest Neighbour Duration Between individuals

Nearest neighbour durations were longer with members of the opposite sex, (Figure 5.1). Results for males and females were non-significant, (Male NN: Mann-Whitney U test: W = 61 P = 0.312; Female NN: Mann-Whitney U test: W = 67, P = 0.122).

Interaction durations were also longer with members of the opposite sex, (Figure 5.2). Results for males and females approached statistical significance, (Male ID: Mann-Whitney U test: W = 54, P = 0.092; Female ID: Mann-Whitney U test: W = 68, P = 0.091).

All age groups spend most time near a member of the same peer group, (refer to figure 5.3). However this result was non significant, (Adult NN: Kruskal-Wallis test: H = 1.66, P = 0.437; Yearling NN: Kruskal-Wallis test: H = 2.57, P = 0.277; Kit NN: Kruskal-Wallis test: H = 2.96, P = 0.228).

Interaction duration was relatively equal across the age groups, with kits showing the greatest variation. All age comparisons were non significant.

Notable differences between interaction duration and NN duration within age groups were shown in the yearling males. They spent an equal time with all three age groups, approximately twice the time spent in interactions. Kits also spent twice the amount of interaction time with yearlings as their nearest neighbour. This suggests that when out of the lodge, yearlings are their primary caregivers/chaperones. In the adults differences in NN durations were less pronounced. Adult males were more often in the company of yearlings, and adult females with adult males.

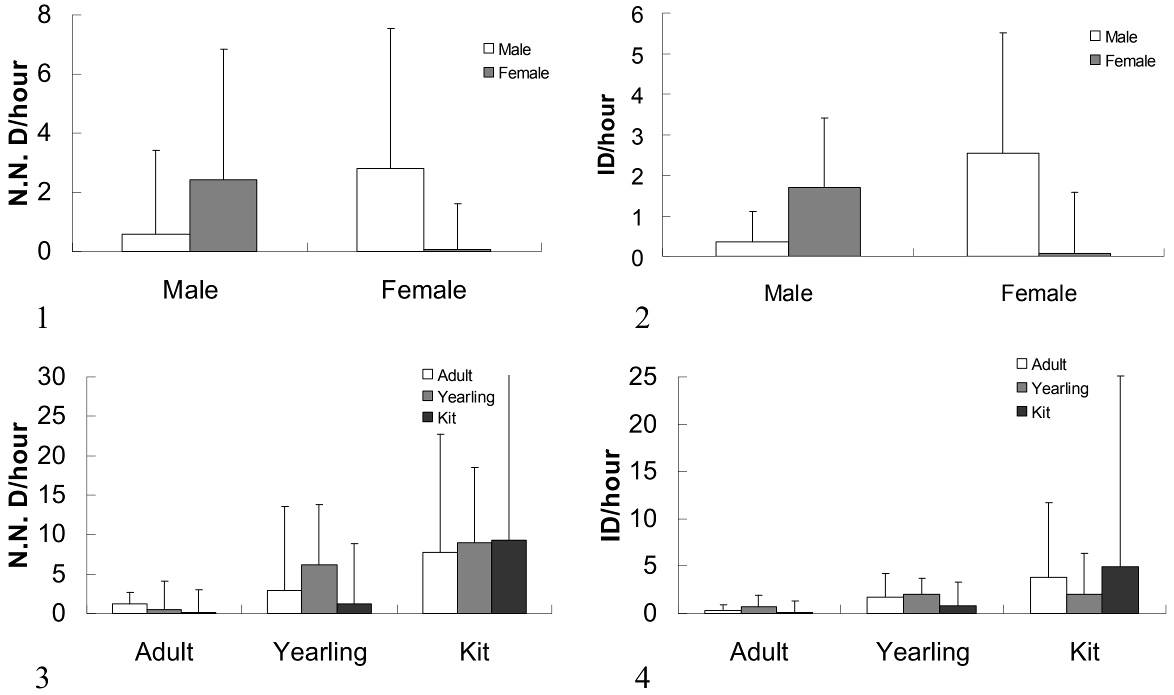

Figure 5 Median and IQR (1) Nearest Neighbour duration per active hour by sex, (male=11, female=9). (2) Interaction duration per active hour by sex, (male=11, female=9). (3) Nearest Neighbour duration per active hour by age, (adult=13, yearling=7, and kit=5). (4) Interaction duration per active hour by age, (adult=13, yearling=7, and kit=5). Collated total number of nights observed; AM =40; AF=35; YM=21; YF=8; KIT=18.

Interaction duration is displayed and compared to nearest neighbour duration in Figure 6. Nearest neighbour and interaction duration differed significantly across all age groups. All animals spent significantly more time in each others company not interacting. (Adult: Wilcoxon signed-ranks test: T = 171, P = 0.002; Yearling: Wilcoxon signed-ranks test: T = 73, P = 0.008; Kit: Wilcoxon signed-ranks test: T = 67, P = 0.028).

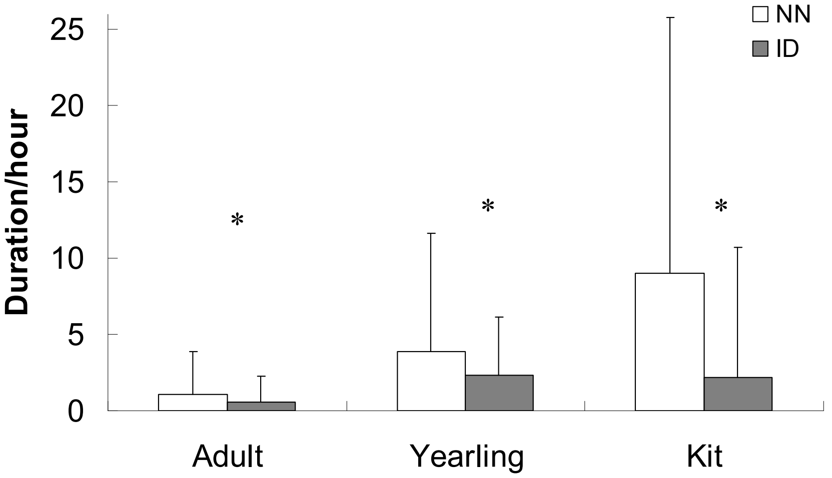

Figure 6 Median (IQR) Rates of nearest neighbour and interaction duration for three age classes of beaver. Adult (n=13), yearlings (n=7), kits (n=5). Collated total number of nights observed; All =122. * P < 0.05

Interaction Initiation and Receiving Rate

A comparison of total interactions initiated, and total received, was made for the three age groups (Figure 7). Adult male and female beavers received significantly more interactions than they initiated. Yearlings and kits initiated more than they received, however this difference only approached significant in the kits, (adult; Wilcoxon signed-ranks test: T = 51, P = 0.017; Yearling; Wilcoxon signed-ranks test: T = 21, P = 0.028; Kit : Wilcoxon signed-ranks test: T = 14, P = 0.080).

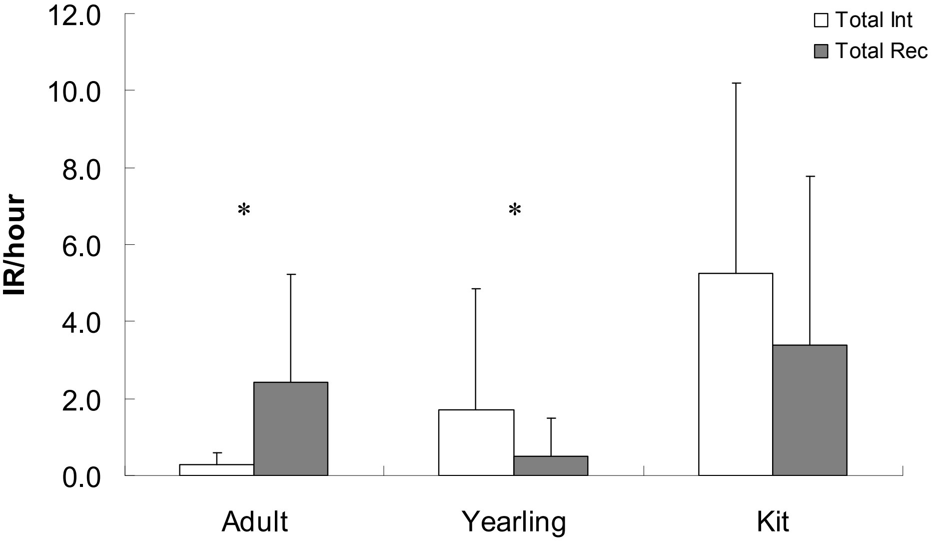

Figure 7 Median (IQR) interaction rate initiated and received by adults, yearlings, and kits. Adults (n=10), yearlings (n=6), and kits (n=5). Animals in territories with no recorded interactions were removed from the analysis. Collated total number of nights observed; Adults =75; YM=29; KIT=18. * P < 0.05

From the results displayed in Table 5, the rank order within the animals studied shows that adult females have the highest index of dominance, followed by adult males, yearling females, yearling males, and then kits.

	Total Initiated	**Total Received**	**Initiated - Received**	**Rank**
Adult Male	0.406	1.365	-0.959	2
Adult Female	0.087	1.350	-1.263	1
Yearling Male	1.714	0.494	1.220	4
Yearling Female	0.949	1.132	-0.183	3
Kit	5.257	3.379	1.878	5

Table 5 Median total initiated and received interactions per age sex group, and corresponding rank.

DISCUSSION

Male and female beavers displayed very little sexual dimorphism, both had similar lengths of principle activity period, time spent in lodge, time budgets, and interaction rates. An absence of sexual dimorphism in body size, (Roberts et al 1998), and a reduction in behavioural sexual dimorphism (Kleiman 1977) are two of the main characteristics of obligate monogamy. Adult male beavers have exclusive mating rights, which create strong selective pressures for male parental participation to ensure maximum offspring survival rates. Young from previous years may also be present in family groups, including yearlings, and sub-adults (two year old offspring). These animals also have a vested interest in ensuring their siblings survival, indirectly increasing their own reproductive success. There are two ways in which adult males and yearlings can show care towards young; direct and indirect care. Direct care includes socialising, mutual grooming, contact with young, retrieving and transporting young (caravanning), and providing food for young (provisioning). Indirect care may include antipredatory behaviour (alert), territorial maintenance (patrolling and scent marking) and in the adult male, investment in the pair bond (Runcie 2000, Svendsen 1989). Age had the most influential affect on time budgets, and social interactions. Principle activity period, time in the lodge, eat, alert, and static behaviours all varied between adults, yearlings and kits. The overall rate of interaction decreased with increasing age. Kits had the highest rate, while adults had the lowest. Time budgets and interaction rates between animals varied greatly, demonstrating individual differences in this population of beavers. The huge behavioural differences observed may be explained by environmental factors such as food availability, need for territorial defence, group size differences (Moncorps et al 1997) and age differences (Busher and Jenkins 1985). A similar variation in time budgets between groups was found by Sharpe and Rosell 2003. Low sample sizes may have resulted in low statistical power and an inability to detect sex, colony and age differences. Previous studies have shown a high correlation between adult male and female behaviour within family groups (Sharpe and Rosell 2003). Only four dominant pairs were radio tracked in this study, so comparisons of pairs was not possible due to small sample sizes.

Variation in time spent eating was demonstrated in the different age groups. Kits spent less time eating (when out of the lodge) than adults or yearlings, as they spend at least some of their time within the lodge eating solid food which is provided by adults and yearlings. Kits remain in the lodge for the first five to six weeks, and are able to eat solid food after only one week. Adults and yearlings provision the lodge with vegetation to supplement the kits diet of milk from their mother. Kits continue to suckle till two months of age (Wilsson 1971, Lancia and Hodgdon, 1983). Kits participated in eating interactions with other family members which could also account for the reduced eating time observed in the time budget data. Time spent in antipredatory behaviour, where the animal was visibly “alert” became greater with increasing age. Adults spent most time alert followed by yearlings, then kits which displayed very little noticeable vigilant behaviour. Adults and yearlings in territories where kits were present showed a slight increase in alert behaviour, thereby providing indirect care for the young. Both adult males and females scent marked their territory and contributed equally to territorial maintenance.

Territories where kits were absent spent more time in swimming, grooming, and static behaviours than territories with kits. Kitless groups may spend more time in territorial defence, which would explain the increase in movement, as beavers mainly scent mark on the borders of their territory (Rosell and Thomsen, 2006).

To determine the extent to which group members contributed to alloparental behaviour, I compared provisioning rates in males and females, as well as adults and yearlings in territories where kits were present. Males provisioned the lodge more frequently than females, but this result was non-significant. Yearlings spend the most time babysitting, (as demonstrated by nearest neighbour results), and contribute most to kit care when out of the lodge. Yearlings provisioned the lodge more frequently than adults. Age had a significant effect on provisioning rate, (Median ± IQR provisioning rate/hour: adults = 0.000 ± 0.171, N = 6; yearlings= 0.567 ± 1.611, N = 5; Mann-Whitney U test: U = 23, P = 0.020). Yearlings provide direct care through time spent socialising and in direct contact (huddling), frequency of caravanning (leading kits to feeding areas), and foraging and eating interactions. Adult males and females also spent time in these activities. Therefore all animals in the family group participated in cooperative breeding to provide maximum survival rates for that years offspring.

Interaction rates were relatively low for a cooperatively breeding social species. However since territory sizes are large (approximately 4km of riverbank) and much time is spent on patrolling the territory, and foraging, it was often the norm for beavers to meet away from the lodge, and participate in eating interactions with each other. Beavers have a very keen sense of smell, and are able to recognise individuals from their unique odour (from anal gland secretions (Sun and Muller-Schwarze, 1998)). Other studies on beaver interactions have focused on the American beaver (Castor *canadensis*) mainly in small ponds/pools and stream systems, where territory sizes are smaller, and there is more chance of beavers meeting in the waterway, or on land, (Brady and Svendsen, 1981; Busher, 1983; and Busher and Jenkins, 1985). These studies reported a higher frequency of interactions than observed in this study. But all reported the same decrease in interactions with increasing age class.

Comparison of agonistic and amicable interaction rates can provide insights into the extent of sociality in a population. Agonistic interactions included wrestling, avoid and ignore. Amicable interactions (or social bonding) included social play, mutual groom, recognition, caravanning, and eat/forage interactions. Agonistic interaction rate differed significantly from social bonding interaction rate, ($P = 0.000$). The ratio of amicable to agonistic interactions between family members for this population of beavers was 4.6. This supports the idea that beavers are more social and less aggressive within family groups, than some other rodent families; such as woodchucks, (Maher 2006) and yellow-bellied marmots (Johns and Armitage 1979). However all interactions observed between beaver groups were always agonistic in nature.

Dominance proved difficult to measure behaviourally, as levels of agonistic interactions observed between family members were very low. Most interactions observed involved social bonding. However adult animals did display mild agonistic behaviour towards younger animals, generally during eating interactions. Eating interactions are important in maintaining social bonds between animals. Eating/foraging interactions were found to be of the longest duration per hour of all interactions. Eating/foraging duration was approximately three times longer in territories with kits at 2.5 min per active hour. The adult male rarely initiated eating interactions with other family members. However he was frequently the receiver of eating interactions (27% of all occasions). Yearling spent less time foraging than adults, but more time eating. Yearlings steal or find food from the adults, as suggested by Brady and Svendsen (1981). They food beg from dominant animals, even though they are perfectly capable of foraging for themselves. Efforts by offspring to “steal” food from adults are often ignored, or actively avoided by removal of the food item, or retaliatory swipes or lunges made by the adult. Results confirmed that only adults avoided/ignored other family members. This behaviour was not displayed in kits or yearlings. Punishment is often used to restrain the demands of offspring, and to establish dominance relationships and mating bonds. Adults could suffer from reduced fitness levels, due to demands of offspring. Therefore adults teach subordinates to behave in a way that avoids reducing the dominant’s fitness, using negative reciprocity, (Clutton-Brock and Parker 1995). The adult male was responsible for 80% of “punishments”, the adult female 20%. Since punishers are generally dominant individuals, this suggests that adult males may be more dominant than adult females. However the cost of punishment may be too high for females to pay. Females need to recover from the costs of reproduction and lactation. They may have adopted a strategy of allowing offspring to share to avoid the costs incurred by preventing them from eating. Adult males do not incur this cost therefore they are free to enforce their authority. Adults avoided/ignored yearlings on 72% of occasions (61% yearling male, 11% yearling female) and kits on 28%. Yearling females used a different strategy, and rather than targeting adults, generally stole food from yearling males, which frequently resulted in bouts of wrestling observed between yearling males and females. Wrestling interaction rate varied significantly with age. Wrestle IR was highest in the kits, then yearlings with adults showing the least occurrences. Wrestle duration was approximately ten times longer in territories with two yearlings present (four animals total). 70% of wrestling bouts were initiated by the younger animals (yearlings and kits).

Recognition interaction rates were very low compared to other interaction behaviours. Recognition behaviours or “greeting” between two individuals required nasal to nasal contact, which is a common behaviour shown by rodents (Eisenberg, 1967). Nearly all nasal to nasal contacts involved two animals approaching each other head-on until their noses touched. Which is in contrast to Brady and Svendsen (1981) definition of nasal to nasal orientations; “beavers initiated nasal-nasal encounters by approaching another from behind”. Brady and Svendsen (1981) concluded that adults rarely initiated but often received nasal interactions, and kits initiated the behaviour most. My results confirm that kits do indeed initiate the most recognition behaviours, closely followed by the adult male and female then yearling male and female. However in this study adults initiated for a much greater proportion of interactions (47% compared to 5% in Brady and Svendsen (1981)). Adults directed most nasal to nasal contacts to each other, then yearling males, and kits.

A comparison of total interactions initiated, and total received, was made for the sex and age groups. Adult beavers received more interactions than they initiated. Yearlings and kits of both sexes initiated more than they received. All adult animals in the study were considered dominant, and were the only ones to breed. Natoli et al 2001, assessed dominance relationships based on aggressive, submissive and affiliative behaviour. The dominance rank based on submissive behaviour was found to be more reliable when studying cats. Since the beavers in this study showed very few aggressive behaviours, (seen in adult animals only), measuring dominance by scoring aggressive and submissive actions was not possible. Only adults were observed to avoid/ignore offspring, and were the only animals to display mild agonistic actions towards younger family members (not including wrestling). An age class dominance hierarchy was considered to exist in this population according to approach avoidance analysis of eating interactions. Based solely on the number of times the adult male was able to secure food from the adult female, and on some occasions displace her entirely from that food, we could speculate that adult males are “dominant” in interactions involving food. However when comparing affiliate behaviour in family groups, the adult female receives the most interactions, suggesting that she most likely to be “alpha”. There are several species where females are dominant to, but not larger than males, such as the Chinese hamster, the ringtailed lemur, the otter and the nutria (Ralls 1976). Thus proving that female dominance can be achieved through means other than physical strength or force. The affiliative behaviour helps to maintain a consistent network of social bonds between the family group, (Macdonald et al 1987) where the adult female is a core figure. A sex age class based hierarchy is suggested to exist when examining only afilliative behaviour.

Further research into social interactions between and within family groups is necessary to explore these initial findings. The role of captive research should be included to allow extrapolation between groups, and could allow further examination of the existence of a possible dominance hierarchy in the family group. Further analysis is needed to examine the interplay between time of year, presence of non-breeding sub adults (two year olds) and time budgets/interaction rates in this northern wild population. Interactions between territorial groups could be examined using bite wounding and body condition data from wild populations. Future research could provide ultimate management and species knowledge benefits.

The data collection methods - lodge watching and radio tracking, produced similar time budgets in adult beavers. However they differed in two behaviours - dive and alert. These behaviours accounted for 6.5% of time in radio tracking and 0.5% in lodge watching. The noise of the boat engine, and/or the lights used to follow the animals during radio tracking caused the adult animals to be more vigilant, but did not significantly affect the animal's nightly activities. Both methods of data collection are viable, and have been used to study beaver populations in Europe and North America. For the purposes of this study lodge watching provided a greater scope for investigating interactions than radio tracking, enabling data on all members of the territory to be collected. Lodge watching could be carried out by one individual if necessary thus increasing the number of territories that could be watched per night.

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