

Distribution and patterns of spread of recolonising Eurasian beavers (*Castor fiber* Linnaeus 1758) in fragmented habitat, Agdenes peninsula, Norway

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The Agdenes peninsula, Sør-Trøndelag, Norway, 1060km², is a heavily dissected mountainous landscape with numerous small watersheds, of mainly steep gradient, flowing separately into the sea or to fjords. Suitable habitat for permanent beaver occupation occurs mainly as isolated patches within these watersheds. Eurasian beavers were directly reintroduced to the area in 1926 and 1928. The last known individual of this population died in 1961. In 1968-69 2 pairs and a young animal were reintroduced on the Ingdalselva watershed. The current population is descended from these animals, and probably from the later 1990s by immigrants from the adjacent Orkla river system. In 2010-11 the area was surveyed and 24 beaver family group home ranges located, 20 of which were currently active and 4 abandoned; the population size was estimated at about 80 individuals within family territories plus in any year a number of dispersing individuals. Eighteen of the active territories were located on just four watersheds, Ingdalselva and three immediately adjacent to it. The remaining two territories were isolated on different watersheds distant from any other known group, requiring multiple crossings between watersheds and/or considerable movements through salt water to reach from them. Signs of vagrant individuals were found widely, including on a number of watersheds not occupied by any family group, though containing suitable habitat for permanent colonisation. Known data on the date of establishment of each family group is given, and the pattern of recolonisation to date discussed. An isolated population of beavers on a section of the Orkla river system, first noted in 1933, has been attributed to spread from the first study area reintroductions. However, there are grounds to suspect that this population may have had a different origin. Genetic studies would be useful to elucidate this point.

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INTRODUCTION

Patterns of spread and population development in beavers have mainly been studied at the scale of large watersheds, and/or in areas where beaver habitat is relatively continuous and groups of territories lie contiguous to each other (e.g. Hartman 1994,

1996; Fustec et al. 2001; Elmeros et al. 2003; Berthelsen 2008; John et al. 2010; Sjöberg & Ball 2011). These studies indicate an overall pattern of rapid spread within a watershed and much more restricted spread between watersheds (Halley & Rosell 2002 for review). However, there is much less information

available on patterns of spread in more fragmented habitat, where areas suitable for beaver territories within a watershed occur as isolated pockets separated by large stretches of unsuitable habitat, and where there are many small watersheds in strongly dissected, mountainous landscapes.

Such areas are of interest as an example of a system where the pattern of movements of dispersing individuals (and of local extinction events) may be particularly important in influencing the realized distribution of the species. They are also of interest with respect to species management, as a model for patterns of colonization in areas of similar topography and hydrology. Such areas include much of western Norway, and northern and western Great Britain (where a trial reintroduction is underway in western Scotland (<http://www.scottishbeavers.org.uk/>), and a population has become established on the largest watershed (Tay) apparently as a result of escapes (Halley 2011).

In this paper we present a study of beaver distribution in an area of active beaver colonisation, the Agdenes peninsula in Sør-Trøndelag, Norway (Figure 1); along with evidence of non-resident beaver movements in the area. The pattern of distribution is interesting in itself, and is intended to provide a baseline to be compared with developments in population and distribution over time. The history of beavers in the study area is reviewed from the information available.

MATERIAL AND METHODS

The study area (Figures 1, 2, 4) consists of all watersheds on the Agdenes peninsula in Sør-Trøndelag province, central Norway, excluding the watershed of the Orkla river system, which bounds the area to the south. This area includes all of mainland Snillfjord and Agdenes kommuner (local government districts), and those parts of Orkdal kommune which are not drained by the major Orkla river system, an area of approximately 1060km². The underlying geology is schists, gneisses and granites of the Caledonian orogeny. Terrain is steeply hilly; elevations range from sea level to 847m. Drainage is via many small watersheds draining separately into fjords or the sea and usually divided from each other by steep ridges, but with low-gradient cols between them in places (as a result of previous glacial action). Rivers and streams are mainly well over 2% in average gradient, the gradient above which beavers rarely establish territories (Slough & Sadleir 1977; Howard & Larson 1985; Beier & Barrett 1987; Zurowski 1992; Rosell & Pedersen 1999; Hartman & Törnlov 2006; Nyssen et al. 2011), with frequent cataracts and waterfalls. Coasts and fjord sides are in most places very steep or precipitous. Sites suitable for colonisation generally occur as isolated patches with sufficient habitat for only a single territory. The vegetation is southern boreal at sea level, sequencing with altitude through middle and northern boreal to alpine on higher peaks. The area is heavily wooded, mainly Scots pine *Pinus sylvestris* Linnaeus, 1753; Norway spruce *Picea abies* Karsten, 1881; and birch

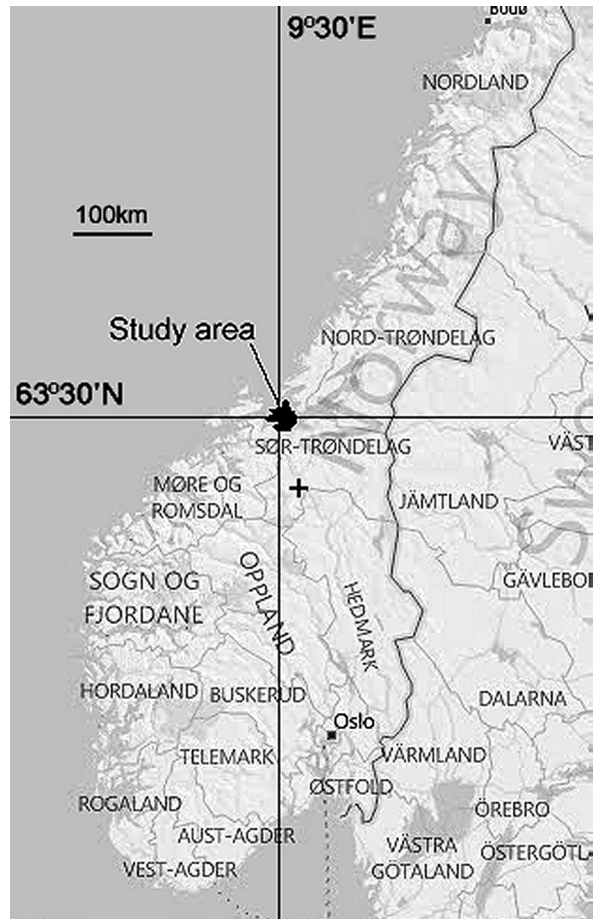


Figure 1. Study area (black) in relation to southern and central Norway. The location of the Ulsberg-Voll section of the Orkla river is indicated by a cross.

Betula spp.; but with rowan *Sorbus aucuparia* Linnaeus, 1753; bird cherry *Prunus padus* Linnaeus, 1753; grey alder *Alnus incana* Linnaeus, 1753; willow *Salix* spp.; and aspen *Populus tremuloides* Linnaeus, 1753 present in varying proportions.

The terrain is such that several of the main watercourses change name as they flow towards the sea, sometimes more than once, reflecting paths of, and barriers to, access for the human population in times past. In this article each watershed is referred to by the name it has where it reaches the sea. Terrain and vegetation can be examined in detail from maps and satellite imagery available at <http://kart.statkart.no/adaptive2/default.aspx?gui=1&lang=1>.

Coppice regrowth of trees felled by beavers is vigorous, despite considerable populations of moose *Alces alces* Linnaeus, 1758; red deer *Cervus elaphus* Linnaeus, 1758, roe deer *Capreolus capreolus* Linnaeus, 1758; and in summer domestic sheep *Ovis aries* Linnaeus, 1758. The climate is oceanic. Summers are generally cool and moist; winters mildly cold with variable, but in most winters appreciable, snow cover. Most slow flowing sections of watercourses and all lakes freeze over for several months in winter.



Figure 2. Part of the study area, showing typical landforms and vegetation. The river and bog at left are the site of beaver territory 10 (see Figure 4). Photo: D.J. Halley

Records of beaver occupation, and collection of historical materials on the population, were made by the first author from 1995 onwards. Although beavers are game animals in many areas of Norway, they have been a protected species in the study area (and on the lower Orkla) throughout the period from reintroduction onwards.

Systematic studies of current distribution were carried out in May-July of 2010 and 2011. All stream and riverbanks, and lake shores, in the field area not clearly unsuitable for sustaining settled beavers (above the tree line or very steep channel gradients, above ca. 4%) were visited by the authors on foot and/or by canoe in each year, and checked for signs of beavers. Known territorial sites were also checked in the autumn of 2010-spring 2011 for signs of food stores and of recent activity. Occupation of a site was confirmed by the presence of beaver structures such as lodges or dams with signs of recent activity, e.g. mud plastering; by fresh tracks; trails in the snow; the assembling of food stores (autumn only); and/or the presence of recently cut stumps, twigs, and chewed sticks. Such activity was normally very obvious. Where there were no signs of recent maintenance of structures, or of any recent stumps, stripped twigs, food stores, etc. (some beavers in our study area live in burrows and most do not build dams (Table 1), so many territories do not have any visible beaver structures at all), the site was assumed to be inactive. Where we found only one or a few stumps or cut twigs remote from established territories these were taken to be evidence of vagrant individuals and not settled family groups. These could be divided into fresh signs, made since the spring of the year of monitoring, and older signs.

From the later 1990s beavers also established territories on stretches of the Orkla river system adjacent to the study

area (Bonvik & Rønning 2006; see below, Figure 4). There are no known beaver populations on the north and northeastern shore of Trondheimsfjord opposite the study area (the Fosen peninsula); on any of the offshore islands to the northwest; or in Hemne kommune or More & Romsdal province, which lie to the west and southwest of the study area.

RESULTS

Historical records and many place names indicate the species was common and widespread throughout Trøndelag in historic times, including the study area (e.g. Bjørbekken, 'beaver stream', Table 1). The original population is thought to have been exterminated by the early part of the 19th century. The last animals in Sør-Trøndelag are said to have been trapped out by a



Figure 3. Release of beavers on the Songli property, 1926 or 1928. Photo from Songli Pictorial Archive; photographer unknown.

“Swedish Lapp” in Selbu/Tydal about 1820-1830 (Collett 1898; Bevanger 1995).

A pair of beavers from “the fringes of Arendal (*Arendalskanten*)”, southern Norway, were reintroduced to the large Songli property, which lies on the Skjenaldelva and Bergselva watersheds, in 1926¹ (*Sør-Trøndelag* newspaper, 28 August 1926). The site of this release was in 1929 reported to have been in Grytdalen, ie upper Bergselva watershed near Melandsøya, current site 14 (Figure 4) (*Sør-Trøndelag* newspaper, 12 September 1929); however, in October 1926 a memorandum from C. Thams which has survived (Songli private records, J. Andøl *pers. comm.*) states “The beavers: we need to find out where the beavers are living, and if it is on Våvatnet (site B, Figure 4) the ice must be broken and necessary measures taken ... so they are not excluded from water”. This clearly implies they were reintroduced at Åmottjønnå near Våvatnet (site A, Figure 4), as stated in Olstad (1937) and by E. Carlsen (*in litt* to K. Brox 7 October 1965); but had moved from the release site.

A further pair were reported to have been released in 1928 ‘by Songsjøen’, the lake holding current site 9, (*Sør-Trøndelag* newspaper, 12 September 1929) probably again meaning Åmottjønnå.

It is probable that a further pair was also released in Grytdalen in 1928 (see above), as sources after this date repeatedly allude to a release also having been made there. E. Carlsen, who lived locally, states this was done (*in litt.* to K. Brox, 7 October 1965). Olstad (1937), however, states that all 6 animals were released at Åmottjønnå.

In 1929 a beaver was seen on 3 consecutive evenings on Våvatnet² (site B, figure 4) and a group of rowans felled at Vådåosen at the west end of the lake (letter in *Sør-Trøndelag* newspaper, 24 September 1929). The writer assumed they had come from ‘the beavers which were released in Grytdalen’. Beavers were reportedly present at Våvatnet until 1938 (Lindsetmo 1974). Beaver-gnawed trees were also noted at Melås on Gagnåsvatnet (midway between current sites 5 & 6, Figure 4) in September 1929 (*Sør-Trøndelag* newspaper, 12 September 1929). A probably vagrant individual was shot at

Hostonvatnet (site C, Figure 4) on the Vormå tributary of the Orkla “at the beginning of the 30s” (Pedersen 1967), apparently mistaken for an otter (E. Carlsen 1965, *in litt* to K. Brox).

Beavers bred at the Melandsøya site within two years of the initial release there (Møller 1967) and also established downstream at Auset in 1928 (current territory 16, Figure 4; Olstad 1937, who assumes spread from Åmottjønnå), where they bred and were present “for many years” (*Sør-Trøndelag* newspaper, 25 April 1959) and noted as being very active in 1936-7 (Lund 1959). Melandsøya was occupied until 1942-43, abandonment of the site being attributed to heavy harvesting of deciduous trees by the then owners; and later beavers were noted at Austvatnet (site D, Figure 4) in the Lena watershed and at Rangvatnet (site E, Figure 4) and Butulsvatnet (site F, Figure 4), and lower Ingdalselva, all in the Ingdalselva watershed. A dead beaver was washed up at Ålmli in Orkdalsfjorden, 3km NE of the mouth of the Skjenaldselva, in the 1930s (E. Carlsen 1965, *in litt* to K. Brox). Old beaver signs were found on an Orkla tributary at Svorkåsen, 3km ESE of current site 4, in the 1930s (Olstad 1937). A beaver was killed at Orkland near the Vormå-Orkla confluence ‘about 1932’ and one killed in a trap in Hemne kommune, SW of the study area, in 1932 (*op. cit.*). This last animal probably dispersed down the fjord from Bergselva. The last known individual descended from this reintroduction died on the Ingdalselva watershed in spring 1961 at Snåkkåsdalbekken, the same location as the current site 13 (Figure 4) (K. Brox *pers. comm.*; Møller 1967; Pedersen 1967).

The present population originates from a new reintroduction to the area, planned from 1965 by Karl H. Brox and Emil M. Carlsen. A pair was obtained in 1968 and was released on the Ingdalselva watershed (which holds current territories 11 – 13) on 1st September. The release was originally planned for Almlisletta (site G, Figure 4; K. Brox *pers. comm.*), a small marshy area at relatively high elevation (390m asl) in Husdal Statsallmenning (*State common land*), but in fact took place at Snåkkåsdalbekken (current territory 13, Figure 4; Møller 1967; *Sør-Trøndelag* newspaper, 3 September 1968; Carlsen 1972)³. By the following year they were present at Butulsvatnet (site F, Figure 4), a small lake at 180m asl on a tributary of the Ingdalselva (E. Carlsen *in litt* to K. Brox, 1969) and had constructed a lodge (*Adresseavisen* 24 September 1969). A further pair and a young animal were reintroduced in 1969, to the same site at Snåkkåsdalbekken, by Sør-Trøndelag Skogforvaltning (*South Trøndelag Forest Authority*) (*Adresseavisen* 24 September 1969; Carlsen 1972; Holgeir Oppdal *pers comm*). All 5 animals were obtained from Åmli, Aust-Agder, southern Norway. Breeding was confirmed in 1970, though the location was not specified (Møller 1970). By the end of 1973 beavers had occupied at least 4 sites on the Ingdalselva watershed (sites F, 11, 12, & 13) and another at Bjørbekken on the Skjenaldelva watershed (site 2); the population was then estimated ‘with certainty’ to be at least

3. Myrberget (1977) states that the releases were at Songli, on the Skjenaldelva watershed near the current site 10, and this is cited in several later sources; but is an error.

1. Published sources vary in the exact location(s), watershed(s), years, and numbers released (4 or 6) given for the 1920s releases though all agree that: the location was the Songli property in the Skjenaldelva and Bergselva watersheds, then owned by industrialist C. Thams and associates and - unusually for Norway - managed as a hunting estate; that releases were in two different years; and that one pair at least (and up to all three pairs) were released near Songli farm, most later sources naming Åmottjønnå, following Olstad (1937). The account here follows information in Songli archives, published sources by individuals with personal knowledge of the area and of the 1920s - 1961 population, accounts in local newspapers of the time, and other published sources in that order of priority.

2. Våvatnet is now regulated as the drinking water supply for Orkanger and shorelines are not suitable for colonisation

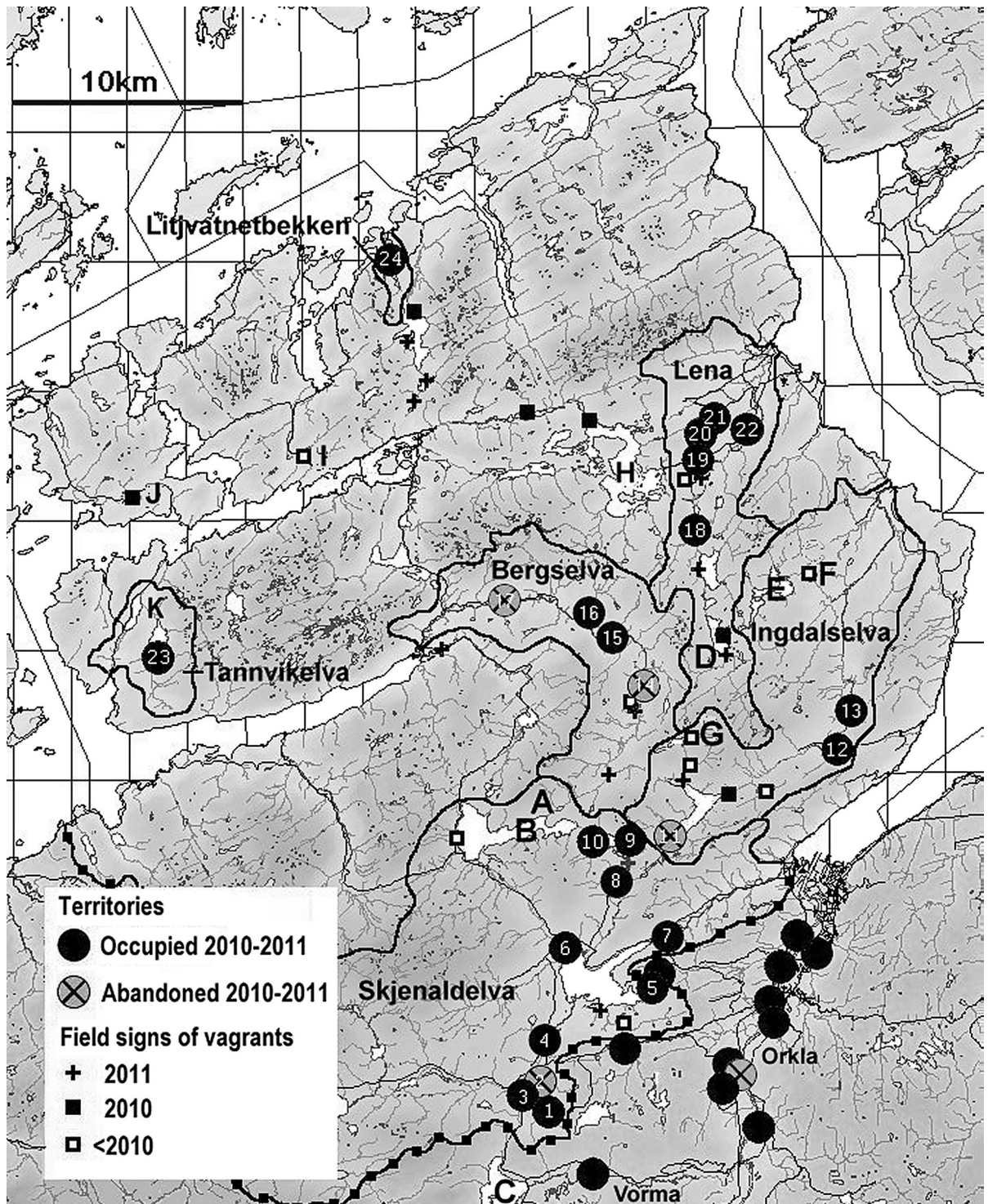


Figure 4. Study area, showing the location of active and abandoned beaver territories in 2010-2011 and of signs of vagrant beavers where no territory is established. The thick black line with squares indicates the land boundary of the study area on the south and west (see text for details), and plain black lines boundaries of watersheds in the study area containing beaver territories. These watersheds are named. The position of the lower Orkla river and its Vormå tributary are indicated. Territory symbols are centred on the active den, or apparent most recently active den for abandoned sites. Numbers for territories are as in Table 1. Territories shown without numbers are outside the study area, on the Orkla river watershed. Letters indicate the position of places mentioned in the text. "Field signs" for vagrants 2010 and 2011 were judged to have been made in the period late April-July of the year named, for <2010 at any time before 2010. Data for the Orkla watershed: Bonvik & Rønning 2006 and *pers. obs.* Map: ArcView/ESRI

27 (Lindsetmo 1974).

An isolated population of beavers on the main Orkla river as far away as the ca. 20km long section between Ulsberg and Voll in Rennebu kommune (Figure 1), first reported at Eggjabakken in 1933, was attributed to spread from the 1926 reintroduction (Olstad 1937). An occupied lodge in this section was recorded in 1933-34; beavers were seen in 1938 and 1940, when another lodge was built at Brattset at the Orkla/Ea confluence (UTM NQ639556). Beavers were noted as present at or near this site in 1941 (Skogdirektøren 1943), but had gone by 1945 (Torp 2000a). 1945-50 beavers were reported on the same section at Flå; and again from 1952-63 (Torp 2000a). In 1961 an entire lodge, apparently not from Flå, was washed downstream from this river section, and 'vagrant' signs were recorded in the Orkla from 1960-65 (Myrberget 1967, 1969). Beavers were also resident on the upper Svorka, a tributary of the Orkla, in the late 1940s (Torp 2000a,b) at Svahyllan (ca. UTM NQ927457), which can be reached from the Ulsberg-Voll section either by swimming down the main Orkla and up the Svorka, or (more probably) by a short overland crossing from side streams of the section.

Myrberget (1977) considered that the species was extinct throughout Sør-Trøndelag in 1965; however, beavers reappeared in the Ulsberg-Voll section of the Orkla from 1974 (signs considered from a vagrant animal, Myrberget 1977). From the late 1970s they were recorded as again established at Brattset and at Voll (Torp 2000a; Bonvik & Rønning 2006), though as late as 1991 Eklid & Grindal (1991) considered there to be only one occupied territory on the Orkla, at Voll. Continuity from the 1970s with the earlier population must be strongly suspected, the alternative explanation being a repeat long-distance recolonisation from the study area, this time involving two watershed crossings or a long movement through Orkdalsfjorden before entering the Orkla. Dispersal into the Orkla from the Glomma watershed to the east (recolonised NE of Røros from Swedish watersheds from the later 1960s (Hartman 1995), and spreading throughout the Glomma 1975-1985 (Bevanger 1995)), is also possible from the 1970s and later. The species recolonised the main Orkla river away from the Ulsberg-Voll section only from the later 1990s, and is still at relatively low densities on tributaries (see Torp 2000a, 2000b, and Bonvik & Rønning 2006 for a review of historical data).

The distribution of beavers in the field area in 2010-11 is shown in Figure 4, and each currently or formerly established territory briefly described in Table 1.

There were 24 beaver territories, 20 currently active and 4 sites which had formerly been the site of territories but were now abandoned. In 10 of the active territories, the main den was a burrow; in 6 a lodge, in 3 burrow-lodges (which begin as burrows but end as lodges), and in one case a lodge-burrow (which begins as a lodge but ends as a burrow). Two of these occupied territories (7 & 12) had been noted as abandoned in 2010 but were reoccupied by 2011. One other territory (9) was certainly new, established in 2011. Two of the abandoned sites

clearly contained insufficient suitable habitat to sustain beavers for more than a few years (site 2 is a small stream in forest bog habitat with at time of colonisation only scattered and small trees; and site 17 is a single pool in a river with long stretches of high gradient rapids above and below the site). All four showed evidence of local depletion of deciduous trees by beavers.

Eighteen of the active sites, and all of the abandoned sites, were located on just four watersheds. Two other watersheds had a single established territory each, and there were signs of non-resident beaver presence on four other watersheds where no territorial groups were established. Fresh beaver signs, indicating the presence of nonresident beavers during the period of the survey, were noted for 3 of these watersheds in 2010; fresh signs of presence were noted for one of these watersheds in 2011 as well. Signs in the remaining watershed all dated from before 2010.

All of the watersheds on which nonresident beaver activity was noted had suitable habitat patches for at least one, and as many as six or more viable beaver territories (site H, Figure 4: Øyangsvatnet lake and the river system into which it drains). Many other watersheds on which no beaver presence was detected also contained suitable habitat of sufficient extent for one or more beaver territories.

DISCUSSION

Beavers are at an intermediate stage in their recolonisation of the study area, and further spread can be anticipated in future. Assuming an average group size of 3.9 (Rosell & Parker 1995; Rosell et al. 2005), the results suggest a current territorially-resident population of about 80 individuals, plus a number of nonterritorial dispersing individuals in any year.

Although it is now 43 years since reintroduction to Ingdalselva, beaver are only securely established on that and three other watersheds (Bergselva, Skjenaldelva, Lena). On those watersheds most or all of the good-quality habitat patches are occupied, with clearly marginal sites such as 1, 2, 7, & 15 either in use or now abandoned. Most stream stretches on these watersheds are too steep to occupy (see Methods), and many lake shorelines too exposed to wave action to build lodges. In both cases many stretches are unsuitably vegetated with pure conifer stands. Some sites on these watersheds are known to have had repeated cycles of occupation and abandonment; at site 13 at least 3 separate periods of occupation are known. This is typical of relatively marginal sites in mature populations, where beavers consume broadleaf woody resources more quickly than they can regenerate and, following resource exhaustion and abandonment, can only reoccupy the site after a period of regeneration. Single groups are relatively recently established on two more watersheds, and these have both selected high quality habitat patches. This pattern is in accordance with other studies, which show a pattern of rapid colonization within watersheds, strong selection for the highest

quality unoccupied habitat available, progressive lowering of the quality of habitat on which settlement occurs as a watershed population grows, and a strong barrier effect of watershed divides on dispersal (Hartman 1994, 1995; Fustec et al. 2001; John et al. 2010; Halley et al. 2002 for review). Beavers are known to have colonised site 2, on Skjenaldelva watershed, within 5 years of the initial release on Ingdalselva. However, the crossing from the early-occupied site 11 into Skjenaldelva near current site 9, is a low col bottomed by forest bog, with site 11's home stream separated by only a few hundred metres from Skjenaldelva headwaters.

While the beavers on the Ulsberg-Voll section of the Orkla (Figure 1) have been attributed to spread from the 1928 Åmotstjønna reintroduction (1930s-1960s population), and again from the 1967-68 Ingdalselva reintroduction (1974- population), this section of the river, about 85km from Åmotstjønna assuming spread via the Vorma tributary of the Orkla (the shortest route by water, with a relatively short land crossing between watersheds), is for most of its length a remote and heavily wooded, steep-sided gorge rising 200m directly from the riverbank, very difficult of access to humans. It emerges into a flatter valley bottom of mixed woodland and fields at Flå, 8km above Voll. The records mainly relate to more accessible points on this stretch. The topography and vegetation in the gorge is such that beavers could live in burrows with few obvious signs of presence, so it is possible these beavers may have been descendants of a remnant of the original population which survived at this location. Colonising beavers usually either occupy sites adjacent to existing territories, or make longer distance dispersals to patches of high quality habitat some distance from existing territories (Fustec et al. 2001; John et al. 2010; Halley & Rosell 2002 for review). The pattern in Ulsberg-Voll from the 1930s-1970s is consistent with short-distance colonisations from a refuge in the gorge, which is then noted by the human population of the wider-bottomed river valley below. Beavers were known to be living in the gorge for 'many years' in the mid-20th century (Voll pers. comm. in Torp, 2000), and do so today. The 1933 occupied lodge would require a colonisation from Åmotstjønna/Våvatnet over at least 85km within 5 years (as the reintroduced pair did not breed in the first year, and dispersal occurs at the earliest at one year old, i.e. in 1928), from a reintroduction stock of at most six animals on a different watershed. Once in the Orkla, colonising animals would have to pass upstream through successive 14km, 7.5km and 5km river sections too steep and fast for beaver occupation, *en route*. Both a male and a female would have to make the trip separately, as dispersal occurs as individuals. The furthest known colonisation distance previously recorded is of 80km, on the Loire, but this did not involve a watershed crossing and was on a river on which beavers were already firmly established (Halley & Rosell 2002; Fustec et al 2001). Conversely, persistence of a population which went unrecorded in print for over a century seems unlikely, even in so remote a location. Genetic studies would be useful to determine the

origins of this population.

Whatever the origins of the Orkla population, the population there was at low numbers and of very restricted distribution until the 1990s. The present population in the field area therefore appears to be mainly descended from the 5 animals released in 1968-9 on the Ingdalselva, probably supplemented since the later 1990s by immigrants from the Orkla watershed. The part of the field area within Orkdal kommune, as well as the middle and lower course of the Orkla and its major tributaries, were surveyed in 2005 by Bonvik & Rønning (2006).

The study area contains many small watersheds; dispersal between them requires either crossing land, or swimming for some distance through salt water and then ascending the terminal stretch of the river/stream, which is in most cases much too steep and rapid to swim through for some distance beginning either at, or very close to, the point where it reaches the fjord/sea. The pattern of distribution suggests that land crossings may have been the way in which the three main occupied watersheds (Skjenaldelva, Bergelva, Lena) to which beavers were not directly reintroduced were colonised. All could have been reached from the headwaters of the Ingdalselva system, and Lena-Bergelva and Skjenaldelva-Bergelva from each other, by single, short overland crossings between side streams in gently sloping cols between hills. Site 23 was most likely colonised by animals dispersing from Bergselva and through the fjord into which it drains, which would involve swimming through ca. 15km of sheltered salt water. The watershed at site 23 is unusual for the area in being of relatively low gradient where it reaches the fjord; while most stretches are nevertheless too steep for colonisation, only one short stretch some way inland is so steep that beavers would have to leave the water and walk (site K, Figure 4; territory 23 lies upstream of this stretch). Site 24 is difficult to interpret, colonisation involving either crossing three watershed divides, swimming for an extended distance through salt water, or a combination of the two. Litjvatnetbekken is a stream which is much too steep to swim through in its final 2km to the sea, so if the animals ascended that way they must have walked in or beside the stream bed.

In 1970 a beaver was found fatally injured (shot) on the coast of Trondheimsfjord at Trolle near Trondheim (*Adresseavisen* newspaper 12 August 1970)⁴. By far the nearest population was the new reintroduction at Ingdalselva. Ingdalselva is 21km away through salt water; 26km assuming following the coastline, including a 5km crossing of the mouth of Orkangerfjord (there is no plausible freshwater route).

There is extensive movement of non-territorial beavers both within colonised watersheds and in watersheds without established territories. Signs of beaver presence are frequently found at sites which would be suitable for settlement, implying that single individuals do not settle permanently at a site unless

4. The newspaper photograph shows an adult size animal. This may have been the third individual of the 1969 Ingdalselva release.

Table 1. Beaver territories in the study area. The table includes all sites where fieldwork in 2009-2010 indicated a territorial family group was, or had been, established. "Watershed" indicates the watershed the territory occurs on, named after the main river of the watershed as given on official Statens kartverk maps where it reaches the sea (NB the name of the main river of the watershed changes along its course in several cases). "Current den" indicates the type of the main den in use in 2011. "Burrow" indicates a hole dug in the bankside; "Lodge" a construction of sticks and mud; "Burrow-lodge" a den beginning as a burrow but leading to a stick lodge; "Lodge-burrow" a den beginning as a stick lodge but leading to a burrow. "Abandoned" indicates a site formerly occupied by a family group but not currently occupied. "Dams" gives the number of dams in the territory; "old" indicates breached dams no longer maintained or affecting water levels. "Established" indicates the information available on when the site was first occupied by a family group. "UTM (den)" gives the 6-figure UTM map reference for the current main den of the family group.

Nr	Territory	Watershed	Current Den	Dam(s)	Established	UTM (den)	Remarks
1	Bjørbekken Øvre	Skjenaldelva	Burrow-lodge	1	ca.2007 ¹	32V 305102	Low dam flooding large forest bog area. Deciduous trees depleted, likely to be abandoned soon.
2	Bjørbekken Nedre	Skjenaldelva	Abandoned	5 old	1973 ²	32V 302116	Stream. Several breached dams and old lodges, deciduous tree supply exhausted.
3	Egga	Skjenaldelva	Burrow	1 & 1 old	ca. 2009 ¹	32V 333108	Stream. Deep 'plug' dam between levee banks on canalized stream, creating new and actively developing stream course through edge of field adjacent. Abandoned dam 300m upstream.
4	Svorkmyran	Skjenaldelva	Burrow	1	ca.1983 ³	32V 303133	Long-established marshland site. Recent (2009-11) small dam on side stream.
5	Gagnåsvatnet Vollaika	Skjenaldelva	Burrow	1	Before 2005 ³	32V 348156	Small 'plug' dam on artificially deepened stream just before enters lake, at burrow location.
6	Gagnåsvatnet Hyllbekken	Skjenaldelva	Burrow-lodge	1 old	ca.1983 ³	32V 312173	Long-established streamside marsh and woodland site. Dam breached by spring floods ca. 2003, 2 years after built, and not repaired.
7	Gagnåsvatnet Bru	Skjenaldelva	Burrow	0	2008 ¹	32V 356178	Narrow arm at outflow of large lake. Occupied, abandoned, and reoccupied since 2008.
8	Songa Trolldalen	Skjenaldelva	Burrow	1 old	2008 ¹	32V 335202	River. Marginal site on pool on river which is otherwise too steep and rapid for occupation.
9	Songsjøen	Skjenaldelva	Lodge	0	2011 ¹	32V 339215	Lake. Newly established 2011, lodge in tiny recess in shore protected from prevailing wind.
10	Songlia	Skjenaldelva	Burrow-lodge	1 old	1999 ¹	32V 324221	River. Large dam at site maintained for several years but now breached.
11	Fjellkjøsvatnet Sør	Ingdalselva	Abandoned	0	1972 ⁴	32V 357221	Stream where enters lake. Deciduous wood supply exhausted but much recent regeneration. Apparently abandoned in 1980s after 'many years' of occupation (Bangjord 1991).
12	Husdalsvatnet	Ingdalselva	Lodge	0	1971 ⁵	32V 431258	Lake. Occupied 1971 and newly abandoned by November 1973 (Sør-Trøndelag newspaper 8 November 1973), possibly due to disturbance. 'Newly occupied' in 2005 (Bonvik & Rønning 2006), but abandoned in 2009-10 and possibly for some years before, reoccupied 2011.

Continued next page.

Table 1. Continued

Nr	Territory	Watershed	Current Den	Dam(s)	Established	UTM (den)	Remarks
13	Snåkkåsdal- bekken	Ingdalselva	Lodge	0	1969 ⁶	32V 430288	River. Pool and riffle habitat in woodland. Last known site occupied by descendants of 1920s releases, to 1961. Release site of all 5 animals in 1968-1969 reintroduction. Not present in 2005, when area surveyed by Bonvik & Rønning (2006), but many recent and older signs of occupation in 2010.
14	Melandsoya	Bergselva	Abandoned	0	<1995 ¹	32V 342296	River. Pool and riffle habitat in woodland/forest bog. Fresh signs every year but not permanently inhabited for some time; dates of permanent occupation unknown but extensive old felling.
15	Ausetøya, Berg	Bergselva	Burrow	0	2009 ¹	32V 333307	River. Short stretch (ca.200m) pool and riffle habitat in woodland, between stretches too steep for occupation. Some fresh signs but not certainly occupied by family group in 2011.
16	Ausetsetra, Berg	Bergselva	Burrow	0	<1995 ¹	32V 323318	River. Meandering low-gradient river stretch with riparian woodland between fields.
17	Saghaugen, Berg	Bergselva	Abandoned	0	?	32V 287323	River. Marginal site on pool on river which is otherwise too steep and rapid for occupation.
18	Valtjørna	Lena	Burrow	0	Long established in 2010 ¹	32V 368353	Long-established forest bog site but deciduous wood near depletion.
19	Fiskeløysa	Lena	Lodge	0	Long established in 2010 ¹	32V 367383	Lake. Exceptionally large lakeside lodge.
20	Frostadvatnet	Lena	Lodge-burrow	0	2010-11 ¹	32V 369393	Lake. Unusual den construction, burrow with stick-built extension into water on shallow, low-gradient bank. Apparently new 2011.
21	Frostadbekken	Lena	Lodge	0	2000 ³	32V 375403	Stream where enters lake. Large old-established lodge by roadside. Establishment date Bolsoø pers.comm. in Bonvik & Rønning (2006).
22	Lena Vadbrua	Lena	Burrow	0	Long established in 2010 ¹	32V 394407	River. Location given road bridge - burrow site unclear. Old-established site on meandering river stretch in farmland.
23	Ø. Heggstad- ssetervatnet	Tannvikelva	Burrow	0	Before 2005 ³	32V 137298	Stream where enters lake. Old established site, occupied by 2005 (A. Monsen pers.comm. in Bonvik & Rønning 2006). No signs activity elsewhere on watershed despite good habitat.
24	Lijvatnet	Litjvatnet- bekken	Lodge	1	2009 ⁷	32V 236471	Lake. Large dam on stream running out of lake, just downstream lodge, under active development 2010 & 2011.

¹ Authors, pers. obs., ² *Sør-Trøndelag* newspaper 8 November 1973; Lindsetmo 1974, ³ Data from historical discussion in Bonvik & Rønning 2006, ⁴ *Sør-Trøndelag* newspaper, 24 August 1972; Carlsen 1972, ⁵ *Sør-Trøndelag* newspaper, 22/07/1971, ⁶ *Sør-Trøndelag* newspaper 9 September 1969; *Arbeider-avis* newspaper 12 September 1969; Carlsen 1972, ⁷ L. Ramvik & A. Staverløkk, pers. comm.

they can find a mate. This may explain the longer distance colonisations of sites 23 and 24, as in part being due to fortuitous meetings of opposite-sex wandering individuals. Almost nothing is known of dispersal behaviour, however. Radio telemetry using GPS tags would be very useful to elucidate this area if the formidable practical problems of capturing dispersing or pre-dispersing individuals, and keeping the tags on them for a long enough period, can be solved. In at least two cases where vagrants were present on short streams connecting directly to a fjord (sites I & J, Figure 4), movements of some distance through salt water in fjords followed by ascending fjord-wall stream stretches much too steep to swim through, appear the only plausible line of approach.

It is intended that the further pattern of recolonisation of the area will be monitored from the baseline established here, in succeeding years. In particular we hope to obtain better information on the strength of watershed crossings as barriers to dispersion, and whether salt water acts as a barrier to, or facilitates, dispersion between watersheds.

For management of populations, the data suggest that in similar dissected landscapes beavers can be limited as an established breeding species to selected watersheds if desired, provided that occasional colonising pairs on new watersheds are removed before they have the chance to breed. The activity required can be measured in interventions per decade. Conversely, if a wide distribution is desired, a strategy of multiple releases to different watersheds is indicated. The

extensive signs of vagrant individuals suggest that where beavers are already established, beaver movements between watersheds will be sufficient to maintain gene flow without further translocations.

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Our sincere thanks are due to Karl H. Brox, who made available considerable material on the history of the 1968-69 reintroduction as well as private correspondence on the reintroduction with E.M. Carlsen and others. Johan Andøl and Holgeir Oppdal provided supplementary information. Livar Ramvik and Arnstein Staverløkk reported new establishments and old and new signs of vagrant beaver. Bonvik & Rønning's 2006 investigation of beavers on the Orkla was invaluable for information on the Orkla population, and on the status of beavers in the Orkdal kommune section of the study area in 2005. This work and Torp's 2000 reports on beavers in Meldal and Rennebu were similarly invaluable for the history of beavers on the Orkla. Kjetil Bevanger provided a fascinating archive of newspaper clippings on beaver in Norway 1959-74 saved from the Department of Nature Management dustbin, which provided



Figure 5. Founders of the study population at the release of the first pair, Snåkkåsdalbekken, 1st September 1968. Left-right: Kåre Klebo (forest manager); Karl H. Brox; Emil M. Carlsen; Einar Møller (leader, S Trøndelag Nature Protection Society); Einar Hjorthol (head of Sør-Trøndelag Forest Authority). Photo: Orkla-Posten newspaper, 12 September 1968.

much detail on the early stages of the 1968-69 reintroduction and cleared up some points where later sources conflicted, such as the exact reintroduction site. Two anonymous reviewers provided constructive criticism which significantly improved the paper. Part of the survey in 2010-11 was carried out in the course of work for the EnviPeak programme of the Centre for the Environmental Design of Renewable Energy (CEDREN).

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