Use of linear and areal habitat models to establish and distribute beaver *Castor fiber* harvest quotas in Norway

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In Norway the Eurasian beaver *Castor fiber* harvest is quota-regulated. Once the annual quota for each municipality has been determined it is distributed to landowner-organized beaver management units. Municipal wildlife managers can choose between two distributional models: the traditional "areal model" whereby each management unit receives its portion of the municipal quota based on the relative *area* of beaver habitat within the township that it contains, or the more recently developed "linear model" based on the relative *length* of beaver-utilized shoreline it contains. The linear model was developed in an attempt to increase the precision of the quota distribution process and is based on the fact that beaver occupy landscapes in a linear fashion along strips of shoreline rather than exploiting extensive areas. The assumption was that the linear model would provide a more precise and just method of distributing the municipal quota among landowners. Here we test the hypothesis that the length of beaver-utilized shoreline is a better predictor of beaver colony density than the area of beaver habitat on 13 beaver management units of typical size (794 – 2200 hectares) in Bø Township, Norway, during 2 years. As hypothesized, the number of beaver occupied sites on management units correlated significantly ($p \leq 0.001$) with the length of beaver-utilized shoreline, but not with the area of beaver habitat. Therefore municipalities should employ the linear model when a precise distribution of quotas is necessary. The density of Eurasian beaver colonies at the landscape scale (>100 km^2) in south-central Scandinavia averages approximately 1 occupied site per 4 km^2. This figure can be employed by municipal wildlife managers to estimate the colony density in their townships, and to calculate municipal quotas, when more precise census information is lacking.

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INTRODUCTION

Following its near extirpation in the latter half of the 19th century, the Eurasian beaver *Castor fiber* (Linnaeus, 1758) has since become reestablished throughout much of its former range (Halley & Rosell 2002; Halley et al. 2012) and many European countries now have viable and harvestable populations. In recent decades, beaver hunting and trapping have resumed throughout much of Fennoscandia, the Baltic region, and countries of the former Soviet Union (Parker et al. 2001a). Internationally, harvest regulation of beaver using quotas is still one of the most commonly employed methods of controlling the annual take-off (Novak 1987; Novak et al. 1987; Hartman 1999; Parker & Rosell 2012). For a species that is relatively easy to trap and hunt, exists at relatively low densities and was nearly extirpated worldwide, quota regulation provides a secure method to control harvests and protect against overexploitation.

Beaver are territorial, semi-aquatic rodents that live in family units commonly referred to as colonies and mark territories with scent mounds (Rosell et al. 1998). They fell trees for food and for building lodges and dams (Rosell & Pedersen 1999).

They occupy riparian landscapes in a linear fashion, i.e. rarely felling trees more than 50 m from the water's edge (Parker et al. 2001b). They use, abandon and reoccupy suitable shoreline habitat on a rotational basis and the remains of this activity are highly visible. Thus habitat both previously occupied and presently in use is easy to record.

Throughout most of Europe, the right to hunt belongs to the landowner and quotas provide a system for distributing the wildlife harvest among them. In Norway, quota-based management of beaver has been employed continually since 1855 (Parker & Rosell 2012). Under current Norwegian law governing beaver management (FOR 2002-03-22 nr 314: *Forskrift om forvaltning av hjortevilt og bever*), municipalities with harvestable beaver populations must first determine an annual harvest quota. This requires some form of information on the number of occupied colony sites within the municipality. Though an autumn ground census provides the most accurate measure of both previously and presently occupied sites (Parker & Rosell 2012), and therefore the best basis for determining the harvest quota, they often involve considerable fieldwork and some expense. Therefore many wildlife managers are reluctant to conduct a municipal census. As an alternative to conducting a census, municipalities that have had a beaver population for at least 25-30 years (Hartman 1994), and that have experienced the initial population peak typical for beaver (Parker & Rosell 2012), may estimate colony density by extrapolating information on colony density gathered in similar landscapes. To date, no review of Eurasian beaver colony densities in Nordic landscapes has been published that managers can employ for this purpose.

Once the municipal quota has been determined it must be distributed among landowners. From 1929 to 1996, municipal beaver quotas were allotted to landowners according to the *area* of beaver habitat that estates encompassed. However, managers often experienced that the area of beaver habitat on estates can be a poor predictor of colony density, particularly on smaller estates. This occurs because beaver are rarely distributed evenly throughout landscapes, but instead occupy them in a linear fashion along shorelines. Therefore in 1997 a new law gave municipal wildlife managers the option to distribute the annual quota among landowners based on the *length* of beaver-utilized shoreline present on their properties, the assumption being that this new linear model would provide a more precise and just method of distributing the municipal quota than the traditional area-based model. To date, this assumption has not been tested.

Here we 1) test the hypothesis that the length of beaver-utilized shoreline is a better predictor of beaver colony density than the area of beaver habitat on beaver management units established within Norwegian municipalities and 2) review the published data on Eurasian beaver colony densities in different Nordic landscapes that municipal wildlife managers can employ to estimate the number of beaver colonies in their municipalities when census information is lacking.

METHODS

Study Area

The study was conducted in Bø Township (59°25'N, 09°03'E; 266 km^2), Telemark County, southeast Norway during 1995 and 1996. The mountainous terrain is interspersed with small streams and lakes and is 77% boreal forest, 9% farmland, 9% above tree line, 3% urban, and 2% water (Parker et al. 2002a). Following local extirpation during the 19th century, beaver first became reestablished in the township through natural dispersion around 1920 (Olstad 1937) and appear to have reached initial peak density around 1970. Trapping and hunting were reopened in 1971 and until 1986 only nuisance animals were taken. From 1986 to 1995 the harvest was light, increasing from 5 to 39 animals annually (Parker 2000). Natural predation is minimal as wolves (*Canis lupus* Linnaeus, 1758), the only major predator on beaver (Novak 1987; Andersone 1999), were not present. Mean density of occupied sites for all area below tree line (242 km^2) was 0.26/km^2 in 1995 (Parker et al. 2002a), which is typical for Scandinavian landscapes (Hartman 1994; Parker et al. 2002b; Parker & Rosell 2012).

Population survey and mapping methods

In both years between 16 October and 15 December, all potential beaver habitat in Bø Township was covered on foot or by canoe. All lodges with food caches were defined as occupied (Bergerud and Miller 1977). Newly built or repaired lodges and bank burrows at sites where caches were not found, but where substantial tree felling and/or dam-building activity had recently occurred were also defined as occupied, because winter caches are not always present or visible at active sites (Semyonoff 1951; Hartman & Axelsson 2004).

Simultaneously we mapped the length of beaver-utilized shoreline, defined as shoreline previously or presently occupied by beaver as evidenced by the past and present location of lodges, dams, tree-felling and scent mounds. Beaver-utilized shoreline lengths were marked in the field on maps scaled 1:10,000 (Norwegian "Økonomisk kartverk" series) and measured to the nearest 100 m. Our goal was to reconstruct the original beaver territorial boundaries established as best possible, often defined by the remains of exploited vegetation and scent mounds (Nolet & Rosell 1994). Beaver occupy shoreline habitat on a rotational basis, apparently deserting an area when vegetation for food and building material becomes insufficient, returning some years later following sufficient regrowth (Hartman 1994; Parker et al. 2001b). Since the remains of beaver cutting and building activity normally remain visible in the landscape for decades, and most sites are reoccupied before old sign disappears, we were able to map most past and present beaver-utilized shoreline in the township. This was possible since most potential sites within the municipality presumably had been occupied at least once following the beaver's return 55 years previous (Hartman 1994; Parker et al. 2002a). Knowing the proportion of previously utilized sites that were occupied in any one year enabled us to also calculate the site occupation rate (occupied sites/all previously utilized sites), an indirect measure of the habitat quality within a township.

Landowner organization and quota allotment

Norwegian forest estates average small (≈50 hectares) (Nedkvitne et al. 1990), so most landowners must organize into alliances in order to receive a quota of at least one beaver. Typically, one beaver would be allotted per 300-500 hectares of beaver habitat (Parker & Rosell 2012). In Bø Township there were 13 landowner alliances (hereafter beaver management units) during the study in 1995 and 1996 that encompassed from 794 – 2200 hectares of beaver habitat, which at that time was defined as forest, bog or small lakes below the conifer tree-line, i.e. excluding most agricultural and urban landscapes (Steifetten & Uren 1997). This size range of beaver management units is typical for Norway (Steifetten & Uren 1997). These same management units were also issued annual hunting quotas for moose (*Alces alces* Linnaeus, 1758), red deer (*Cervus elaphus* Linnaeus, 1758) and roe deer (*Capreolus capreolus* Linnaeus, 1758). In 2002, new beaver management by-laws in Norway modified the definition of beaver habitat to encompass all habitat used regularly by beaver, i.e. now including agricultural and urban areas. Therefore many of the studies of colony density summarized in Table 1 encompass farmland.

Statistics

We determined whether the area of beaver habitat (areal model) or length of beaver-utilized shoreline (linear model) best predicted the number of occupied sites on beaver management units using least squares regression analysis. Means are shown with standard deviations. The level for statistical significance was set at $p \leq 0.05$.

RESULTS

Areal vs. linear model

Eleven of the 13 municipal beaver management units censused contained at least one occupied beaver site. For these 11 units there was no significant correlation ($p > 0.05$) between the area of beaver habitat on units and the number of occupied sites for both years (Figure 1). In contrast, the length of beaver-utilized shoreline on beaver management units correlated significantly ($p \leq 0.001$) with the number of occupied sites both years, explaining 82% of the variation in number of occupied sites in 1995 and 78% in 1996 (Figure 1).

Colony density in different Nordic landscapes

Though the published data on colony density for Eurasian beaver near carrying capacity in different Nordic landscapes is limited, the highest densities appear to exist in farmland and along low gradient rivers, followed by forest and alpine regions (Table 1). Pooling the areal data on colony density for forest, agricultural and low-gradient riverine landscapes gave a mean density of 0.26 colonies per km^2 (Table 1). The site occupation rate varied considerably from 28-100% but was 40% in the only study to date conducted on a larger landscape scale (Table 1).

DISCUSSION

Our results indicate that for the beaver management unit sizes (794-2200 hectares) and landscape types involved in this study, which are typical for Norway (Steifetten & Uren 1997), use of the areal model to allocate quotas to landowners is unreliable. In contrast, the linear model was a good predictor of the presence of occupied beaver sites. For many municipalities, gathering the initial background information on the location of beaver-utilized shoreline will entail an economic field-work expenditure, though in townships where the beaver population has already peaked and stabilized (Hartman 1994; Parker & Rosell 2012), gathering this information needs to be conducted only once. In contrast, mapping the area of potential beaver habitat in a township can usually be accomplished from the office using modern mapping technology only, e.g. Geographic Information System (GIS), which explains its popularity. In the future, managers should strive to gather more information on site occupation rate since it provides a measure of both habitat quality and the beaver harvest potential of different landscapes.

In those municipalities with little interest for beaver hunting and trapping (Parker & Rosell 2012), the extra precision provided by the linear model may not justify the added cost. Indeed, the present national harvest rate for beaver in Norway appears to be well below the estimated limit for sustainability (Parker & Rosell 2012). However, in those townships where the interest for beaver hunting and trapping is considerable or increasing, and where beaver management units are within the size range of those studied here, the linear model should provide the most effective means of predicting colony density and fairly dividing the quota among landowners. Use of the areal model to distribute the municipal quota to management units will also tend to under-harvest the population, since the smaller management units in particular will often receive a quota where no beaver exist.

As the area of beaver management units increases, so should the predictive power of the areal model, since progressively larger landscapes will increasingly include a more typical mixture of beaver habitat quality. Likewise, the areal model should function well in relatively small landscapes where good beaver habitat is evenly distributed. However, these landscapes are less common in Norway, so we suspect that areas in excess of 100 km^2 will often be necessary to attain acceptable precision using the areal model. This suspicion is supported by the small variation in colony density (mean = 0.26 per km^2, range = 0.20 – 0.32) reported from typical landscapes in southeastern Norway and south-central Sweden ranging in area from 105 – 10,580 km^2 (Table 1).

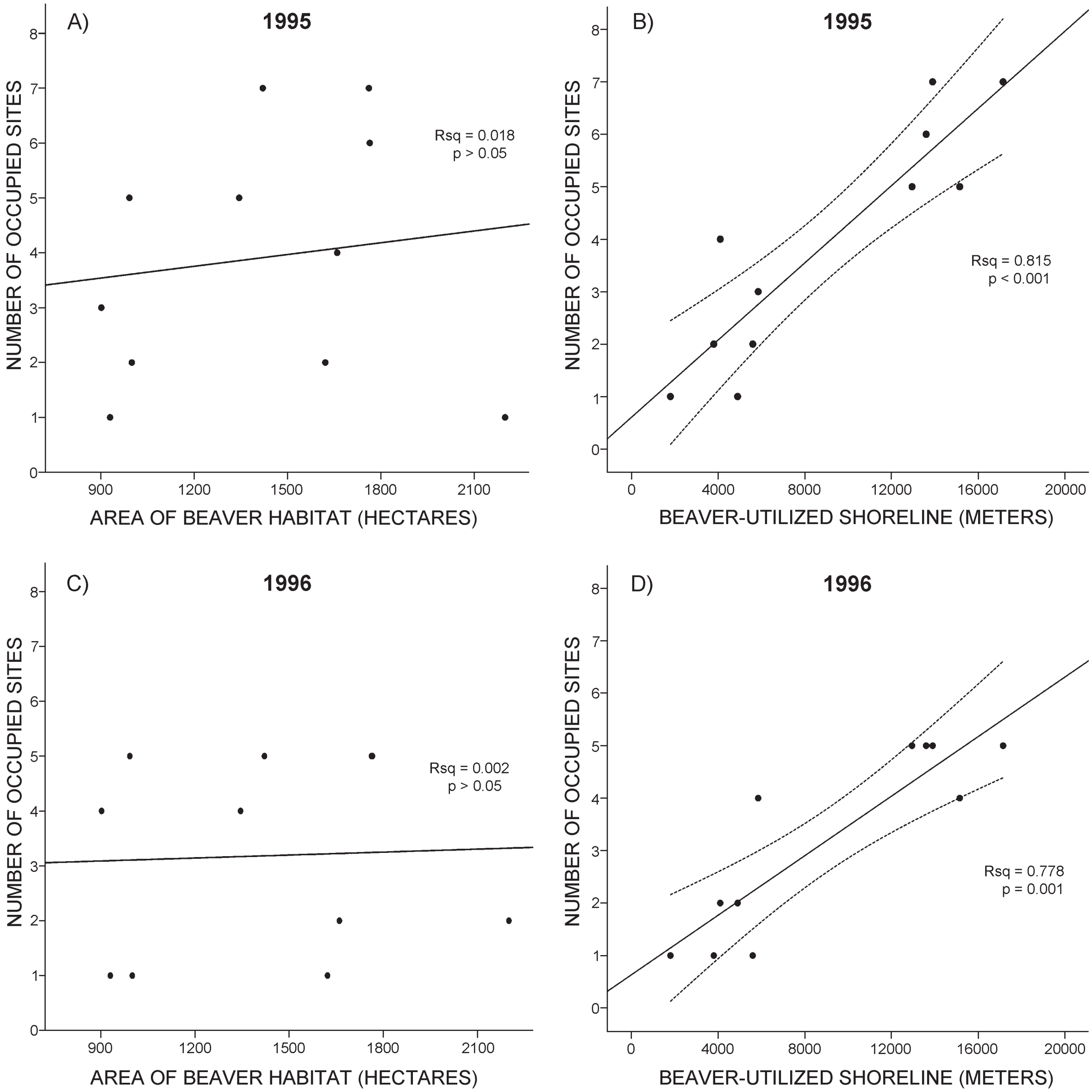

Figure 1. Regression of the number of occupied beaver *Castor fiber* sites on the area of beaver habitat (A and C) and the length of beaver-utilized shoreline (B and D) present on 11 moose hunting units in October 1995 and 1996 in Bø Township, Telemark County, Norway (2 points coincided in figure C). "Beaver habitat" here is defined as the combined area of forest, bog and small lakes below the conifer tree-line, i.e. excluding most agricultural and urban landscapes. "Beaver-utilized shoreline" is defined as all shoreline in rotational use by beaver within this same area of "beaver habitat", based on the presence of scent-marks, tree-felling, dams and lodges.

Management implications

For those Norwegian municipalities where the interest for beaver hunting and trapping is substantial and beaver management units range from normal to small in size, use of the linear model to allot the municipal quota to beaver management units will usually lead to a more precise and just distribution of the quota among landowners than the areal model, and most likely a better and less variable harvest success. In municipalities where interest is minimal, model selection will be of less consequence for population management since few animals will be felled in any case. The areal model will tend to increase in precision with increasing landscape scale, though presently we lack a sufficient data base to enable the development of predictive models. For all but the smallest municipalities in south-central Norway and Sweden with beaver populations at least 30 years old, a mean density estimate of one occupied site per 4 km^2 of beaver habitat should prove sufficiently precise for many management purposes.

Table 1. Mean areal density of beaver *Castor fiber* colonies in different landscapes and the mean linear density along low gradient rivers in Norway and Sweden. Hunting pressure at all locations varied from nothing to light, with seemingly little effect on colony density. Densities were measured after a minimum population occupation time of 25 years after which most populations, at the landscape scales presented here, appear to have stabilized near carrying capacity following initial peaks (Hartman 1994). Values in parentheses represent the landscape areas (km^2) and river lengths (km) involved in each study. The "Total" column shows density values for combinations of landscapes. Means are shown with standard deviations.

	Landscape Category							
Reference	Forest (F)[a] (colonies/km^2)	Agricultural (Ag)[b] (colonies/km^2)	Alpine (Al)[c] (colonies/km^2)	River (R)[d] (colonies/km)	Total[e] (colonies/km^2) (landscapes)	Census form[f]	Site occupation rate (%)[g]	Approximate Population Age (years)[h]
Campbell et al. 2005				0.50 (22 km)		Total count	100	70
Parker & Rønning 2007				0.40 (65 km)	0.32 (105 km^2) (F,Ag,R)	Total count		47
Hartman 1994					0.25 (10,580 km^2) (F,Ag,R)	Moose hunting teams		34
Hartman 1994					0.20 (3385 km^2) (F,Ag,R)	Moose hunting teams		25
Eikeland 2004		0.43 (30 km^2)				Total count	59	40
Bergan 2003	0.24 (128 km^2)					Total count		80
Parker et al. 2002b	0.22 (217 km^2)	0.50 (26 km^2)			0.26 (242 km^2) (F,Ag,R)	Total count	40	80
Mossing 2005			0.04 (165 km^2)			Total count	28	60
Mean values:	0.23±0.01	0.47±0.05		0.45±0.07	0.26±0.05			

[a] Primarily boreal forest < 600 m above sea level including smaller lakes and all streams.
[b] Primarily farmland. Most water sources have a forested edge.
[c] Primarily sub-alpine birch (*Betula pubescens*) forest or shrub willow (*Salix. spp.*) heathland 880-975 m above sea level.
[d] "River" refers to low gradient, meandering streams normally 20-80 m wide. Beaver territories encompassed both sides of the river. Therefore, territory length is measured midstream. Due to their low gradients, most sections of these rivers would typically be included in a territory.
[e] "Total" refers to the colony density when several landscape forms are combined into a single area, including rivers.
[f] All censuses were performed in mid to late autumn after most single beaver or family units had established a site location for the winter, usually with a food cache. Counts were either total ground counts made on foot or with a canoe, or based on counts made by moose hunting teams using a method reported to be reliable (Lavsund 1979, Hartman 1994).
[g] Proportion of previously occupied sites that were occupied at the time of each study.
[h] Approximate time in years from the first established colony in the area to the date the census was conducted. Figures were rounded off to the nearest decade when exact values were not provided.

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