

Colonization, riparian habitat selection and home range size in a reintroduced population of European beavers in the Loire

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SUMMARY

1. Colonization in a reintroduced population of European beavers in the Loire Valley was studied between 1974 and 1999. It followed a discontinuous remoteness model and a scattered distribution, beavers occupying only 25% of the river system over the 2800 km explored.
2. After 5 years, the colonization rate reached 104.2% year⁻¹ of new sites occupied (SD 75% year⁻¹), before dropping over the next 20 years. Nevertheless, the number of new colonies per km (0.125) remained stable throughout the years.
3. *Populus nigra*, *Salix alba* and *Fraxinus angustifolia* were the dominant woody species in beaver sites, often associated with some herbaceous species.
4. The length of willow grove dominated by *S. alba* and *P. nigra* (x) was the best predictor of beaver home range (y), fitting the equation $y = -0.742x + 5.9$. Long-term maintenance of the population requires a minimum of 1.79-km of willows per colony.
5. In cutting tree trunks, beavers stimulate shoot development from the remaining stumps. They rejuvenate riparian forests, increase the number of tree stems and help stabilize the banks. Their effect on woody plant morphogenesis may have consequences for the helophyte communities used as food or habitat by other aquatic species.

Keywords: aquatic vertebrate, dispersal, reintroduced species, territory size, willow grove

Introduction

Introductions of wild caught animals have been used on several occasions to restore populations lost from parts of their former range (Griffith *et al.*, 1989; Primack, 1993). Thus, after the Eurasian beaver *Castor fiber* L. 1758 declined over large regions in Europe, many animals were transferred back to areas from which the species had disappeared (Richard, 1980; Véron, 1992; Macdonald *et al.*, 1995; Nolet & Rosell, 1998). Local extinction had often resulted from a degradation in habitat quality, however, limiting the potential for re-colonization.

Despite the need for careful considerations of the factors likely to contribute to success (Yalden, 1986; Braun, 1990; Breitenmoser & Haller, 1993; Nolet & Rosell, 1998), many re-introductions have been performed on the grounds of urgency, without proper assessment of the factor that determine the long-term maintenance of populations. For example, after a release of nine beavers in 1965–67 in the Der Lake Forest (Champagne, France), the population extended to 20 sites during the 1970s but then quickly declined after 1980 so that there remained only four occupied sites (Léger, 1996). Similarly, a translocation of 58 beavers in the Elbe basin (Germany) in 1988–94, resulted in the death of 22 individuals from infectious disease in their new habitats (Nolet *et al.*, 1997). Moreover, although several re-introductions have allowed the establishment of a permanent population,

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beavers have not always succeeded in expanding into the surrounding areas of Brittany (France) since 1968.

The Eurasian beaver *Castor fiber galliae* Geoffroy 1803 disappeared from the Loire Valley at the beginning of the 19th century (last recorded around 1820, near Sully sur Loire). Thirteen individuals, originating from the Rhone Valley, were successfully re-introduced between 1974 and 1976 through five successive releases near Blois (Hesse & Jollivet, 1978; Sénotier, 1986; Rouland & Migot, 1997; Fig. 1). Recently, two further releases have been carried, one between 1994 and 1996 near the Forez Region in the Massif Central (though its success is unclear) and another earlier, between 1970 and 1973, on the Creuse tributary (Fig. 1), which failed (Richard, 1980). Despite the small number of individuals released, leading to genetic founder effects (Mayr, 1963), beavers have been colonizing large areas of the Loire Valley from Blois. Determining the influence of habitat characteristics is essential for understanding the distribution of beavers. It may be that habitat properties, especially the structure of the deciduous riparian forest, have favoured the restoration of a population on the Loire.

Beavers play an important role in freshwater ecosystems in modifying the stream and water level with dams, but also in regenerating riparian forests (Naiman, Melilla & Hobbie, 1986). They exploit the available resources of their habitat assiduously.

Principally using ligneous species, they cut trunks and branches to build lodges and dams, feed on leaves and twigs and strip bark from trees (Hoffman, 1967; Richard, 1980; Fryxell & Doucet, 1991; Nolet, Hoekstra & Ottenheim, 1994; Kostkan, 1999). Woody plants need several years to regenerate, a lag that could affect the long-term survival of beavers. Beavers exhibit strong territorial behaviour, however, which might regulate the population and preclude resource depletion (Aleksuik, 1968; Richard, 1970; Nolet & Rosell, 1994). Therefore, the distribution of animals should reflect habitat suitability and we might predict that resource dispersion directly influences home-range size. In populations of American beaver *Castor canadensis* Kuhl, studies have been carried out to determine habitat suitability by quantifying several environmental characteristics (Atwater, 1940; Howard & Larsson, 1985; Beier & Barrett, 1987; Snodgrass, 1997). Slough & Sadleir (1977), emphasized that density was enhanced by the conservation of aspen (*Populus tremuloides* Michx) stands. Previous studies on Eurasian beaver have mainly provided only a general habitat description (Zarkhov, 1970; Heidecke, 1983; Zurowski & Kasperczyk, 1988; Rahm, Baetti & Baumgartner, 1995). Habitat selection should be regarded as a hierarchical process, ranging from the selection of a geographical range to preference for a particular plant. The only investigation on habitat

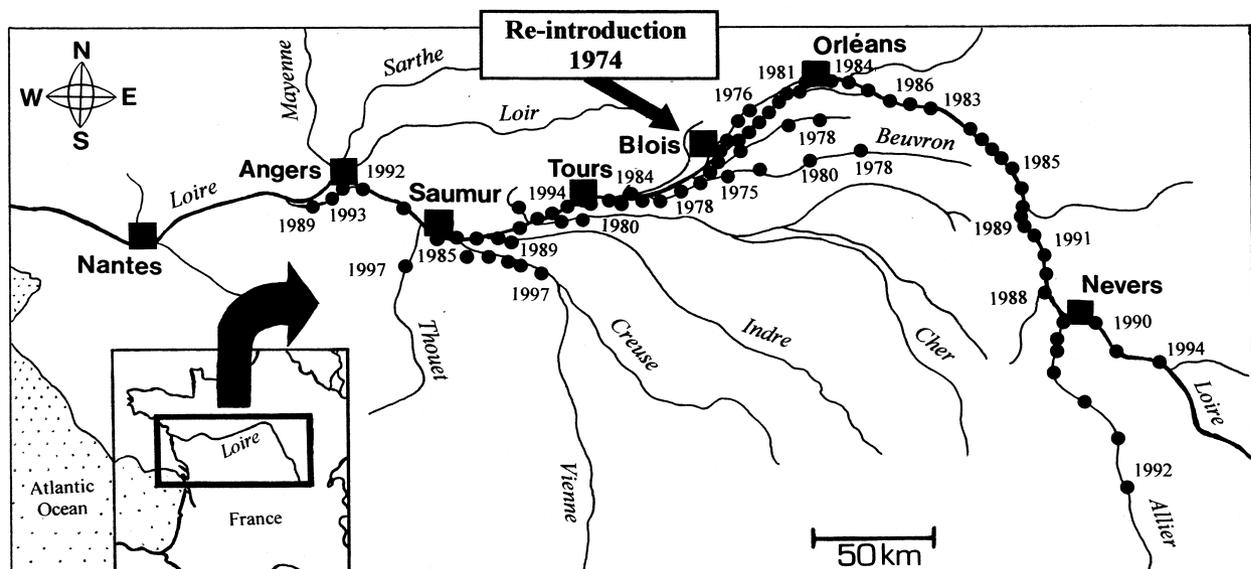


Fig. 1 Distribution map of Beaver *Castor fiber* colonies (●) in the Loire Valley and dates of settlements from 1974 to 1999; (■) urban areas located on the Loire River.

selection in Eurasian beaver concerns boreal coniferous forest (Hartman, 1996). Habitat selection within deciduous riparian habitat is still poorly documented.

This long-term study was designed to analyse the relationships between habitat features and beaver settlement and to assess the response of colonizing beavers to habitat constraints. We investigated (1) the progress in beaver colonization since the reintroduction to the Loire Valley in 1974, (2) the characteristics of the habitats selected, inferred from beaver distribution, (3) the variation in exploitation of plant species according to available habitats in the Loire riparian forest, and (4) the potential for regrowth of the woody species exploited by the beavers.

Methods

Study area

The Loire River exhibits periodical flooding. Normally receiving little precipitation in summer, its minimum discharge is reached in September ($160\text{--}180\text{ m}^3\text{ s}^{-1}$ at Saumur-Montjean), while riparian forests are flooded in winter with a maximum discharge in January–February ($1320\text{--}1500\text{ m}^3\text{ s}^{-1}$). Abandoned river channels form backwaters called 'boires' and several embankments restrict the extent of flooding in some areas. The elevated central portion of the Loire's active zone forms numerous islands during winter high flows. Sometimes, tributaries run parallel to the river in lateral depressions (Fig. 1). Downstream from Orléans, the river flows slowly between unstable sand and gravel banks and islands. The Loire is subject to a mild and humid oceanic climate (mean temperature August $20\text{ }^{\circ}\text{C}$, and mean temperature February $5\text{ }^{\circ}\text{C}$, annual precipitation 650 mm).

Over 120 plant species compose the riparian and instream flora of the Loire (Corillion, 1982). There are few aquatic plant species in the unstable active zone of the Loire River. In summer, sandy banks favour thermophilous therophytes. Riparian forests are characterized by three natural plant communities. First, the lower willow grove ($< 5\text{--}6\text{ m}$ tall) may remain submerged for several weeks during each year and includes pioneer species such as purple osier *Salix purpurea* L., with almond-leaved willow *Salix triandra* L. and common osier *Salix viminalis* L., associated with reed canary-grass *Phalaris arundinacea* L. The presence of this community decreases markedly from Orléans

to the estuary. Secondly, the intermediate willow grove is dominated by white willow *Salix alba* L., crack willow *Salix fragilis* L. and black poplar *Populus nigra* L., combined with box elder *Acer negundo* L., common elder *Sambucus nigra* L., hedge bindweed *Calystegia sepium* (L.) R. Br., hop *Humulus lupulus* L., and broad-leaved dock *Rumex obtusifolius* L. Thirdly, on top of the river bank, narrow-leaved ash *Fraxinus angustifolia* Vahl and smooth-leaved elm *Ulmus minor* Mill. dominate, accompanied by common oak *Quercus robur* L. and dewberry *Rubus caesius* L. (Corillion, 1982). This last community becomes more common downstream from Saumur to the estuary: the frequency of *Salix fragilis* increases, while that of *S. alba* drops. Hybrid black poplars *Populus* \times *canadensis* Moench, often grow widely along the river.

Colonization

Colonization of the Loire Valley by a re-introduced beaver population has been studied in a 25-year survey, which commenced in 1974, at the time of the first re-introduction of two animals near Blois. The Loire and its tributaries (a linear distance of 2800 km), were explored for beaver evidence from the bank or by canoe, although the individuals released latest in the extreme upstream river (Forez Region in 1994) were excluded. Since 1974, varied evidence of beaver activity has been recorded during periodical surveys, including the presence of dens, tracks, cut trees and branches, bark stripping, refectories, faeces, ano-genital secretion deposits (castoreum) or dams (Hesse & Jollivet, 1978; Sénotier, 1986; Miège, 1989; Pailley & Pailley, 1994; Le Jacques & Lodé, 1996; Bourand, 1997; Cabard & Le Gall, 1997). Permanent occupation was checked between 1993 and 1999 on at least four separate visits. Den building was regarded as indicative of a regular settlement. Each settlement on a new site was listed by year and a colonization rate was estimated from the annual number of new sites occupied and the number of previous sites. The maximum distance of colonization was measured as the distance separating each newly discovered site from the nearest site recorded previously.

Habitat characteristics

Field study of habitat features was performed between Blois and Angers from July to September

(1998–99), a low flow period allowing an easier study of plant communities across the 15 m wide band from the water's edge. Vegetation was sampled in 73 randomly located areas on some tributaries and on the banks and islands of the Loire River. These areas were 100–150 m long and 6–10 m wide, parallel to the river-edge. On 70 of these areas, trees and branches cut by beaver and dens were recorded. In the three other areas, no sign of beaver was noticed. Ligneous and herbaceous species were listed and their respective percentage cover was estimated using the Braun–Blanquet scale (see Guinochet, 1973) which depends on the size and number of individuals. The percentage cover was recorded as nil when the riverbank was strengthened with riprap. Plant nomenclature followed *Flora Europae* (Tutin *et al.*, 1972–89). Vegetation data were compared using the Welch approximate *t*-test for the main ligneous species.

Signs of beaver presence around active dens were recorded between Angers and Nevers including cut trees and branches, tracks, castoreum deposits and faeces. Because beaver territory in a river system is linear, two territories A and B could be easily differentiated by measuring the spacing between four successive signs (s1, s2, s3, s4). Each beaver's home-range size was assessed by the distance separating each newly found sign (s2) from the previously found sign (s1). When the distance between s2 and s3 (s2, s3) was greater than both distances (s1, s2) and (s3, s4), s1 and s2 were attributable to territory A, s3 and s4 to territory B. Home ranges were in most cases found to be clearly separated. Multiple regression analysis was used to investigate relationships between home-range size and the 15 most common woody plants recorded on corresponding vegetation data. Linear regression was then performed between the home range size and the percentage cover of these plants to analyse the relationship with resource dispersion and therefore to detect important determinants.

Exploitation of woody plants and their regeneration potential

Beavers exploit woody plants for food and to build their lodges and dams. A systematic search for trees cut by beaver was carried out on a monthly basis from 1994 to 1999. All cut trees ($n = 757$) were classified by genus into five categories: *Populus*, *Salix*, *Fraxinus*, *Ulmus* and others (*Prunus* and *Sambucus*). The

diameter of each cut trunk was measured immediately below the cut section and the season of the cutting was estimated. Data were log-transformed to avoid inequality of variances, and variation in diameter between genera categories was analysed using one-way ANOVA.

In September 1999, the re-sprouting level of 156 trees, that had been cut since the previous winter and belonged to the four most exploited genera (*Salix*, *Populus*, *Ulmus*, *Fraxinus*), was evaluated. For each cut tree, any new basal shoots developing from the stump were counted and the long axis measured. Differences in length between genera were analysed using the Kruskal–Wallis non-parametric ANOVA test.

Results

Colonization pattern

Over 25 years, beavers have colonized the Loire Valley and settled on 82 sites (Fig. 1), including 29 sites on 11 tributaries. This corresponds to an average of 0.117 colonies per km or one beaver site per 8.56 km of river length. Of the 2800 km of river length explored, 702 km (25%) of the river system was occupied by beavers. Therefore, the total number of adult beavers may have reached a minimum of 160 (based on two adults per colony). The distance travelled by colonizing beavers averaged 8.87 km year⁻¹ (SD 12.89) but varied greatly between years (range 0–80 km). Beavers dispersed with two distinct patterns: regular dispersion averaging 3.2 km year⁻¹ (SD 2.14), and long distance movements that reached 37.6 km year⁻¹ (SD 25.86). From previously settled sites, distant sites were often colonized before the nearer sites. The intervening river was progressively then occupied by dispersers from one or other sites. This colonization pattern could be regarded as both distant and irregular according to colonization by the discontinuous remoteness model.

At the beginning of the study period, the number of sites occupied by beaver increased rapidly, reaching 20% of the present number of sites during the first 5 years and 43.8% during the first 10 years (Fig. 2). The mean colonization rate for the first 5 years 1974–78 reached 104.2% year⁻¹ of new sites occupied (SD 75% year⁻¹), while it was only 9.5% year⁻¹ (SD 10.4% year⁻¹) during the next 20 years 1979–99 (Welch's approximate $t = 2.82$, d.f. = 4, $P = 0.048$).

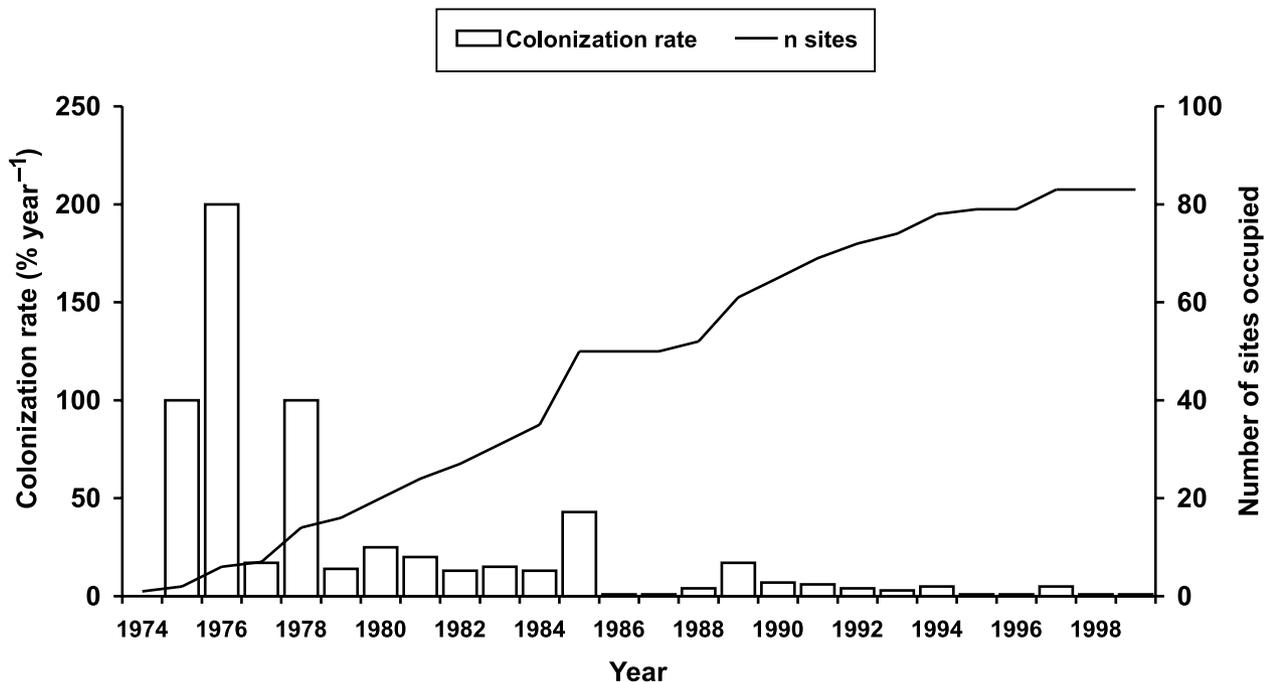


Fig. 2 Colonization rate and number of occupied sites by reintroduced Beaver from 1974 to 1999.

Although there was a major decrease in colonization rate, the number of new colonies km^{-1} did not significantly differ between 1974 and 1979 (0.104 colonies km^{-1} , $n = 16$) and 1980–99 (0.120 colonies km^{-1} , $n = 66$; Welch's approximate $t = 1.29$, d.f. = 25, $P = 0.209$). The number of new colonies km^{-1} even showed a small increase after 1985 with 0.125 colonies km^{-1} ($n = 48$); there were only 0.107 colonies km^{-1} between 1974 and 1984 (Welch's approximate $t = 1.94$, d.f. = 71, $P = 0.057$).

Habitat features

Riparian habitats in our samples were characterized by 33 ligneous and 78 herbaceous species (see Appendix 1). On the riverbanks and islands occupied by beaver, vegetation cover was, on average, composed of 61.6% ligneous and 63.4% herbaceous plants (Appendix 1). About 34% of the bank had no vegetation.

Black poplar *P. nigra* was the dominant woody species in beaver sites (13.3%), with *S. alba* and narrow-leaved ash *F. angustifolia* (11.9 and 6.9%) also important. Of 80 recorded herbaceous species, eight predominated (*Elymus repens* (L.), *Urtica dioica* L.,

Aristolochia clematidis L., *Paspalum dilatatum* Poir., *P. arundinacea* L., *Carex riparia* Curtis, *Hedera helix* L. and *C. sepium* (L.) R. Br.), totalling 50.6% of the total herbaceous plant cover. Ruderal plants like *Ur. dioica*, *Berteroa incana* (L.) DC., *Datura stramonium* (L.) and *Lamium maculatum* (L.), helophytes such as *P. arundinacea* and *C. riparia*, and understory plants (*A. clematidis* and *Hedera helix*) were common species on the banks.

Exploitation of woody plants

Among the 757 trees cut by beaver, there were more Salicaceae (84%) than Oleaceae (12.1%), Ulmaceae (3.4%) or other woody species (0.5%). Willows and poplars were exploited throughout the year. The number of cut Salicaceae increased significantly in spring and summer ($\chi^2 = 63.64$, d.f. = 3, $P < 0.0001$), whereas *Fraxinus* and *Ulmus* were mainly used in winter and autumn (Table 1). The diameter of the cut trunks averaged 5.54 cm (SD 5.93 cm, range 62.4–0.17, $n = 757$) and differed among genera ($F_{4,756} = 4.81$, $P < 0.001$). The mean diameter of cut trunks belonging to Ulmaceae and Oleaceae was larger than that of Salicaceae.

	Number of cut trees				Frequency (%)	Mean diameter \pm SD (cm)
	Winter	Spring	Summer	Autumn		
Salicaceae						
<i>Salix</i>	84	75	58	60	36.6	3.91 \pm 3.21
<i>Populus</i>	110	129	39	81	47.4	5.98 \pm 5.85
Oleaceae						
<i>Fraxinus</i>	23	22	1	45	12.1	7.57 \pm 5.99
Ulmaceae						
<i>Ulmus</i>	3	0	0	23	3.4	10.15 \pm 5.59
Others	2	0	2	0	0.5	3.10 \pm 1.24

Table 1 Seasonal variation in the number of cut trees and mean diameter per woody plant genus

Habitat selection

The length of beaver home ranges averaged 5.54 km of river bank ($n = 82$, SD 0.74, range 4.2–7.4). The mean distance between two consecutive territories was 3.02 km (SD 5.24) and ranged from 0.225 km, showing some gaps (mean length 17.13 km, SD 4.93) in the occupation of the valley. Considering the main ligneous species, multiple regression analysis ($r_{\text{multiple}} = 0.998$, $F = 57.56$, 99.65% of variance, $P < 0.003$) revealed that home range size was only significantly explained by the abundance of *S. alba* ($\beta = -0.658$, $F_{1,2} = 162.33$, $P < 0.00001$), *P. nigra* ($\beta = -0.821$, $F_{1,2} = 101.18$, $P < 0.001$).

The size of beaver home ranges was inversely correlated with the cover of intermediate willow grove ($r_{\text{Pearson}} = -0.972$, d.f. = 64, $P < 0.001$), an assemblage of *S. alba*, *S. fragilis* and *P. nigra* combined with *A. negundo*, *S. nigra*, *C. sepium*, *H. lupulus* L. and *Rumex* spp. (Fig. 3a). The ash-elm grove and the lower bank willow grove with *S. triandra* and *S. viminalis* showed no significant correlation with the size of beaver territory ($r_{\text{Pearson}} = -0.311$, $r_{\text{Pearson}} = -0.156$, respectively, d.f. = 30, $P > 0.05$). Thus, the beaver home range size was directly dependent on resource dispersion. On beaver territories, the riparian forest consisted of 32.3% of intermediate willow grove, a mean length of 1.789 km per home range. The length of intermediate bank willow grove appeared as the best predictive determinant of the beaver home range ($r_{\text{Pearson}} = -0.917$, d.f. = 64, $P < 0.001$, Fig. 3b). Home range tended to become larger when the intermediate willow grove was insufficient. Not surprisingly, the proportions of *Fraxinus* and *Ulmus* tree cuts significantly increased ($r_{\text{Spearman}} = 0.672$, d.f. = 18, $P = 0.0023$) with territory size, further suggesting the insufficiency of

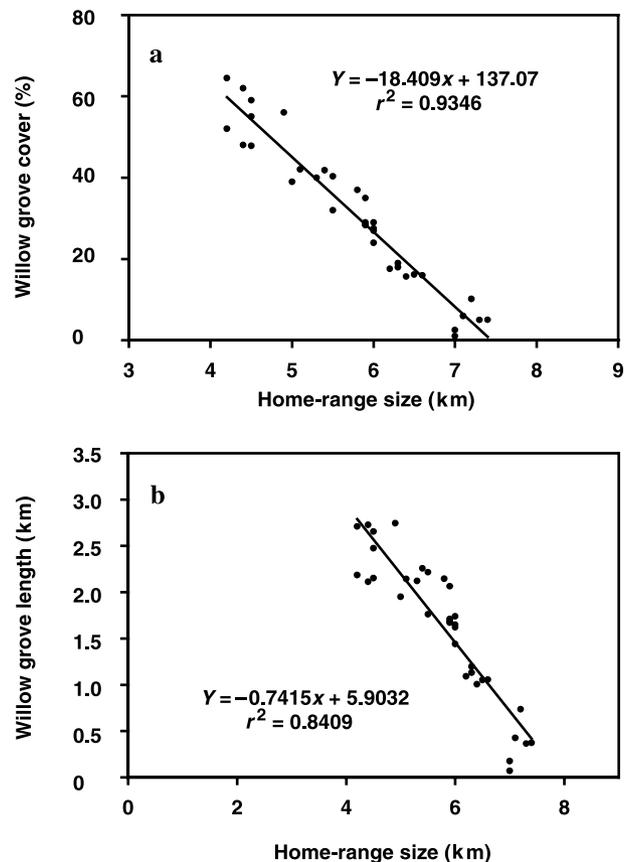


Fig. 3 Linear regressions showing relationships between beaver home-range size and the willow grove in the Loire valley: (a) willow grove cover related to home-range size and (b) willow grove length related to home-range size.

the willow cover. On the basis of these results, it could be predicted that long-term maintenance of beaver requires at least a 1.789-km of intermediate willow grove on the river bank.

Woody plant regeneration

In trees cut by beavers in autumn or winter, basal buds began to grow from the stumps in the following April. Salicaceae produced numerous basal shoots developed from buds located immediately below the cut. Willows and poplars showed a good potential to re-sprout, the two genera producing 6.85 (SD 5.49), 4.38 (SD 4.97) basal axes per individual, respectively (Table 2). In September, the longer proximal shoot was significantly taller in willows (mean length 69.35 cm, SD 37.50) than in poplars (mean length 50.44 cm, SD 28.33; paired *t*-test, $t = 2.862$, d.f. = 33, $P = 0.048$). *Fraxinus* could re-sprout from basal buds similar to those of willows (mean number of basal shoots 5.27 cm, SD 4.80, Welch's approximate $t = 0.899$, d.f. = 71, $P = 0.372$). As for *U. minor*, numerous shoots developed from buds formed in the cambial zone of the section (mean 7.59, SD 7.56). They usually reached lesser lengths than in other genera (mean 34.86 cm, SD 16.67, KW = 20.99, $P < 0.0001$).

Discussion

The main results were that (1) colonization by beavers has been spatially discontinuous, (2) they have an irregular distribution along the river and (3) extensive willow grove on the banks is necessary to maintain a population. These raise numerous issues for biological conservation and management of reintroduced species.

Re-introduced populations of autochthonous species do not generally become invasive. It has been presumed that reintroduced populations in their former natural range are regulated by similar environmental constraints as existed before their extinction (Stanley-Price, 1989). From a 11-year survey in Sweden, Hartman (1994, 1996) described a development pattern of a beaver population with a rapid

increase followed by a decline. In accordance with Caughley's (1970) model for ungulates, this development pattern was attributed to a density dependent effect (Hartman, 1994). Such a development could also be recognized in our beaver population colonizing the Loire Valley. Beaver colonization rate was high during the first 5 years and decreased over the following 20 years. Nevertheless, beaver abundance never reached more than 0.125 colonies km⁻¹ in the Loire Valley and is clearly lower than 0.20–0.25 colonies km⁻¹ estimated in Sweden (Hartman, 1994). The abundance even slightly increased despite a decrease in the rate of colonization to 4.1% of new sites occupied per year after 1987. Therefore, the decrease in colonization rate might not be density-dependent but could have resulted from a despotic distribution, inferring that beaver occupied the richest habitats first. Nolet & Rosell (1994), who surveyed translocated beavers in the Netherlands, found that they established their home ranges successively in rich than poor habitats. Thus beaver colonization showed an irregular pattern in both time and space. This pattern was also found in *C. canadensis* (Bergerud & Miller, 1976). In the sequential settlement model, Maynard-Smith (1974) stressed that territorial behaviour forced dispersers to avoid settlement between two territories. Beavers are able to disperse long distances, up to 170 km (Heidecke, 1984). In the Loire Valley, they colonized upstream and downstream around a new site, following a discontinuous remoteness model. Long distance bridge heads, on average 37.6 km from the nearest site but up to 80 km distance, were followed by many settlements in the immediate vicinity (mean 3.23 km) of previous and new sites. We propose that this particular colonization pattern might be linked, first, to the territorial organization of beavers, with dispersers constrained to travel far from the home-range of adults and, secondly, to the duration of puberty. Beavers become mature later than other rodents (2–3 years old, Wilsson, 1971), so subadults disperse and must settle far away to avoid costly aggressive interactions. Future re-introduction programmes should pay attention to this particular dispersal mode.

The colonization pattern led to a scattered distribution, with only one colony for an average of 8.56 km of riverbank. Moreover, in the Loire Valley, beaver home range was 5.54 km long. Such a home range size was relatively close to the territory size estimated in

Table 2 Regeneration potential of the main genera exploited by beaver. All values are mean \pm SD, n = number of studied trees cut by beavers

Plant genera	Basal shoots per cut tree	
	Number	Size of the longer axis (cm)
<i>Populus</i> ($n = 45$)	4.38 \pm 4.97	50.44 \pm 28.33
<i>Salix</i> ($n = 49$)	6.85 \pm 5.49	69.35 \pm 37.50
<i>Ulmus</i> ($n = 37$)	7.59 \pm 7.56	34.86 \pm 16.67
<i>Fraxinus</i> ($n = 25$)	5.27 \pm 4.80	63.62 \pm 17.29

Germany, ranging from 3.1 to 6.5 km (Heidecke, 1986) and in American beaver, from 3.9 to 5.2 km (Davis, 1984). Nevertheless, European beaver might require a larger home range, averaging 7.9 km as revealed by a radiotracking survey in the Netherlands (Nolet & Rosell, 1994). In *C. canadensis*, distance travelled along the stream ranged from 8 to 16 km (Hibbard, 1958; Leege, 1968). Occupying 25% of the river system, beaver colonies remained relatively distant from each other in the Loire Valley. In contrast, beavers settled on 35% of the river system in the Rhone Valley (Rouland & Migot, 1997). In France, beavers are present on about 4500 km of river (Loire Valley, Brittany, Lorraine, Alsace, Der Lake and Rhone Valley) corresponding to around 500–580 colonies (2000–2500 beavers), thus reaching only a half of the total number expected by Macdonald *et al.* (1995). Populations in the Loire Valley represented 15% of the total number of beaver colonies in France.

In the Loire, variation in home range size was directly dependent on vegetation cover, especially on intermediate bank willow grove. Beaver exploited potential habitat very selectively. Salicaceae often make up the bulk of the diet, but they are also used to build lodges and dams (Richard, 1980; Fryxell & Doucet, 1991; Doucet, Adams & Fryxell, 1994; Nolet & Rosell, 1998). In *C. canadensis*, the percentage cover of trembling aspen (*Populus tremuloides* Michx) was clearly correlated with the number of colonies (Slough & Sadleir, 1977). In contrast, the availability of deciduous woods dominated by birch *Betula* sp. appeared of a lesser importance for Eurasian beaver in Sweden (Hartman, 1996). Nolet & Rosell (1994) observed in Netherlands that beaver territories included around 3 km of wooded banks with many places poorly exploited. The accuracy of model predictions relies upon the biological variables used. Our results emphasized beaver preference for tender woody species (Rameau, Mansion & Dume, 1989): *P. nigra*, *S. alba*, and to a lesser extent, *S. fragilis* and *S. nigra*. Although *Populus × canadensis* and *P. canescens* could be utilized, poplar plantations did not provide suitable habitats for the rodent. Moreover, the structure of the riparian forest clearly affected habitat exploitation: when ligneous plants showed bushy shapes offering basal shoots, beaver could easily find branches to build lodges or twigs to feed, without cutting the trunk at its base. Other ligneous genera (*Fraxinus*, *Ulmus*) were only used when the willow cover percentage was low.

While the lower willow bank grove and the ash-elm grove had little effect on beaver colonization, a particular assemblage of ligneous plants, the intermediate bank willow grove, influenced the probability of settlement. According to a linear regression, beaver required at least 1.79-km long willow grove on their territory. More than the wooded bank length, home range size was linked to resource dispersion, i.e. the percentage cover of willow grove.

In the Loire, beavers did not modify flow and water level by building dams (only one dam was observed). On the other hand, beaver had a major effect on the structure of riparian forests, increasing the number of woody shoots. They cut trees to eat leaves and to build hut-burrows on the steep banks (more often on islands). Willows and poplars, but also ash and elms were able to produce shoots from the base of their trunk. Stem cuttings, and particularly coppicing, are known to increase the number of basal shoots, stimulate their growth and reduce senescence (Bonduelle, 1979). The new shoots are often more vigorous than those of uncut trees and contribute to a quick renewal of lost biomass. Winter cuttings are more favourable for the development of vigorous shoots because they occurred just after reserves of carbohydrates have reached their maximum (Libby, Brown & Fielding, 1974). Moreover, in cutting tree trunks, beavers prevent the development of tall arborescent individuals that are sensitive to storms and which may be uprooted from the sandy bank and fall into the river. Thus beaver may contribute to a reduction in bank collapse.

Nevertheless, several years are required for regeneration of ligneous plants, and so the willow grove length should correspond to a rate of renewal just balanced by consumption. Below the threshold value of 32.3% of willow cover, beaver used other tree species. Beaver also need herbaceous plants, they use as food. Grassé & Dekeyser (1955) noted the consumption of *Rumex* and *Urtica*. Herbaceous plants provide a substantial source of phosphorous and nitrogen and should be mainly consumed in summer (Heidecke, 1988; Nolet *et al.*, 1997). In several beaver refectories recorded in the Loire Valley, *Xanthium*, *Carex*, *Paspalum* and *Phalaris* were identified. Although beaver can feed on a large number of plant species, our study indicates that intermediate bank willow grove had the highest predictive power in relation to beaver habitat selection in riparian forest.

This results in precise conservation and management implications and guidelines. Where the percentage cover of Salicaceae is insufficient, long-term survival of beaver populations might be affected and the impact on other woody plants should increase. The resulting modification in riparian forest structure might have consequences for herbaceous plants used as food and habitat by other aquatic animals.

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Appendix 1 Mean percentage cover of plant species recorded in 70 areas chosen in deciduous riparian forests inhabited by Eurasian beaver in the Loire valley

Species	Mean cover
<i>Acer campestre</i> L.	0.0188
<i>Acer negundo</i> L.	0.9178
<i>Acer pseudoplatanus</i> L.	0.0250
<i>Achillea ptarmica</i> L.	0.0021
<i>Aesculus hippocastanum</i> L.	0.0033
<i>Alisma plantago aquatica</i> L.	0.0016
<i>Alnus glutinosa</i> (L.) Gaertn.	0.5560
<i>Arctium lappa</i> L.	0.2715
<i>Aristolochia clematitis</i> L.	7.2387
<i>Arrhenatherum elatius</i> (L.) Beauv.	0.8487
<i>Artemisia vulgaris</i> L.	0.5851
<i>Asparagus officinalis</i> L.	0.0561
<i>Berteroa incana</i> (L.) DC.	0.5041
<i>Bidens frondosa</i> L.	0.1314
<i>Brassica napus</i> L.	0.0479
<i>Bromus sterilis</i> L.	0.0016
<i>Calystegia sepium</i> (L.) R.Br.	6.2942
<i>Carex riparia</i> Curtis	2.6059
<i>Castanea sativa</i> Mill.	0.0273
<i>Chaerophyllum temulem</i> L.	0.0125
<i>Cirsium arvense</i> (L.) Scop.	0.0686
<i>Clematis vitalba</i> L.	0.1207
<i>Conium maculatum</i> L.	0.2344
<i>Convolvulus arvensis</i> L.	0.0244
<i>Cornus sanguinea</i> L.	0.4577
<i>Crataegus monogyna</i> Jacq.	0.2604
<i>Cucubalus baccifer</i> L.	0.0404
<i>Cyperus esculentus</i> L.	0.1170
<i>Cytisus scoparius</i> (L.) Link	0.0411
<i>Dactylis glomerata</i> L.	0.1285
<i>Datura stramonium</i> (L.)	0.0659
<i>Dipsacus fullonum</i> L.	0.0028
<i>Echinochloa crus galli</i> (L.) Beauv.	0.7803
<i>Elymus repens</i> (L.)	10.0698
<i>Epilobium hirsutum</i> L.	0.0016
<i>Equisetum</i> L.	0.0276
<i>Eragrostis pectinacea</i> (Michx) Nees	0.0711
<i>Erysimum cheiranthoides</i> L.	0.0507
<i>Frangula alnus</i> Mill.	0.6107
<i>Fraxinus angustifolia</i> Vahl	6.9068
<i>Fraxinus excelsior</i> L.	4.7879
<i>Galium aparine</i> L.	1.1727
<i>Glechoma hederacea</i> L.	1.1105
<i>Filaginella uliginosa</i> (L.) Opiz	0.0335
<i>Hedera helix</i> L.	1.7828
<i>Heracleum sphondylium</i> L.	0.3802
<i>Hordeum murinum</i> L.	0.0016
<i>Humulus lupulus</i> L.	0.0343
<i>Impatiens glandulifera</i> Royle	0.0391
<i>Iris pseudacorus</i> L.	0.0220
<i>Juglans regia</i> L.	0.1563
<i>Juncus conglomeratus</i> L.	0.1563
<i>Lamium maculatum</i> L.	0.1978
<i>Linaria vulgaris</i> Mill.	0.0030

Appendix 1 (Contd.)

Species	Mean cover
<i>Ludwigia uruguayensis</i> (Camb.) Hara	0.0844
<i>Lycopus europaeus</i> L.	0.2135
<i>Lysimachia vulgaris</i> L.	0.5211
<i>Lythrum salicaria</i> L.	0.1690
<i>Matricaria perforata</i> Mérat	0.4905
<i>Mentha aquatica</i> L.	0.0083
<i>Mercurialis annua</i> L.	0.0016
<i>Myosotis scorpioides</i> L.	0.0391
<i>Oenothera suaveolens</i> Pers.	0.0228
<i>Panicum capillare</i> L.	0.0627
<i>Parthenocissus inserta</i> (Kerner)Fritsch	0.0384
<i>Paspalum dilatatum</i> Poiret	6.6555
<i>Phalaris arundinacea</i> L.	6.4915
<i>Phragmites australis</i> (Cav.) Trin.	0.0488
<i>Plantago major</i> L.	0.0197
<i>Plantago arenaria</i> Waldst. & Kit.	0.1593
<i>Polygonum amphibium</i> L.	0.0043
<i>Polygonum hydropiper</i> L.	0.3808
<i>Populus alba</i> L.	0.0521
<i>Populus × canadensis</i> Moench	3.0098
<i>Populus canescens</i> (Ait.) Sm.	0.0298
<i>Populus nigra</i> L.	13.3438
<i>Portulaca oleracea</i> L.	0.0438
<i>Potentilla anserina</i> L.	0.0521
<i>Potentilla reptans</i> L.	1.0938
<i>Prunus avium</i> L.	0.3613
<i>Prunus spinosa</i> L.	0.0781
<i>Quercus robur</i> L.	0.2460
<i>Ranunculus repens</i> L.	0.0016
<i>Ribes rubrum</i> L.	0.0419
<i>Robinia pseudoacacia</i> L.	2.6797
<i>Rorripa sylvestris</i> (L.) Besser	0.3833
<i>Rosa canina</i> L.	0.6629
<i>Rubus caesius</i> L.	4.4272
<i>Rumex</i> L.	0.0016
<i>Salix alba</i> L.	11.9309
<i>Salix atrocinerea</i> Brot.	0.8167
<i>Salix babylonica</i>	0.0078
<i>Salix fragilis</i> L. and <i>S. × rubens</i> Schrank	2.9759
<i>Salix purpurea</i> L.	0.2954
<i>Salix triandra</i> L.	0.5186
<i>Salix viminalis</i> L.	0.3121
<i>Sambucus nigra</i> L.	0.9638
<i>Saponaria officinalis</i> L.	0.0236
<i>Scrophularia nodosa</i> L.	0.0680
<i>Solanum dulcamara</i> L.	0.5891
<i>Sonchus asper</i> (L.) Hill	0.0031
<i>Stachys palustris</i> L.	0.0722
<i>Symphytum officinale</i> L.	0.3947
<i>Tanacetum vulgare</i> L.	0.1521
<i>Torilis arvensis</i> (Hudson) Link	0.0016
<i>Ulmus minor</i> Mill.	4.1263
<i>Urtica dioica</i> L.	9.4345
<i>Veronica anagalloides</i> Guss.	0.0029
<i>Vitis vinifera</i> L.	0.9013
<i>Xanthium orientale</i> L.	0.3206