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Territory and group sizes in Eurasian beavers (*Castor fiber*): echoes of settlement and reproduction?

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Abstract According to current theories of territoriality, an animal is expected to defend the smallest area that can provide resources for maximisation of reproduction, known as the 'economically defendable' area. In group territorial species however, the strategies behind resource defence are likely to be more complex with corporate territoriality, cooperative breeding, delayed dispersal and intra-group competition all potentially playing a role. Here we examined group territoriality in a social herbivorous rodent, the Eurasian beaver *Castor fiber*. Beavers in our study do not inhabit economically defendable territories. Instead the sequence of arrival of pairs into unoccupied areas seems to play a more important role in determining the size of the territory, whereas group size is determined by past reproductive success. We argue that the settlement pattern and reproductive history have a lasting impact in the territorial system of beavers due to a combination of the low adult mortality, high dispersal costs, and avoidance of resource depletion.

Introduction

Animals defend territories to gain exclusive access to a critical limiting resource (Davies and Houston 1984). Theoretical studies of territoriality concentrate on the pay-offs between costs and benefits associated with this behaviour (Davies and Houston 1984). Costs such as the energetic and opportunity costs of patrolling and the risk of border conflict are likely to increase as the size of the defended area increases. Balanced against this, the benefits such as resources for reproduction will also increase with territory size until such resources held within the territory are greater than required for maximizing reproductive output. Under these conditions, the optimal territory size a resident requires is the size where the difference between benefits and costs is maximized, where the territory holder experiences the greatest *net* benefit of resource defence. In describing this, Brown (1964) called such a territory the "economically defendable" area. Such 'economic' strategies have been classically shown in nectar-feeding birds such as Golden-winged Sunbirds (*Nectarina reichenowi*) (Gill and Wolf 1975) and the Hawaiian Honeycreeper (*Vestiaria coccinea*) (Carpenter and MacMillen 1976) as well as recently in side-blotched lizards (*Uta stansburiana*) (Calsbeek and Sinervo 2002) and steelhead trout (*Oncorhynchus mykiss*) (Keeley 2000).

The economics of territoriality may not be so clear-cut for group living species. Individuals will not only be experiencing costs and benefits to sociality such as reproductive suppression, intra-group competition and alloparenting, but the very presence of additional group members will have implications for resource depletion and defence (Jennions and Macdonald 1994; Clutton-Brock et al. 1998a; Clutton-Brock et al. 1999; Baker et al. 2000; Chapman and Chapman 2000). These factors can all work to

affect the strategies of all group members in terms of dispersal decisions, intra-group and inter-group aggression and consequent optimal territory configurations.

Alloparenting has been found to be one of the clear benefits to group territoriality in species such as the long-tailed tit (*Aegithalos caudatus*) (McGowan et al. 2003), meerkat (*Suricata suricatta*) (Russell et al. 2002) and African wild dog (*Lycaon pictus*) (Courchamp and Macdonald 2001). However, it has been suggested that delayed dispersal and social queuing in saturated habitats might be the primary reason why groups form, whereas alloparenting is simply one of the subsequent benefits (Emlen 1982; Kokko and Ekman 2002). For example, in the Seychelles warbler (*Acrocephalus sechellensis*) group members appear to derive a kin-selective benefit to alloparenting in that helping behaviour can increase reproductive success and non-breeders only tend to help relatives (Komdeur 1994a,b). At the same time, availability of good breeding opportunities appears to play a role in that delayed dispersal and alloparenting ceases when high quality territories are available (Komdeur et al. 1995). However, larger groups have lower reproductive success, possibly due to reproductive or resource competition (Komdeur 1994b) suggesting that the dispersal decisions taken by Seychelles warblers may be more complex.

Furthermore, group living and its associated benefits may require the defence of greater resources to accommodate the needs of all group members and would be more likely where corporate strength allows greater success in territorial conflicts, leading to the formation of 'empires' (*sensu* Kruuk and Macdonald 1985). Indeed, numerical advantages in territorial conflict have been shown (e.g. Bowen 1982; McComb et al. 1994; Radford 2003; Seddon and Tobias 2003) though it is unclear whether this will necessarily translate into greater territory sizes. Territory size has been shown to correlate with group size in capybaras (*Hydrochoerus hydrochaeris*) (Herrera and

Macdonald 1989) though whether there was a numerical advantage to larger groups in this species was unknown. Thus in many social species, the strategies behind group living are ambiguous.

Beavers, both the North American beaver (*Castor canadensis*) and the Eurasian beaver (*C. fiber*), are also known to be territorial and to live in family groups. The basic social unit consists of a monogamous adult pair with kits of the year (juveniles), yearlings, and sometimes two-year-olds (subadults) (Bradt 1938; Wilsson 1971). However, the dominant adult pair are the only breeders in these family groups (Wilsson 1971; Müller-Schwarze and Sun 2003). All age classes and both sexes participate in marking the territory boundaries at scent mound sites close to the water's edge (Aleksiuk 1968; Wilsson 1971; Rosell et al. 1998). All group members also appear to participate in the provisioning of young before and just after their emergence from the natal den at c. two months of age (Wilsson 1971; Patenaude 1983; Müller-Schwarze and Sun 2003). Beaver populations vary markedly in both group size (Bradt 1938; Wilsson 1971; Rosell and Parker 1995) and territory size (Collins 1976; Heidecke 1986; Nolet and Rosell 1994; Herr and Rosell 2004), and are therefore an ideal species on which to examine the economics of defensibility within group territorial systems.

Based on the rational outlined above, we might expect beavers to be maintaining some minimum economically defendable area that decreases in size with increasing habitat quality. However, given the group nature of beaver territoriality, we might expect this simple economical relationship to be more complex with the defended area increasing with group size so that area is a function of both habitat quality and group size. Furthermore, we might expect that, since group members appear to assist the breeding pair in rearing young, there will be a direct reproductive advantage (for the dominant pair) to group living. In this study we test these predictions in Eurasian

beavers and compare two populations, one recently re-introduced population in the Biesbosch (Netherlands) and one established population in Telemark (Norway).

Methods

Study sites

The Biesbosch (area c. 100 km^2) is a national park in the freshwater estuary of the rivers Rhine and Meuse in the Netherlands (51°45′ N, 4°50′ E). The climate is mild and wet with a mean annual temperature of 10.0 °C and an annual precipitation of 800 mm. The mean number of ice-days (i.e., maximum temperature on a given day < 0 °C) is eight per year. The central part of the Biesbosch is a nature reserve (about 50 km^2) with a tidal amplitude of 30 cm. The nature reserve consists of willow (*Salix* spp.) coppices and reed (*Phragmites australis*) beds no longer exploited by humans, and is intersected by a network of creeks. The reserve is surrounded by agricultural fields with former creeks that have stable water levels and banks with predominantly natural vegetation. Forty-two beavers were re-introduced here in 1988-1991 (Nolet 1995). Because of the tidal water movements, beavers do not build dams in the central part of the Biesbosch. Beavers are legally protected throughout the Netherlands.

The Telemark study site is centred on two rivers, the Saua and the Gvarv, in southern Norway (59°25′ N, 09°03′ E). The climate is cold and wet with a mean annual temperature of 4.6 °C and an annual precipitation of 790 mm. The mean monthly temperature dips below 0 °C for five months a year between November and March. Both rivers flow through a semi-agricultural landscape interspersed with riparian woodland dominated by grey alder (*Alnus incana*) and, to a lesser extent, willow (*Salix*

sp.) and bird cherry (*Prunus padus*), with some dry deciduous and coniferous forest. Both rivers are regulated along part of their length, resulting in only limited fluctuations in water temperature and reduced ice cover in winter. Both rivers are linear, i.e. without braided channels. The Saua river forms part of the Telemark Canal and the section used in this study was bound at each end by canal locks and weirs. The Gvarv river follows a less restricted flow regime and empties into Lake Nordsjø. The section used in the study forms the lower reaches including part of Lake Nordsjø. There are no beaver dams in the study area as both rivers are either too large for beavers to dam or large enough to make damming unnecessary. Beavers have been in the area since the 1920s (Olstad 1937) and face little or no hunting pressure.

In both study sites natural predation is minimal as wolves (*Canis lupus*), the only known major predator on adult beavers (Novak 1987, Andersone 1999), have not been resident locally for more than 100 years.

Determination of territory size

Territory boundaries in the Biesbosch were determined by mapping scent mounds and sight observations together with additional radio-tracking in peripheral colonies. In Telemark, all territories were mapped solely using radio-tracking.

All radio-tracking observations were conducted from a boat either powered with an outboard motor or where possible by rowing and, when dark, spotlights were used to illuminate the study subject (Buech 1985). Binoculars were used when needed. Given the range of behaviours displayed by the beavers in both study sites (see Nolet and Rosell 1994; Sharpe and Rosell 2003; Herr and Rosell 2004) it would appear that with due care, the effect of the spotlight, noise and the presence of the motorboat appeared to be minimal and we suggest that such disturbance is unlikely to have had an effect on the

beavers' behaviour. Indeed, on several occasions, animals approached the observers to within a distance of two metres and generally ignored the observers whilst doing so.

Animals were followed for a full night (Telemark) - from when the individual first emerged from its day resting place in the evening, until it entered a lodge or burrow the following morning and remained inside for at least 30 minutes – or a half night (Biesbosch) – either from emergence until midnight or from midnight until the following morning. When in view, an animals location could be easily recorded based on a visual assessment of position. While on land beavers spend the vast majority of their time at or close (<6 m) to the water's edge (Nolet et al. 1994), and therefore when out of sight, it was possible to record their location every 15 minutes by taking the crossing of one bearing and the bank, on average about 50 m away.

Biesbosch

The founder group comprised 17 adults, seven subadults, 10 yearlings and eight kits. Before their release, animals were sexed according to the presence or absence of the os penis on an X-ray picture, and marked with coloured plastic and aluminium eartags for visual identification. A 30 MHz-radio-transmitter with a life span of 1-2 years, depending on the size of the transmitter (52-92 g), was implanted intraperitoneally in 31 beavers in 1988-1991 (Nolet and Rosell 1994). Of these 22 survived their first year after release (which was by far the most critical; Nolet & Baveco 1996). We determined the resting sites of these beavers once a week, yielding 1236 daytime resting site determinations. At first, the beavers repeatedly switched sites but after some time they settled down and did not change anymore (apart from moving later to a summer daytime resting site within the same territory). We determined the date of settlement as

the average of the dates of first appearance at their later territory of the two pair members involved.

From April 1 to August 31, 1993, we mapped 10 territories by locating scent mound sites. A scent mound is a pile of mud, grass or twigs upon which a beaver scent-marked at least once in the study period; scent mounds <5 m apart were considered one site. We traversed the study area once a week with a small boat equipped with an outboard motor, except for territory G (Fig. 1a) which we visited once a month as it was relatively time consuming to visit (a dyke blocked the main waterway and we needed to bring a canoe along to enter). Scent mound sites were marked with twigs. Scent mound sites were attributed to a territory based on the identity of the individual sighted nearest to it. In three territories on the periphery (J, H, L), where little marking took place, four adult beavers (two males and two females) were radio-tracked between 1 April and 31 August for an average of 20.3±0.6 SD half-nights per territory. In 1992 we had found that territory sizes determined in this period were the same as in winter (Nolet and Rosell 1994). The beavers tracked in 1993 had been in the Biesbosch for almost two years. In three territories (A, C and F), scent mounds, sightings and radio-tracking did not provide enough information, and we found it necessary to supplement the data with locations of fresh feeding-sites and additional sight observations (see Rosell and Nolet 1997 for further details). Drawing of the territorial borders was aided by experience from radio-tracking a total of 22 beavers for c. 20 nights per territory per year in all territories except one (B) in 1989-1992 (Nolet and Rosell 1994).

Between April 20 and June 18, 1998, territories were again mapped by traversing the nature reserve once every two weeks to locate scent mound sites. Territorial boundaries were drawn based on the locations of scent mound sites (Rosell

and Nolet 1997; Rosell et al. 1998) and without direct reference to the 1993 map (Fig. 1b).

Data from scent mound sites, sightings and radio fixes (n=1241) were digitised from a 1:10,000 scale map into a Geographical Information System (GIS) (ARC/INFO).

[Fig. 1a,b near here]

Telemark

Between October 1999 and April 2000, 18 beavers were trapped from a boat using landing-nets (Rosell and Hovde 2001). This trapping technique allowed us to select the dominant adult individuals of each sex from each territory based on previous trapping records of weights, incidents of lactation, and behavioural observations (see Sharpe and Rosell 2003; Herr and Rosell 2004). Both the dominant male and female were trapped in seven territories (territories A, D, E, F, G, I and K – Fig. 2), in three territories only the dominant male (B, C and H) was trapped and in one territory, only the dominant female (J), thus providing us with a total of 10 males and eight females from 11 territories (Fig. 2). Each animal was implanted with an Alterra TX30.3A1 intraperitoneal 30 MHz-radio transmitter (63g) equipped with a temperature sensor and movement sensor (Alterra-DLO, Wageningen, the Netherlands) (Ranheim et al. 2004). Each animal was released within five hours of the initial trapping and allowed a minimum of one week before tracking began, thereby enabling it to recover from the operation (Ranheim et al. 2004).

Radio tracking took place between March 1 and August 15, 2000, resulting in an average of 8.3±4.2 SD tracking nights per territory. In northern latitudes, beavers

generally rely on food caches built in autumn over the winter (Wilsson 1971) and thus observations conducted from spring into early autumn are likely to reflect habitat requirements for the entire year. All fix locations (n=3306) were recorded on 1:5000 scale field maps and later digitised into GIS (ArcView version 3.1).

Beaver may occasionally travel significant distances from their usual ranges (0.5-1.5km) into adjacent territories (personal observation). Such incursions may serve to gain information on neighbouring territories and where witnessed, this behaviour was classified as "on-tour", and excluded from measures of territory size.

[Fig. 2 near here]

Determination of group size and reproductive rate

In defining the size of a group in terms of its ability to defend a resource, all individuals within a group who contribute in some form to the defence of that resource must be counted (i.e. effective group size). Since Eurasian beavers exhibit fully developed territorial behaviour by approximately five months of age (Wilsson 1971), yearlings are included in the determination of the group size. The kits in this study were <5 months of age and were therefore excluded from the calculation of group size but were counted to determine reproductive rate. Reproductive rate was defined as the number of offspring surviving until emergence from the natal lodge.

Biesbosch

In the summers of 1989-1999, we regularly traversed the study area by boat to spot as many beavers as possible. Observations were made with binoculars and a telescope. When dark, a flashlight was used to identify beavers by their eartags. In addition to the released beavers, four recruits (beavers born in the Biesbosch) were caught with Hancock live traps, sexed by external palpation of the os penis (Osborne 1955) and marked with coloured eartags in 1991-1992. Animals that had not been seen for a full year were assumed to have died in the last year in which they had been observed. This means that the 1999 season was necessary to obtain group size data for 1998 and the 1994 season for group sizes in 1993. Between 1989 and 1998, attempts were made in May, June and July to assess the presence of kits inside dens by sound recordings using an AV- recorder (Nokia, model ITT SL 537 AV), and subsequently, in June, July and August, litter sizes were determined by watching the kits emerging from the dens in the evening (at approximately two months of age, Wilsson 1971).

Telemark

Since 1998, the beavers in the study areas have been subject to an extensive live-trapping programme. All captured individuals have been marked with unique coloured plastic ear-tag combinations or metal ear-tags (Rosell and Hovde 2001). Animals were sexed by examining the colour of the anal gland secretion (Rosell and Sun 1999). Animals were assigned to an age class (kit, 1-year-old, 2-year-old and adult) based on body weight and size following Rosell and Pedersen (1999) and Parker et al. (2001a,b). The number of kits in 1998, 1999 and 2000 emerging from the natal lodge or burrow was determined through sight observations and/or live-trapping. Non-breeding adults were beavers >2 years of age other than the dominant male and female within a

territory. Throughout the radio tracking sessions, the presence or absence of group members within the focal individual's territory was monitored by identifying individuals from ear-tags.

Determination of territory quality

In our study areas, Eurasian beavers strongly preferred deciduous habitat and consumed mainly deciduous trees (Nolet and Rosell 1994; Nolet et al. 1995; Campbell, unpublished MSc thesis). Studies of North American beavers have shown that simple measures of food abundance, in broad categories, can explain features of their social system (Smith 1997; Fryxell 2001). We therefore chose deciduous habitat as the resource in the analysis.

Biesbosch

The banks of waterways >5 m wide (615 km in total) were classified based on the dominant vegetation in 25 m sections. In the Biesbosch, surveys of foraging signs have shown that very little foraging occurs beyond 6 m from the waters edge (Nolet et al. 1994) indicating that this method is appropriate. The 1:10,000 map from 1987 and the 1:25,000 map from 1988 of the Topografische Dienst (Delft) supplied the basic information, and this information was complemented by panoramic pictures taken of banks at 80 sites throughout the Biesbosch in 1989. The banks were classified as dominated by woodland (184 km), herbs (126 km), reeds (217 km) or barren (88 km). The classifications based on maps and photos were verified by visiting these waterways

by boat in 1991. The banks were digitised from a 1:10,000 scale map into a GIS (ARC/INFO).

Telemark

Along both rivers, all deciduous habitat blocks greater than approximately 100 m^2 (corresponding to a minimum of about 10 m of river bank) within 40 m of the shore were delineated into polygons on 1:5000 field maps. The rivers, and habitat blocks were digitised onto ArcView GIS (Version 3.1). No correction was made for slope. Rivers were digitised from 1:5000 scanned maps (Gvarv river) or obtained in digitised vector format (Saua river).

Due to the more heterogeneous nature of the habitat in the Telemark area, it was felt that this method would result in a more accurate representation of deciduous availability within Telemark than the simple linear measurement used in the Biesbosch. The cut-off point of 40 m was used based on a study of an adjacent population of beavers in southern Norway where the mean maximum distance of beaver-damaged woody plants from the river was found to be 36 m ± 32 SD (Parker et al. 2001a). This was later confirmed as suitable from research on our study population that found a gradual drop in foraging with distance from water with approximately 70% of woody stems being cut by beaver within the first 10 m of the waters edge, compared with over 20% between 10-20 m dropping to approximately 5% between 30-40 m from the waters edge (Orsolya Bozsér unpub.).

Data analysis

Because beavers defend territories as a group, location fixes from members of the same family group were combined to obtain territory sizes. All fixes were used to delineate territories. We considered territories to be one rather than two-dimensional, and thus, territory sizes were expressed as the total length of banks between extreme fix locations. This method has essentially the same assumptions as the minimum convex polygon method and so autocorrelation of the data sets could be ignored (Harris et al. 1990).

Because some variables showed slight deviations from a normal distribution (Kolmogorov-Smirnov test), non-parametric statistics were applied in some cases (Siegel and Castellan 1988). Differences between Biesbosch and Telemark were tested using the Mann-Whitney U test with SPSS. Spearman's rank correlations were performed with Statistica and SPSS. Probability values are two-tailed, and 0.05 was used as the level of significance.

A general linear model (procedure GLM, SAS 1989) was used to determine which of the measured variables affected territory size, with study site, group size and the proportion of deciduous habitat as independent variables. Study site was a class variable (Biesbosch or Telemark). Group sizes were those in 1998 for the Biesbosch and 2000 for Telemark. The proportion of deciduous habitat was arc-sine transformed. We started with the full model, including all interactions, and used a manual stepwise approach to determine the best model (all type III $P>0.05$). A Poisson regression (using Statistica) was performed to assess the determinants of group size, again using an manual stepwise approach ($P<0.05$) with study site (class variable), reproductive rate, territory size and proportion of deciduous habitat as independent variables. Mean values are given with standard deviation. Sample sizes are n=13 (Biesbosch) n=11 (Telemark) and n=23 (both sites), unless otherwise stated. As advocated by Colegrave and Ruxton

(2003), all fully reported non-significant results are provided with 95% confidence intervals (denoted as *CI*).

Results

Territory and group sizes

Biesbosch

In 1993, 28 beavers (excluding kits) were sighted. Of these, 23 (82%) had been released and five (18%) were recruits from the released population. There were 13 pairs, in 11 of which both animals were older than two years, the exceptions being territories C and H (Fig. 1a). Two pairs were also accompanied by one yearling (territories D and M); thus group size (excluding kits) varied only from 2-3. In 1998 by contrast, group size varied from 1-7, mean 3.0±1.9. Between 1989 and 1998, the average reproductive rate was 1.0±0.8 kits per territory per year.

A total of 214 scent mound sites were located in 1993. The average territory size was 12.8±5.5 km, of which 4.8±3.1 km of bank (36±12%) was wooded. In 1998, a total of 402 scent mound sites were located. From the locations of these and the location of active main resting sites in territories G, H and J it was clear that the 13 territories that had been established by 1993 still existed in 1998 (cf. Fig. 1a and 1b). In eight of them at least one of the 1993 territory holders was still present in 1998 (territories A, B, D, E, F, H, L and M). In that year, 57 beavers (excluding kits) were counted.

Telemark

A total of 50 beavers of all ages were recorded in the 11 territories studied. There was no significant difference between the Saua and Gvarv rivers in terms of territory sizes (Mann-Whitney U = 12, *CI* = -3.65 to 3.78, *P*=0.788), group sizes (U = 13.5, *CI* = -7.00 to 2.00, *P*=0.927) and deciduous vegetation (U = 12, *CI* = -0.26 to 0.19, *P*=0.788). Group sizes in 2000 ranged from 3-11, mean 4.5±2.4 animals per territory. Group sizes were significantly larger than those found in the Biesbosch in 1993 (U = 5, *P*<0.0001) but, though still larger, were not significantly so from those in the Biesbosch in 1998 (U = 39, *CI* = 0.00 to 3.00, *P*=0.063). Between 1998 and 2000, 10 of the 11 territories studied reproduced successfully with territory 'B' (Fig. 2) failing to reproduce over the three years. The average number of kits per territory in any year was 0.9±0.8, which was not significantly different from the reproductive rate of the Biesbosch (U = 68, *CI* = -0.67 to 0.67, *P*=0.865).

The average territory size was 4.0±2.1 km, of which 47±13% was deciduous habitat (Fig. 2). The territory sizes in Telemark were found to be significantly smaller than those in the Biesbosch (U = 9, *P*<0.0001).

Testing the predictions

Territory size was not correlated with group size, neither in the Biesbosch (Spearman's rank correlation coefficient r_S=0.25, *CI* = -0.35 to 0.70, *P*=0.420) nor in Telemark (r_S=0.44, *CI* = -0.22 to 0.82, *P*=0.180). For Telemark, excluding the large group-size territory did not result in a significant correlation (r_S=0.55, *CI* = -0.08 to 0.89, *P*=0.102). The general linear model indicated that, after controlling for the difference in territory size between the study sites ($F_{1,21}$=34.4, *P*<0.0001), territory size

was dependent only on the proportion of deciduous habitat ($F_{1,21}$=5.1, P=0.034). Together study site and the proportion of deciduous habitat explained 62% of the variation in territory size (interaction terms were not significant). However, contrary to the prediction of the 'economic' strategy, territory size and the proportion of deciduous habitat were positively correlated (Fig. 3).

[Fig. 3 near here]

Territory size and date of settlement in the territory were negatively correlated (r_S=-0.65, P=0.017) (Fig. 4). The proportion of deciduous habitat within a territory also decreased significantly with the date of settlement (r_S=-0.63, P=0.021) (Fig. 4). These data were only available for the Biesbosch.

[Fig. 4 near here]

Reproductive rate (all years) was found not to correlate with territory size, neither in the Biesbosch (r_S=0.28, CI = -0.53 to 0.57, P=0.929) nor in Telemark (r_S=0.20, CI = -0.65 to 0.54, P=0.552). Mean annual reproductive rate was also not correlated with the proportion of deciduous habitat in a territory, again neither in the Biesbosch (r_S=0.18, CI = -0.41 to 0.66, P=0.553) nor in Telemark (r_S=0.35, CI = -0.29 to 0.80, P=0.289). The Poisson regression indicated that group size was affected by reproductive rate (Chi^2_1=10.9, P<0.001) after controlling for study site (Chi^2_1=4.4, P=0.036), the deviance of the model being 12.62 (df = 21) (Fig. 5). To explore the causality of this relationship between reproductive rate and group size, we constructed a GLM of reproductive rate against group size for each year in each territory where both variables were known. Territory, nested within site (Biesbosch or Telemark), was used as a

blocking variable. The GLM indicated that group size actually had a negative impact on reproductive rate *within* territories ($F_{1,30}=12.13$, *P*=0.0015) suggesting that the positive relationship found in the regression was due to variation *between* territories (Fig. 6). Thus some territories have a consistently greater reproductive rate than others which results in larger groups sizes and therefore a measure of mean reproduction and group sizes for territories will indicate a positive relationship between the two variables.

[Fig. 5 and 6 near here]

Discussion

Despite the difference in population development, the Biesbosch population being still in its growth phase, whereas the Telemark population appears to be at carrying capacity (Rosell and Hovde 2001; Parker et al. 2002; cf. Zurowski and Kasperczyk 1986), the results from these populations are strikingly similar. Both sites exhibit no correlation between territory sizes and group sizes, and positive trends between territory size and proportion of deciduous habitat. Furthermore, neither site shows a correlation between either reproductive rate and territory sizes, or reproductive rate and proportion of deciduous habitat, suggesting that territory size or the amount of deciduous habitat do not influence reproductive rate. In both populations, group size was correlated with reproductive rate. Territory sizes were smaller in Telemark suggesting that the higher population density there was influencing territory size. However, by 1998 beaver group sizes in the Biesbosch were not different from those in Telemark and we would expect border intrusions to be similar in each site. Differences in territory sizes between sites may therefore be due to some factor other than population pressure.

Within our study systems it appears that territories are not configured to a minimum economically defendable size based purely upon resource abundance. In fact, it appears that larger territories are also proportionately richer in terms of resource abundance. This is in contrast to a study on a newly established Eurasian beaver population in the Loire river valley, France that reports a highly significant negative correlation between home range size and proportion of suitable foraging habitat (Fustec et al. 2001). In that study, home range boundaries were determined by investigating changes in density of beaver signs along the river rather than more directly by radio-tracking or mapping scent mounds. However, given that individual beavers are known to use and develop trails, ditches and feeding stations created by other colony members (Wilsson 1971; personal observation) and that individuals can spend a significant proportion of their activity near territory borders (Herr and Rosell 2004), we are tempted to conclude that variation in the density of beaver signs may be as much a product of heterogeneous use of preferred habitat within territories as any perceived spacing of colonies.

If territory sizes are not decreasing with increasing habitat quality, then perhaps they are primarily responding to variation in group sizes. However, this was also not supported; group size had no effect on territory size in either population. This result is in agreement with the study of Bergerud and Miller (1977), who found a similar pattern among North-American beavers living in low population densities.

What then determined the territory size of beavers in our two study populations? It is of course conceivable that some other factor governs habitat quality in beavers. To be in accordance with the economically defendable area hypothesis, this 'other' factor should negatively correlate with proportion of deciduous habitat for *both* our study populations. We consider this to be an unlikely scenario. In fact, a multi-factorial

analysis of many environmental variables in the Telemark site found no clear negative relationship between territory size and any variable (Campbell, unpublished MSc thesis). Furthermore, Adams (2001) in a review of 40 studies examining food availability and territory size, found 14 studies where no resource effect was found. Indeed, a similarly positive relationship between territory size and absolute amount of resources has been found in other rodents (e.g. Lacher and Mares 1996; Steury and Murray 2003). This suggests that factors other than resources can influence territory sizes.

Settlement pattern

In the Biesbosch, new beavers were released every year. The territories of the first beavers were very large, but those released in later years claimed territories roughly half the size from those released a year earlier. In addition, they were more and more likely to settle in poor habitat and most of the last releases became floaters (Nolet and Rosell 1994). This settlement pattern is in line with a value asymmetry for territory owners and intruders (Maynard Smith 1976; Tobias 1997). Here we demonstrated that early arrivals still occupied larger and higher quality territories than late arrivals after more than six years. Though we might expect territory size to decrease and group size to increase with increasing beaver density in the Biesbosch, any initial variation in territory size due to settlement pattern might not entirely disappear as the population reaches carrying capacity.

During natural colonisations of beavers in Sweden and France, distant sites were often colonised earlier than those closer to previously occupied sites, before filling up of the habitat took place (Hartman 1995; Fustec et al. 2001). This pattern is analogous to a

sequential settlement. A sequential settlement is therefore likely to be the natural settlement pattern during colonisation events and may have occurred within the Telemark population, as it did (artificially) within the Biesbosch.

The echo of settlement

How might the settlement effect be retained in the long term? Once the territory pattern is established, change may only be possible through the vacation of adjacent territories, which would then allow replacements to repack territories within the newly created space (Knapton and Krebs 1974). Such a scenario is less likely in species with a low adult mortality since the likelihood that adjacent territories are simultaneously vacated will be lower (Knapton and Krebs 1974). A territory shared by a pair or a group is likely to have an even lower chance of becoming vacant. For example, in beavers, if we assume an annual (sub)adult mortality of 0.09 (Nolet and Baveco 1996) and assume that mortality is *independent* of territory, a territory with just two owners will lose one beaver approximately once every six years (annual risk of one of a pair dying is $2(0.09)(0.91) = 0.164$, or 1:6 chance). The risk of a territory losing both adults within a year is $(0.09)(0.09) = 0.0081$, 1:123 chance or approximately once every 123 years. As group size increases, the likelihood of a territory becoming vacant decreases rapidly (e.g. 1,372 and 15,242 years for groups of three and four respectively). Obviously, in reality, mortality is likely to be influenced by some independent variable such as habitat quality or predation risk. Furthermore, removal of one of the pair could allow a neighbour of the same sex to expand its territory and obtain a second partner, though to our knowledge there is no evidence of such behaviour in the monogamous beaver.

These simplistic calculations however, do serve to illustrate how low mortality and group living could reduce the chances of gaps appearing in the territory array.

In the course of our studies in the Biesbosch and Telemark, five examples of new pair formations were observed that did not lead to new territory borders. In Telemark, the unlikely event was observed in which the two territory owners in one particular site died shortly after each other. A male from an adjacent territory upstream then occupied the empty territory. At this point, a preliminary radio telemetry analysis suggested that the downstream border remained, but the beaver was additionally utilising parts of its former territory upstream. Previously, a single vacancy in the same territory had not affected its borders, thus, only a complete territory vacancy resulted in a (partial) change in territory borders.

The echo of reproduction

In our study, group size did correlate with reproductive rate, which could suggest that alloparenting is one of the advantages of philopatry. Yet, an examination of the variation in group sizes and reproductive rates in different years within each territory suggests that the causal relationship was from reproductive rate to group size, and not the other way around, thus groups are built up by past reproduction. Moreover, the negative relationships between these variables indicate that reproduction falls as group size increases. Smith (1997) and McTaggart and Nelson (2003) also found no evidence of larger group sizes benefiting reproductive rate in North American beavers. Similar costs to group living have been found in communally breeding mammals such as the European badger, *Meles meles* (Woodroffe and Macdonald 2000) and the tuco-tuco, *Ctenomys sociabilis* (Lacey 2004). However, the benefits of cooperative breeding may

occur in other currencies, such as reduced provisioning costs (Crick 1992; Clutton-Brock et al. 1998b), which may apply to beavers, since provisioning by sub-dominant beavers has been observed (e.g. Wilsson 1971). Mortality of offspring in their first six months of life has been found to exceed 50% in the North American beaver (McTaggart and Nelson 2003), but to our knowledge, no studies have been conducted on either the mortality of beaver kits before they leave the lodge or the longevity of beavers in relation to group size.

However, cooperative breeding does not have to be the proximate cause of delayed dispersal by offspring. In an established population, bites by other beavers can be a major cause of death particularly in yearlings and subadults during the dispersal phase (Piechocki 1977). Where dispersal costs are high, natal philopatry can be a viable strategy in improving recruitment success of a territory owner's offspring by allowing the offspring a safe 'haven' from which to find a breeding vacancy (Stacey and Ligon 1987; Ekman et al. 1999; Ekman et al. 2000; Kokko and Ekman 2002). Thus kin-selection can operate between parents and their philopatric offspring without any benefit through cooperative breeding. Furthermore, the large investments in engineering activities (lodges, ditches and dams) in certain habitats may further contribute to the sociality of beavers.

The synopsis

An economic perspective of territoriality (*sensu* Brown 1964) assumes that by holding a larger territory than is necessary for minimum breeding requirements, territory owners should incur extra costs such as increased travel to territory border or increased border intrusion and territorial aggression. It is presumed that such costs must be balanced by

some benefits. Beavers maintain territories over several years and play host to philopatric offspring, thus a long-term approach to their territory economics must be taken. Here, the advantage could be a long-term payoff in reducing the rate of resource depletion within the site and thus increasing the long-term viability of the territory. Beavers selectively forage on their preferred food source of woody plants, a resource that is not rapidly renewed. Such selective foraging can cause a shift in the woody plant community structure towards non-preferred species and result in a depletion of resources over time (Nolet et al. 1994; Fryxell 2001). Site abandonment, due to resource depletion has been frequently recorded both in populations of the North American beaver (e.g. Donkor and Fryxell 1999; Fryxell 2001) and those of Eurasian beaver (Tyurnin 1983). Presumably, abandoning a site and attempting to occupy a novel site has associated costs such as increased predation risk (or increased building costs to reduce predation risk) (Metzgar 1967; Larsen and Boutin 1994), exploration (Nolet & Rosell 1994) and intra-specific competition (Piechocki 1977). The latter cost is particularly great at high population density where there may be few, if any, unoccupied suitable habitats. Thus, by retaining large territories as a form of prospective resource defence (*sensu* Stamps and Tollestrup 1984), beavers may avoid these future costs. We suggest that further long-term research is needed to examine the viability of beaver territories over time.

We believe that important questions remain unanswered: if large territories are maintained to increase the survival of philopatric offspring or the capacity of territories to hold them, why do larger territories not contain larger groups? If dispersal success is decoupled from territory size (this seems quite likely since the chance of finding a breeding vacancy will depend on number of and distance to neighbouring territories, not natal territory size) then why do these larger territories not increase reproductive output?

Indeed, the mechanism where by reproduction decreases as group size increases remains unclear. It maybe that avoiding resource depletion is the most important factor determining the territorial and reproductive strategies of beavers but further study is required to examine the effects of population pressure (inter- and intra-group) on the territorial, reproductive and philopatric strategies of beavers.

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Figure legends

Fig. 1 Beaver territories in the Biesbosch, based on scent mound sites and sight observations of marked animals and radio-tracking in 1989-1993. (a) Summer 1993. The edge territories H, J and L were determined by radio-tracking (after Rosell and Nolet 1997). (b) Summer 1998 The boundaries of the edge territories (G, H and J) (dashed lines) were not determined but redrawn from the 1993 data, except for a shift of the boundaries of G based on the relocation of the main resting site and the building of a new dyke with pumping engine at the (new) NE-corner. ● scent mound sites ○ main resting sites. The hatched areas indicate no-man's land. Note that only streams and ditches up to 25 m wide are depicted on the maps.

Fig. 2 Beaver territories in Telemark as minimum convex polygons based on radio-fixes. (a) the Gvarv river and (b) the Saua river. Territories of which no telemetry data were collected are represented with dashed lines; the numbers indicate group sizes of these territories. ○ main resting sites.
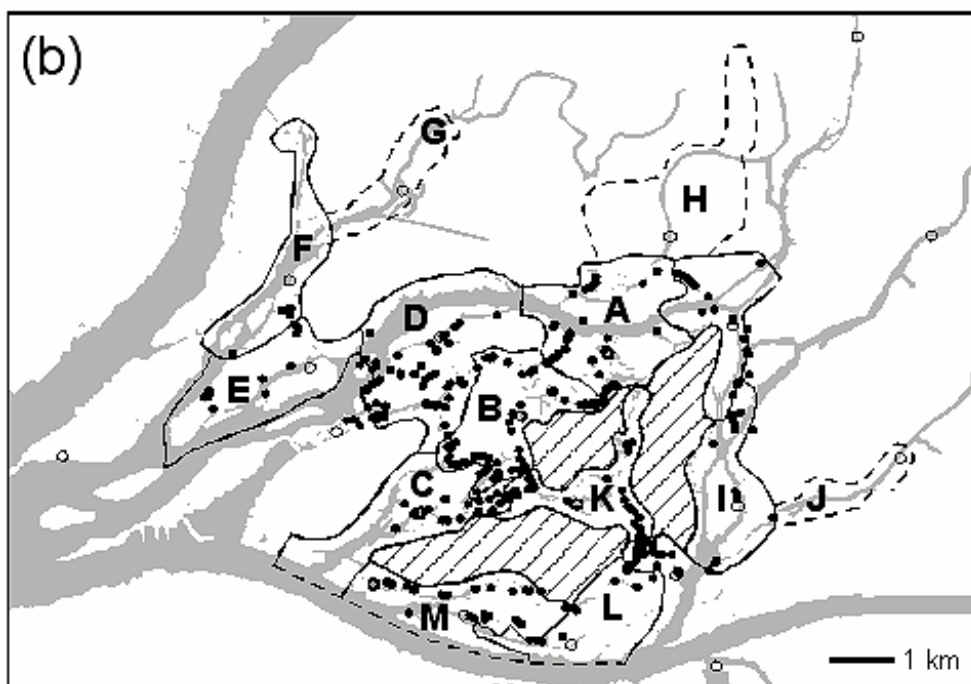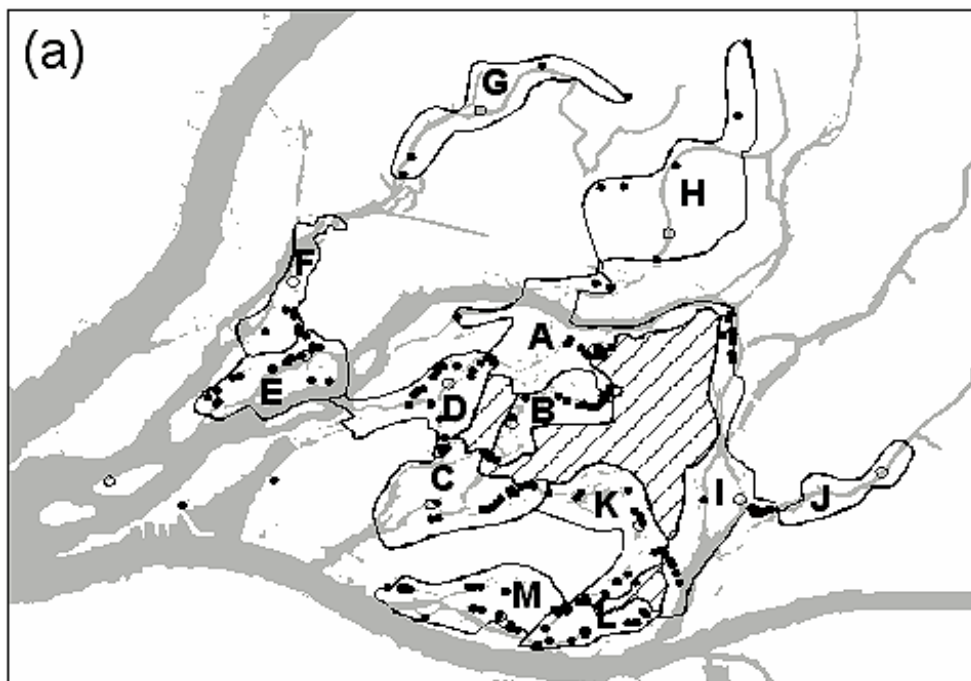
Fig. 3 Beaver territory sizes (km) against the proportion of deciduous habitat of these territories, with the selected general linear model, in the Biesbosch (solid symbols and lines) and Telemark (open symbols and dashed lines).

Fig. 4 The date of settlement within the Biesbosch territories against territory size and against the length of deciduous habitat. Lines are linear regressions (r^2=0.58 and 0.41, respectively).

Fig. 5 Reproductive rate against group size, with the selected Poisson regression. Data from Biesbosch in solid symbols and lines, and data from Telemark in open symbols (the numbers indicate coinciding data points) and dashed lines.

Fig. 6 Reproductive rate against group size for each year within each territory showing the negative relationship between the variables at territory level. Data from Biesbosch in solid symbols and data from Telemark in (larger) open symbols. Lines connect data points within each territory. Numbers indicate total number of data points / number of territories. In general, group sizes tended to increase and reproduction to fall over time, thus in the figure time can be considered to flow from lower right to upper left.
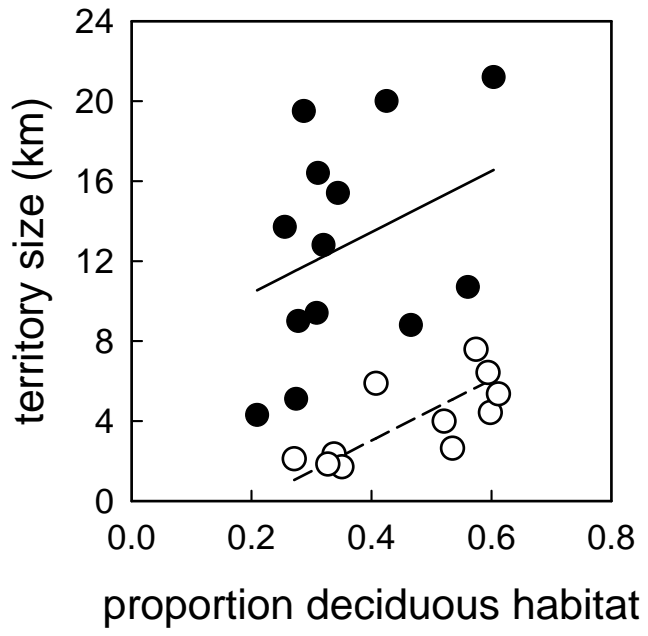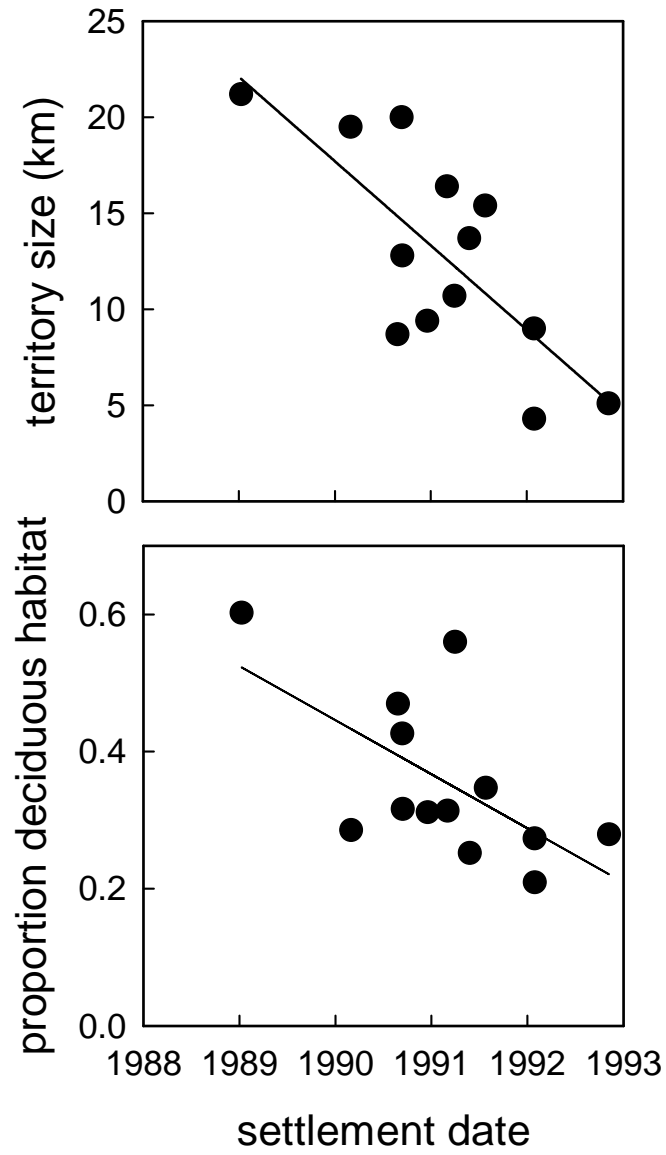
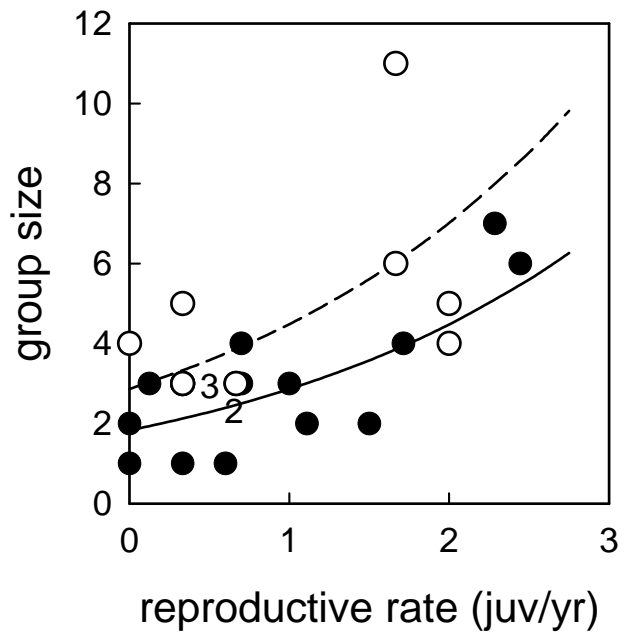**[Figure 1; Campbell et al.]**
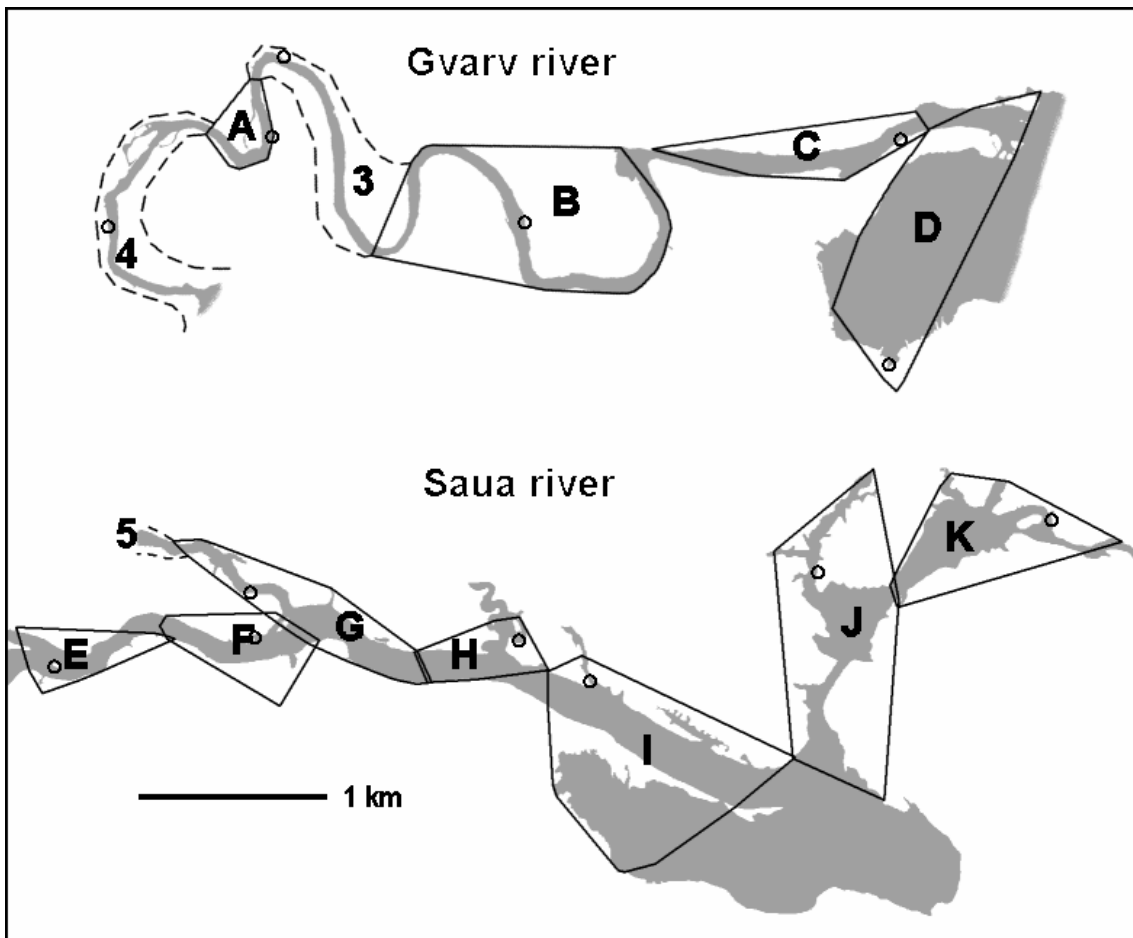
[Figure 3; Campbell et al.]

[Figure 4; Campbell et al.]

[Figure 5; Campbell et al.]