The habitat potential of the downstream Loire River for European beavers (*Castor fiber*)

Joëlle Fustec[1] & Jean-Paul Cormier[2]

[1] Ecole Supérieure d'Agriculture d'Angers, LEVA, 55 rue Rabelais, BP 30748, F-49007 Angers cedex 01, France, e-mail: j.fustec@esa-angers.educagri.fr

[2] Laboratoire d'Ecologie Animale, UFR Science, 2 boulevard Lavoisier, F-49045 Angers cedex, France

Abstract: During the 19th century the European beaver (*Castor fiber*) disappeared from most parts of France, except for the Rhône Valley. In the 1970s, beavers caught from the river Rhône were released in the Loire River, near the city of Blois. While this reintroduction was successful and led to the progressive recolonisation of the Loire River and its tributaries, the density of beaver colonies has remained low. Furthermore, habitat quality has decreased in the downstream part of the Loire, and beavers might not find enough suitable sites to settle. This study was designed to estimate the number of suitable places for beaver settlement in a downstream segment of the Loire River, which is still uncolonised, but already explored by pioneer individuals. For this purpose, we searched for relationships between signs of beaver presence (lodges, cut trunks, and remains of browsed plants) and vegetation features, bank characteristics, and human disturbance in a presently colonised region of the Loire River. Beavers selected sites dominated by 10-15 m tall trees to build lodges, irrespective of the tree species. Sites with cut trees were dominated by Salicaceae. Beavers fed on Salicaceae and numerous herbs. Based on these findings, vegetation features in the uncolonised stretch of the river are expected to be favourable to beaver settlement and feeding. However, beavers will have to face river bank protections and more intense levels of human activity in most of the uncolonised area. These factors may dramatically limit the number of sites suitable for lodge building.

Keywords: Castor fiber, France, Loire, habitat selection, river colonisation, Salicaceae, diet, aquatic mammal.

Introduction

The European beaver (*Castor fiber* L., 1758) had all but disappeared from France at the end of the 19th century because of human persecution. The sole exception was the Rhône Delta where small populations remained (Halley & Rosell 2002). After their protection in the Rhône Valley in 1909, their populations expanded along the river Rhône and its tributaries. In 1968, the species came under protection throughout France, and about 250 individuals from the Rhône Valley were caught and released at different sites across the country (Rouland 1991, Halley & Rosell 2002, Anonymous 2003; figure 1).

In the Loire River, 13 individuals were released near the city of Blois between 1974 and 1976 (figure 1). Reintroductions along this river were successful, and beavers settled in more than 80 sites over 25 years; they now occupy 25% of the Loire River system (Fustec et al. 2001). However, beaver density along the Loire River is approximately 0.125 colonies/km, which is lower than densities estimated in other European countries (Hartman 1994, Ulevicius 1999, Fustec et al. 2001).

In previous studies focusing on the Loire River downstream from Blois, we have shown relationships between home-range size and the canopy cover by white willows (*Salix alba*) and black poplars (*Populus nigra*) (Fustec et al. 2001). Nevertheless, we have also shown that bank characteristics, human disturbance, and vegetation structure may be more important than a high density of Salicaceae for lodge site selection (Fustec et al. 2003). Further information about cut trees and feeding sites would provide a more complete understanding of habitat utilisation.

In the downstream parts of the Loire River, pioneer individuals are just beginning to explore

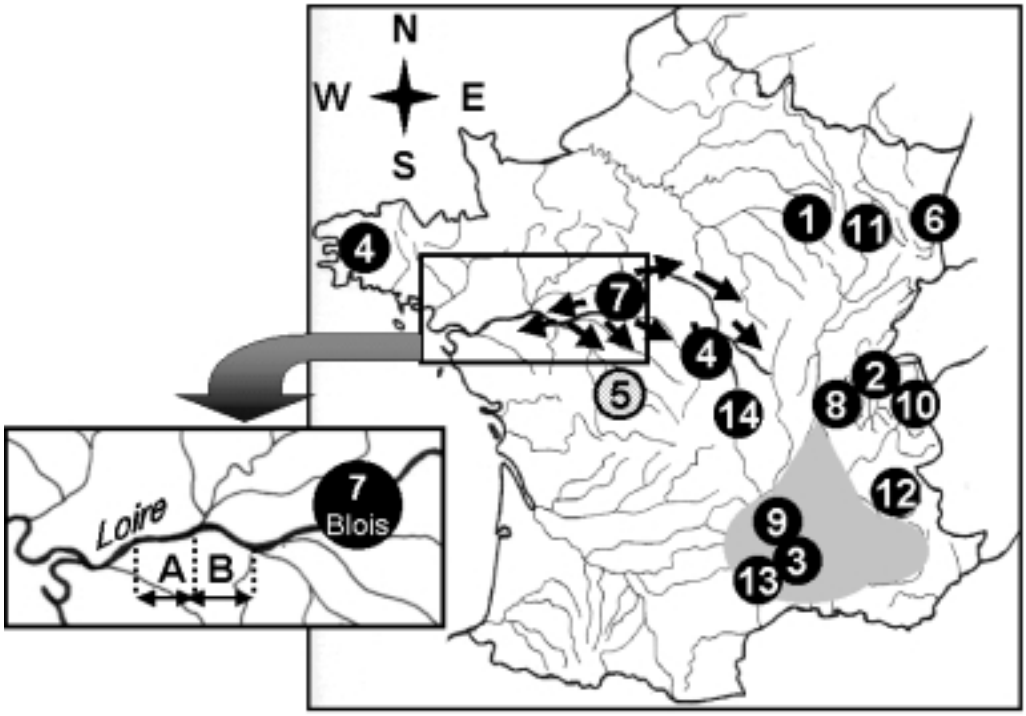

Figure 1. Distribution map of beaver colonies in France after reintroductions (modified from Rouland 1991). Grey area = populations of the Rhône Valley; black circles = areas with one or several successful reintroductions; dotted circle = unsuccessful reintroduction; black arrows = colonisation of the Loire River valley by beavers; numbers indicate successive reintroductions; A = uncolonised stretch, and B = colonised stretch of the Loire River.

a developed part of the river that is equipped for fluvial traffic. It is unclear whether this stretch of the river contains sufficient suitable sites for settlement of the beavers. This study, of an already colonised part of the river, was designed to identify the characteristics of sites where beavers fell trees, and sites where they browse cut branches and herbs (refectories). Our aims were (1) to compare site selection to the various animal needs, and (2) to estimate the habitat potential of the uncolonised stretch of river.

Material and methods

Study area

The Loire Valley (France) is a vast alluvial plain composed of sand and clay interspersed with limestone and loess. The study area was located in this valley, about 127 km downstream from Blois (47°45' N, 0°75' E; figure 1). Two river sections were distinguished: (1) the A-stretch, which is not yet colonised but occasionally explored by beavers, and (2) the B-stretch, colonised by beavers since 1983. The Loire River bed is some 200-300 m wide and the stream carries huge quantities of sand and gravel that form numerous islands held by riparian woods, or continuously shifting sandbanks (figure 2). With little precipitation in the summer, the Loire River has its lowest flow in September (160-180 m^3s^{-1} at Saumur Montjean), while riparian forests are flooded in winter (maximum 1320-1500 m^3s^{-1} in January-February). Riparian woods are characterised by three main woody plant communities: the pioneer willow grove, the tall willow grove, and the ash-elm community (figure 2). The humid and mild climate is favourable to the growth of numerous

herbs that colonise banks and sandbanks at-periods of low flow. Banks and islands are sometimes protected from erosion by ripraps. Only the very downstream part of the Loire River (from the A-stretch to the estuary) is modified and equipped for fluvial traffic.

Data collection

The field study has been conducted over four consecutive years (2000-2003). The riverbanks were surveyed for signs of beaver presence by canoe and on foot from June to September, when low water levels allow better access to sandbanks in order to search for signs of beaver activity. The surveys included both sides of the Loire River and island banks (88 km of shoreline in the A-stretch and 105 km in the B-stretch). The whole bankside was divided into 10 m wide and 0.6 to 1.5 km long contiguous plots. Borders between plots corresponded with obvious changes in plant community (structure and/or species composition), or river bank characteristics. In each plot (n=89 in A-stretch, n=104 in B-stretch) human activity was qualitatively assessed using a scale ranging from 1 (low disturbance) to 5 (very high disturbance), and the bank slope was classified as (1) <20%, (2) 20-50% or (3) >50%. Woody plants were classified in three categories based on plant morphology: tall trees (10-15 m), small trees (5-10 m), and tall bushy plants (>5 m). In our classification, a 'tree' was defined as a plant with a trunk and no basal branches touching the water at flood time, 'bushy' qualified plants without a main trunk, but with basal branches accessible to beavers even at low water levels. In each plot, the canopy cover for each plant morphological category was

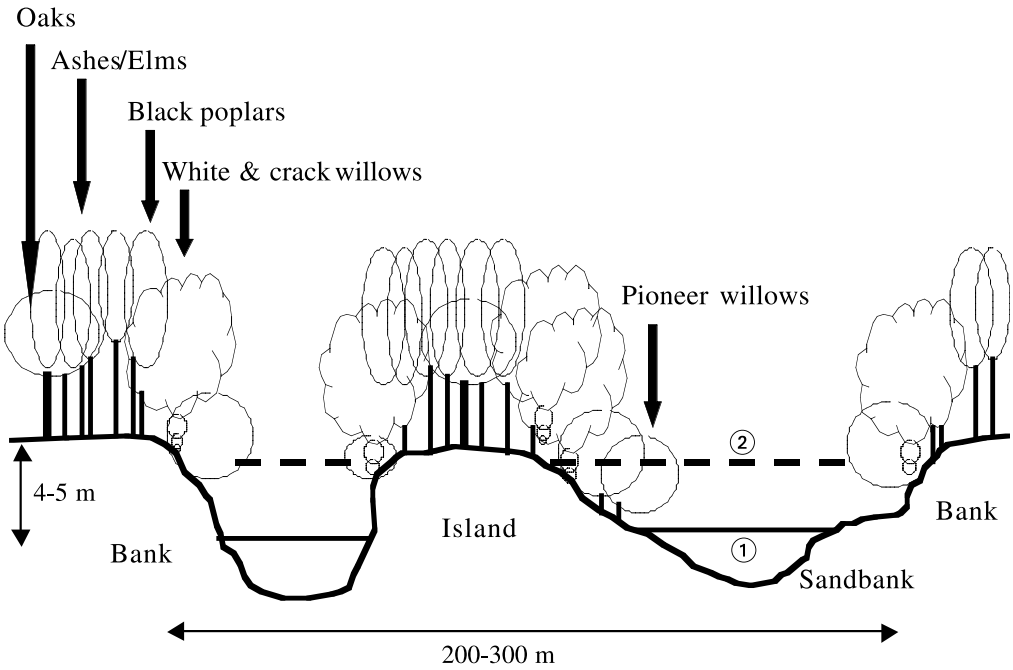

Figure 2. Woody plant communities of the minor bed of the Loire River. The pioneer willow grove is dominated by purple osiers (*Salix purpurea*), common osiers (*Salix viminalis*), and almond-leaved willows (*Salix triandra*). The tall willow grove is dominated by white willows (*Salix alba*), crack willows (*Salix fragilis*), and black poplars (*Populus nigra*) with some hybrids (*Populus* x *canadensis*). The ash/elm community is dominated by narrow-leaved ashes (*Fraxinus angustifolia*), smooth-leaved elms (*Ulmus minor*) and common oaks (*Quercus robur*). (1) low water level reached in September, (2) high water level reached in February.

estimated for each woody and herbal plant species, using an Abundance-Dominance scale (AD) ranging from 1 to 5: (1) <5%, (2) 5-25%, (3) 25-50%, (4) 50-75%, (5) 75-100%, and (+) isolated plants (Guinochet 1973). In each plot, we recorded beaver signs: lodges (burrows and hut-burrows) and tree-felling (hereafter stump sites). We discovered 28 sites with remains of browsed twigs and herbs in the water (hereafter refectories). Plant species found in the 28 refectories were identified, but the characteristics of the plant community covering the bank were recorded in only 17 of these sites. Neither dams, nor huts were found on the Loire River.

AD-values were transformed into mean canopy cover values: (1) 2.5%, (2) 12.5%, (3) 37.5%, (4) 62.5%, (5) 87.5%, (+) 0.5%. In earlier work (Fustec et al. 2003) we compared plots with and without lodges using the non-parametric Mann-Whitney test, which is based on medians equality and does not assume a Gaussian distribution or equal standard deviations. The same method was used here to compare plots without beaver signs with stump plots. Comparisons were also made between refectory plots and those without beaver signs. Plots combining lodges and stumps (n=3) were not included in the analysis.

Results

In the colonised part of the river, stump sites were strongly characterised by a canopy cover of tall Salicaceae (table 1). Crack willow (*Salix fragilis*) cover was markedly higher in stump plots than in those without beaver signs (U=1519, P=0.001; table 1), and a similar trend was found for *Populus nigra* and *Populus* x *canadensis* (U=863, P=0.011). There was no difference between these plots in the canopy cover of white willows, pioneer Salicaceae, and non-Salicaceae trees (table 1). Cover by bushy plants and bushy Salicaceae was higher in stump plots than in plots without beaver signs (U=817, P=0.046 and U=800, P=0.035; table 1). No difference was found between the two types of plots in mean cover of tall or small trees (table 1). Beavers fell trees on plots with steep banks (U=1416, P=0.011), and low human activity (U=742, P=0.005; table 1).

Occurrence of refectories did not depend on the bank slope (U=676, P=0.303), or on human disturbance level (U=622.5, P=0.174). Only one significant difference in vegetation structure and species composition was found between refectory plots and plots without beaver signs, that of cover by small Salicaceae trees: mean 0.26% (n=17) in refectory plots and 0.75% (n=36) in plots without beaver signs (U=1249, P=0.002). Eighty-two percent of the refectories examined (n=28) contained young twigs removed from Salicaceae (poplars, white willows, and crack willows; table 2). Browsed herbs belonged to various locally abundant species, particularly Monocotyledons. Five species of Poaceae and Cyperaceae were found in 49% of the refectories (table 2).

Discussion

Lodge sites in the colonised part of the Loire River

European beaver and American beaver (*Castor canadensis* Kuhl, 1820) are known to be able to live in places without Salicaceae, but when available, they prefer plants from this family as both food and building material (Nolet & Rosell 1998, Donkor & Fryxell 1999, Parker et al. 2001). Previously, Fustec et al. (2001) showed that on the Loire River, the home range size of the European beaver varied from 4.2 to 7.4 km, and was inversely correlated with the canopy cover of white willows and black poplars. However, vegetation is not homogeneous throughout a given home-range, and despite Salicaceae occurrence, lodges are sometimes built on sites where this plant family is poorly represented. According to Fustec et al. (2003), woody plant morphology seems to be a more important determinant of lodge site selection than Salicaceae abundance: beavers build lodges in sites with more than 37.5% canopy cover by 10-15 m tall

Table 1. Comparison of habitat variables between stump sites (with cut trees) and sites without beaver signs in the colonised part of the Loire River (B-stretch). Values are means (median / min-max). *U*-values are based on Mann-Whitney tests. *P*-values are two-tailed: ** = significant at the 0.01 level, * = significant at the 0.05 level.

	Stump sites (*n*=60)	No beaver signs (*n*=36)	*U*	*P*
Species mean cover (%)				
Salicaceae				
Populus alba	0.13 (0 / 0-2.5)	0.11 (0 / 0-2.5)	1104	0.752
Populus nigra & *P.* × *canadensis*	3.42 (12.5 / 0-62.5)	7.01 (2.5 / 0-37.5)	1400	0.011*
Salix alba	3.04 (0.5 / 0-37.5)	5.29 (0.5 / 0-37.5)	1025	0.658
Salix fragilis	2.90 (2.5 / 0-37.5)	1.51 (0 / 0-12.5)	1519	0.001**
Salix purpurea	0.09 (0 / 0-0.5)	0.07 (0 / 0-0.5)	1128	0.574
Salix triandra	0.29 (0 / 0-12.5)	0.04 (0 / 0-0.5)	1189.5	0.176
Salix viminalis	0.17 (0 / 0-2.5)	0.11 (0 / 0-0.5)	1082	0.983
Main other woody species				
Fraxinus angustifolia	8.05 (2.5 / 0-37.5)	10.83 (2.5 / 0-62.5)	1056.5	0.851
Quercus robur	0.88 (0 / 0-37.5)	0.18 (0 / 0-2.5)	1244	0.135
Sambucus nigra	0.06 (0 / 0-0.5)	1.09 (0 / 0-37.5)	1052.5	0.717
Ulmus minor	2.51 (0.5 / 0-37.5)	3.25 (0.5 / 0-37.5)	1105	0.840
Bank characteristics				
Slope (1-3 increasing scale)	2.85 (3 / 1-3)	2.50 (3 /1-3)	1416	0.011*
Human disturbance (1-5 increasing scale)	1.50 (1 / 1-3)	1.97 (2 / 1-4)	742.5	0.005**
Mean cover by different plant structure (%)				
10-15 m tall trees	23.96 (12.5 / 0-87.5)	19.23 (12.5 / 0-62.5)	1193	0.372
10-15 m tall Salicaceae trees	8.04 (2.5 / 0-62.5)	5.41 (2.5 / 0-37.5)	1298	0.082
5-10 m small trees	12.79 (2.5 / 0-62.5)	10.62 (7.5 / 0-62.5)	1147	0.829
5-10 m small Salicaceae trees	4.14 (0 / 0-37.5)	1.58 (0.3 / 0-12.5)	1135	0.648
>5 m bushy plants	15.75 (12.5 / 0-87.5)	12.03 (2.5 / 0-37.5)	817	0.046*
>5 m bushy Salicaceae	6.02 (2.5 / 0-37.5)	4.67 (2.5 / 0-37.5)	800.5	0.035*
Herbs	25.80 (12.5 /0.5-87.5)	31.38 (12.5 / 2.5-87.5)	884	0.432

trees, with about 33% Salicaceae. As is the case on the river Rhône, the beavers along the Loire River dig burrows or hut-burrows on steep banks (slope >50 %), rather than building huts (Richard 1973, Erome 1984, Fustec et al. 2003). Since the Loire River banks have a sandy substrate that is prone to collapse beavers require the strong root system of a 10-15 m tall tree as a burrow frame, irrespective of the plant species. They avoid sandbanks and most kinds of ripraps, but select quiet places, such as islands, to build lodges (Fustec et al. 2003).

Stump sites in the colonised part of the Loire River

On the Loire River, European beavers mainly fell poplars and willows, and to a lesser extent non-Salicaceae species (Fustec et al. 2001). These results concur with other studies conducted in areas where Salicaceae are available (Gorshkov et al. 2002). However, several authors report that both European and American beavers do cut numerous non-Salicaceae species such as Ulmaceae, Oleaceae, Aceraceae, Betulaceae, Rosaceae, and

Table 2. Occurrence of plant species identified from remains of browsed branches and herbs in refectory sites (*n*=28).

Plant species	Occurrence in refectories (%)
Salicaceae (4 sp.)	**82.3**
Populus nigra	32.1
Salix fragilis	21.6
Populus x canadensis	14.3
Salix alba	14.3
Other woody species (3 sp.)	**14.3**
Ulmus minor	7.1
Fraxinus angustifolia	3.6
Prunus laurocerasus	3.6
Monocotyledons (5 sp.)	**49.5**
Carex riparia	21.0
Paspalum paspalodes	10.7
Echinochloa crus-gallii	7.1
Phalaris arundinacea	7.1
Cyperus esculentus	3.6
Dicotyledons (13 sp.)	**82.2**
Xanthium orientale	17.8
Artemisia vulgaris	10.7
Calystegia sepium	10.7
Polygonum amphibium	7.1
Conyza sp.	7.1
Cirsium sp.	3.6
Arctium lappa	3.6
Bidens frondosa	3.6
Lycopus europaeus	3.6
Rorippa sylvestris	3.6
Rorippa palustris	3.6
Ludwigia grandiflora	3.6
Erysimum cheiranthoides	3.6

Pinaceae (Nolet et al. 1994, Hartman 1996, King et al. 1998). In some cases, non-Salicaceae species are positively selected, even when they are uncommon compared to Salicaceae (Nolet et al. 1994, Collen & Gibson 2001). The differential use of woody species, either for construction or for food has implications for preference indices (Doucet et al. 1994). For instance, branch or trunk diameter may influence the selection of woody species for construction purpose (Barnes & Mallik 1997). According to our results, European beavers in the Loire River fell trees in plots with a high Salicaceae cover, in particular poplars and crack willows. This concurs with the findings of Fustec et al. (2001) that beavers of the Loire River use 4 cm mean diameter branches of willows and 6 cm of poplars for construction. Such branches (1.5-2.5 m length) can be commonly found in the roof frames of hut-burrows, where they are covered with either willow or non-Salicaceae twigs (ashes and elms; J. Fustec & J.P. Cormier, unpublished data). Because of the specific development traits of trees, beavers from the Loire River can only get frame branches, of these characteristics, from Salicaceae (poplars, white willows, and crack willows), whatever their morphological category. The rodent either cuts the trunk of trees to get the required branches, or directly removes basal branches of bushy plants. Plant morphology therefore appears to be less important in plant selection by beavers, although the abundance of bushy plants varies significantly between plots with and without beaver activity. Nevertheless, this result must be considered with some caution, as willows naturally tend to form bushes, and poplars have a high potential to resprout from the stump after being felled by beavers. This result may be simply linked to the high Salicaceae cover observed in stump plots.

Refectory sites in the colonised part of the Loire River

As discussed previously, Salicaceae twigs are, when available, the main food of the European beaver (Nolet et al. 1994, Barnes & Mallik 1997, Dzieciolowski & Misiukiewicz 2002). As this study shows, the beavers of the Loire River mainly use the same species for food as for construction, but have a preference for 5-10 m trees. Nolet et al. (1994) suggested that beavers positively select non-Salicaceae woody species, such as ash. In the Loire valley, ash is rarely eaten, even though it is very common. By contrast, various herbs are frequently used as food by beavers, when they are available, and it is likely that these provide important nutrient complements (Nolet et al. 1994, Nolet et al. 1995, Ganzhorn & Harthun 2000).

The habitat potential of the uncolonised stretch of the Loire River

In the uncolonised river stretch, canopy cover by poplars, white willows, and crack willows is markedly higher than in the colonised stretch, particularly for 10-15 m tall trees (P=0.0009). Canopy cover by 5-10 m trees (P<0.0001) and herbs (P<0.0001) is also higher (Fustec et al. 2003). Therefore, vegetation in the uncolonised stretch of the Loire River seems more favourable for feeding than in the colonised stretch. On the basis of a minimum cover of tall trees of more than 37.5%, we have identified 28 suitable sites for settlement along the 88 km surveyed in the uncolonised stretch, compared to 12 in the colonised stretch (Fustec et al. 2003). Unfortunately, the uncolonised stretch has been developed and equipped for fluvial navigation, which means that beavers will have to face a significantly more intense level of human activity (P=0.016; Fustec et al. 2003). Another factor is that river banks in the uncolonised stretch have been extensively altered: 78% of the bank length is protected by ripraps, and groynes have been built along the riversides to retain sand and maintain a channel for boats in the middle of the river. Taking these factors into account, only three of the 28 sites might be suitable for beaver settlement. It is possible that the beavers may adapt to this altered part of the Loire River. Alternatively they may find better living conditions along the tributaries.

Acknowledgements: We thank the Parc Naturel Régional (PNR) Loire Anjou Touraine, who supported this study, and two anonymous referees who helped us to improve the paper.

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Samenvatting

De vestigingsmogelijkheden voor de Europese bever (*Castor fiber)* in het benedenstroomse deel van de Loire, Frankrijk

In de jaren '70 vond een herintroductie plaats van de bever (*Castor fiber*) in de Loire, dichtbij de stad Blois. De dieren waren afkomstig uit de Rhône, waar zich lange tijd de enige overgebleven beverpopulatie van Frankrijk ophield. De introductie bij Blois was succesvol; de dieren verspreidden zich langzaam maar zeker over dit deel van de Loire en haar zijrivieren. Het was echter de vraag in hoeverre de bever zich ook meer stroomafwaarts zou kunnen vestigen. Om hierover een uitspraak te kunnen doen is allereerst in een door bevers bewoond deel van de Loire de relatie onderzocht tussen het voorkomen van beversporen (burchten, vraatsporen) en kenmerken van de vegetatie, de rivieroever en menselijke verstoring. Bevers bleken hun burchten bij voorkeur te bouwen op plaatsen die gedomineerd worden door 10-15 meter hoge bomen, ongeacht de boomsoort. Het voedsel bestond in hoofdzaak uit wilgen en populieren (Salicaceae) en een aantal soorten kruidachtige planten. De gevonden resultaten, alsmede de uitkomsten uit eerder onderzoek, zijn vergeleken met de eigenschappen van een naburig, meer stroomafwaarts gelegen traject van de Loire. Dit deel van de rivier was niet gekoloniseerd, maar wel zijn hier geregeld bevers waargenomen, mogelijk op zoek naar geschikte vestigingsplaatsen. Uitgaande van de vegetatie, bleek dit gebied enkele tientallen gunstige vestigingsplaatsen te herbergen, zelfs meer dan in het onderzochte bewoonde traject. Echter, het onbewoonde traject is grotendeels ontwikkeld voor de scheepvaart. Op vele plaatsen zijn stroomdammen aanwezig en is het oevertalud verstevigd. Als deze factoren in aanmerking worden genomen, blijven er naar verwachting slechts drie plaatsen over met goede kansen voor vestiging van de bever.

Received: 31 October 2003
Accepted: 27 January 2004