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Including wildlife habitat in the definition of riparian areas: The beaver (*Castor canadensis*) as an umbrella species for riparian obligate animals

Patricia Stoffyn-Egli and J.H. Martin Willison

Abstract: Riparian wildlife is as important as vegetation in maintaining watercourse ecological integrity, yet present riparian buffer guidelines often fail to maintain sufficient terrestrial habitat for a variety of riparian species in North America. This is of particular concern for the conservation of riparian obligate animals, defined as freshwater-dependent species for which the terrestrial habitat immediately adjacent to watercourses is indispensable to complete their life history. Terrestrial habitat requirements of riparian obligate species are reviewed in this paper using the North American beaver (*Castor canadensis*) as a focal species. As an ecosystem engineer, the beaver has a profound influence on the shape and function of riparian ecosystems and creates diverse habitat patches. Published data show that 95% of woody plants cut by beavers on land are obtained within 50 m of the water's edge. A review of riparian invertebrates, amphibians, reptiles, mammals, and birds indicates that a 50 m-wide riparian buffer (measured from the high water mark) in its natural state (intact native vegetation) is the minimum area for supporting the majority of riparian obligate species. Exceptions are moose and some amphibian species that also need habitat well beyond 50 m from the water's edge to complete their life history. To conserve these wide-ranging species it is recommended that riparian buffers be continuous and integrated in a connectivity plan including upland reserves. Such a watershed-wide plan will also ensure that riparian buffers can serve as travel and dispersal corridors for both riparian and upland wildlife.

Key words: *Castor canadensis*, riparian obligate, home range, conservation buffer, riparian area, stream habitat.

Résumé : La faune riveraine peut être aussi importante que la végétation pour maintenir l'intégrité écologique d'un cours d'eau, et pourtant les directives présentes de réglementations riveraines n'arrivent souvent pas à maintenir suffisamment d'habitat terrestre pour diverses espèces riveraines d'Amérique du Nord. Ceci concerne en particulier la conservation des animaux riverains obligatoires, définis comme des espèces dépendant de l'eau douce pour lesquelles l'habitat terrestre immédiatement adjacent aux cours d'eau est indispensable pour compléter leurs cycles vitaux. Les auteurs passent en revue les besoins en habitats terrestres des espèces riveraines obligatoires, en prenant le castor nord-américain (*Castor canadensis*) comme espèce focale. En tant qu'ingénieur de l'écosystème, le castor exerce une profonde influence sur la forme et la fonction des écosystèmes riverains et crée des parcelles d'habitat variées. Les données publiées montrent que 95% des plantes ligneuses terrestres coupées par les castors proviennent de 50 m au plus du bord de l'eau. Une revue des espèces riveraines incluant les invertébrés, les amphibiens, les reptiles, les mammifères et les oiseaux indique qu'une zone tampon large de 50 m (mesurée à partir de la ligne des hautes eaux) dans son état naturel (végétation indigène intacte) constitue une surface minimale pour satisfaire la majorité des espèces riveraines obligatoires. L'orignal et certains amphibiens font exception, ayant besoin d'un habitat allant bien au-delà de 50 m du bord de l'eau pour leur cycle vital. Pour conserver ces espèces aux habitats étendus, on recommande des tampons riverains continus et intégrés dans un plan de connectivité incluant des réserves en hautes terres. Une telle planification des bassins versants assurera que les tampons riverains puissent également servir de corridors pour les déplacements et la dispersion des espèces animales riveraines et des hautes terres.

Mots-clés : *Castor canadensis*, espèce riveraine obligatoire, domaine vital, tampon de conservation, zone riveraine, habitat fluvial.

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Introduction

The land bordering watercourses, usually called riparian area or corridor, interacts with the adjacent water body through reciprocal exchanges of materials and energy (NRC 2002; Verry et al. 2004; Naiman et al. 2005). As such, ripar-

ian areas strongly influence the ecological integrity of freshwater ecosystems. It is now well established that riparian vegetation (particularly trees) and soil perform various riparian functions including (i) thermal regulation of the water and, more generally, establishment of unique microclimates (wind, light, temperature, and humidity conditions); (ii) the

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supply of coarse organic matter (e.g., leaves), a food source for many benthic invertebrates; (iii) the supply of large woody debris that affect channel shape and water flow while providing refugia for fish and substrate for aquatic invertebrates; (iv) water purification and regulation of nutrient inputs to streams and lakes; (v) dampening of floods and droughts by decreasing surface run-off and helping replenishment of groundwater by infiltration of precipitation; and (vi) bank stabilization, control of erosion, and corresponding stream-bed sedimentation (see reviews by NRC 2002 and Naiman et al. 2005). It has been suggested that the minimum riparian area width to fulfil these functions is on the order of one site-potential tree height (FEMAT 1993; Naiman et al. 2000a), which is approximately 30 m in eastern North America and 50 m in the west (O'Laughlin and Belt 1995; Reid and Hilton 1998).

The widespread alteration of riparian areas by human activities has resulted in the loss of many of the ecosystem services they provide, such as water purification and maintenance of fish populations (Naiman et al. 2002; Dudgeon et al. 2006). In attempts to reverse this trend, most jurisdictions in North America have adopted guidelines (recommended or mandatory) to control land use within a specific distance from the water's edge, commonly called riparian "buffer" or "special management zone" (Blinn and Kilgore 2001; Lee et al. 2004). These guidelines tend to focus more on mitigating detrimental impacts of human activities on streams, lakes, or wetlands (e.g., fertilizer and pesticide sequestration) than on overall protection of riparian ecological functions and biodiversity (Lee et al. 2004; Crawford and Semlitsch 2007; Goates et al. 2007). Although highly variable, current riparian guidelines prescribe buffer widths of 30 m or less in many cases, and (or) allow some level of resource extraction such as partial timber harvest (see Blinn and Kilgore 2001 and Lee et al. 2004 for details).

Riparian areas are known to support high levels of biodiversity on relatively small areas of the landscape (Anthony et al. 2003; Dudgeon et al. 2006). As a result, the stated goals of riparian buffer guidelines increasingly include the conservation of terrestrial wildlife, and many studies have attempted to assess the value of riparian buffers as habitat for wildlife, particularly in forested areas where timber extraction is taking place (see reviews by Semlitsch and Bodie 2003 and Marczak et al. 2010). A number of these studies concluded that riparian buffers wider than those prescribed in their study area were needed to maintain species abundance and diversity similar to those of undisturbed sites (e.g., Hagar 1999; Vesely and McComb 2002; Shirley and Smith 2005). This conclusion is not surprising as these studies considered all species present in the undisturbed sites, including terrestrial species preferring interior habitat. Riparian buffers are typically linear reserves with high perimeter-to-area ratios where edge effects dominate (Brososke et al. 1997; Mascaraúa López et al. 2006), and are thus poor representatives of interior habitat. For example, Hannon et al. (2002) point out that edge effects from both the water's edge and the clear-cut edge make 100 m-wide buffers essentially all edge habitat, and suggest a buffer width of 200 m to preserve the preharvest bird community. Moreover, increased incidence of wind-throws at the clear-cut edge further reduces the forest habitat value of a buffer (Reid and Hilton 1998; Whitaker

and Montevecchi 1999). Yet, buffer widths of 200 m have little chance of being implemented because of their impact on resource extraction and competing land uses. It has been argued that conservation of interior species would be better served by protecting large blocks of inland habitat (Whitaker and Montevecchi 1999; Potvin and Bertrand 2004).

Riparian buffers may not, by themselves, preserve all terrestrial fauna but they are indispensable for riparian obligate wildlife. Riparian obligate species are species that "absolutely require streams or riparian areas for some portion of their lives" (Richardson 2004; see also Naiman et al. 2000a; Anthony et al. 2003). Thus, inadequate protection of the riparian area may result in their extirpation (or even extinction), and for this reason the riparian buffer width should include the terrestrial range needed by riparian obligates. Moreover riparian obligate species are as instrumental as vegetation in maintaining riparian ecological functions through their activities (e.g., predation, damming, burrowing) which influence the fluxes of matter and energy between terrestrial and aquatic ecosystems (Naiman et al. 2000b; Baxter et al. 2005; Butler 2006).

1.1 The beaver – a riparian ecosystem engineer

The North American beaver (*Castor canadensis*) is one of the most typical and important riparian obligate species. Beavers find shelter and food (aquatic plants) in water but also eat terrestrial vegetation (forbs, grasses, bark) and cut woody vegetation on land for building lodges, dams and food caches (NRC 2002; Müller-Schwarze and Sun 2003; Parker et al. 2007). Through these activities, the beaver (i) changes the flow regime of sections of a river and thus erosion and sedimentation patterns (Gurnell 1998; Butler and Malanson 2005; Butler 2006); (ii) shifts the aquatic environment from lotic to lentic upstream of the dam (Collen and Gibson 2001; Rosell et al. 2005); (iii) increases wetland area through flooding (Naiman et al. 1988; Cunningham et al. 2006; Hood and Bayley 2008a) with attendant shifts from terrestrial to hydrophilic or aquatic vegetation (Ray et al. 2001; Rosell et al. 2005); and (iv) affects the composition, structure, and succession of the terrestrial vegetation in the riparian area (Martell et al. 2006; Donkor 2007; Wright 2009). The beaver is such an important species in the creation and maintenance of riparian areas that it is considered an ecosystem engineer (Müller-Schwarze and Sun 2003; Wright et al. 2004; Rosell et al. 2005). In fact, it has been argued that today's watercourses are not representative of their historical characteristics as beaver abundance, although increasing, amounts only to about 10% of the numbers that existed before commercial trapping for the North American fur trade (Naiman et al. 1988; Müller-Schwarze and Sun 2003; Butler and Malanson 2005). Indeed, Hood and Bayley (2008a) consider that removal of beavers is a detrimental wetland disturbance, and reintroduction of beavers in degraded stream reaches has been both proposed and used for rehabilitating human-impacted watercourses and restoring wetlands (Albert and Trimble 2000; McKinstry et al. 2001; Müller-Schwarze and Sun 2003).

Beaver activities result in a variety of habitat patches (both aquatic and terrestrial) and, therefore, more biodiversity (Naiman et al. 1988; Anthony et al. 2003; Wright et al. 2004). Studies documenting how beavers create or enhance habitat for a multitude of species include effects on the occurrence,

number and diversity of aquatic plants (Ray et al. 2001; Parker et al. 2007), invertebrates (Collen and Gibson 2001), fish (Collen and Gibson 2001; Pollock et al. 2004; Rosell et al. 2005), birds (McKinstry et al. 2001; Aznar and Desrochers 2008; Nummi and Hahtola 2008), amphibians (Cunningham et al. 2006; Stevens et al. 2007), and mammals (Anthony et al. 2003; LeBlanc et al. 2007). As such, the beaver can be considered an umbrella species for conservation purposes (Beazley and Cardinal 2004; Roberge and Angelstam 2004) throughout much of North America, as its geographic range extends from coast to coast and from the arctic tundra to northern Mexico (Müller-Schwarze and Sun 2003; Butler 2006).

1.2 Goals and definitions

The overall goal of this paper is to estimate the minimum riparian buffer width that spans the riparian habitat necessary for the survival of riparian obligate wildlife. In the first part of the paper we evaluate the riparian width that meets the terrestrial habitat requirements of the North American beaver on the basis of published data on its foraging ranges. In the second part we review which animal species can be considered riparian obligates and assess to what extent the riparian width necessary for the beaver will also provide sufficient terrestrial habitat for these species. For this purpose, we refine the definition of riparian obligate animal to mean a species for which aquatic (or semi-aquatic such as a wetland) environment is *essential* for at least one of its life-history needs (i.e., feeding, shelter, breeding, or hibernation but not dispersal) and which also needs the terrestrial environment *immediately* adjacent to the aquatic or wetland habitat. Thus, fish, for example, are not considered riparian obligates, nor are terrestrial species that are present in riparian areas but for which the adjacent water body is not indispensable to complete their life history.

When considering buffer width or a riparian species' terrestrial range, it is implicitly assumed that the reference point is the water's edge. Yet the position of the water-land boundary may vary considerably with seasons. In this paper we consider that the water's edge is the *limit of the watercourse at high water mark*, a recommended definition that is independent of the type of water body and includes intermittent streams (Ilhardt et al. 2000; Verry et al. 2004). According to this definition, regularly flooded areas such as adjacent wetlands or lateral channels are part of the watercourse.

The water's edge lies within the *riparian ecotone*, the transition between fully aquatic conditions (e.g., the permanent part of a lake or the main river channel) to fully terrestrial conditions, where biophysical parameters (e.g., microclimate, soil humidity) stop being significantly influenced by the proximity of water (Palik et al. 2000; NRC 2002; Verry et al. 2004). To avoid any ambiguity, we use the term riparian area to designate the most landward portion of the ecotone uphill from the water's edge. The riparian buffer is measured from the same water-land boundary, but this term refers to a managed area within which land-use restrictions are specified, having a width not necessarily equal to that of the riparian area itself.

2. Beaver terrestrial foraging ranges

In this section we use "forage" to mean woody stems cut

by beaver for food and dam or lodge building. Beavers are quite selective in the woody species they harvest at a given location; generally, they prefer poplar (*Populus* spp.), willow (*Salix* spp.), and alder (*Alnus* spp.), and usually avoid conifers (Müller-Schwarze and Sun 2003; Gallant et al. 2004 and references therein). Nevertheless, beavers are very adaptable and will settle in areas where preferred species are scarce (e.g., mostly coniferous forests of Newfoundland: Northcott 1971), which explains the wide range of the species' distribution across North America (Müller-Schwarze and Sun 2003).

As central-place foragers, beavers bring back the trees and stems they cut to the central water-based colony for construction or consumption (Barnes and Mallik 2001; Gallant et al. 2004; Hood and Bayley 2008b). Energy maximization models predict that the species and size of stems selected by beavers, as well as the distance from the water at which they are harvested, are controlled by the need to optimize the consumer's net energy gain (Basey et al. 1988; Fryxell 1992; Gallant et al. 2004). The models explain why beavers concentrate their foraging near the shore around the body of water they occupy (Johnston and Naiman 1990; Donkor and Fryxell 1999, 2000). This behaviour is reinforced by the fact that beavers are likely more vulnerable to predators on land than in water and thus gain by spending as little time as possible on land (Basey and Jenkins 1995; Müller-Schwarze and Sun 2003; Hood and Bayley 2008b). For example, in a comparison of two islands in Lake Superior with similar vegetation, Smith et al. (1994) found that beavers concentrated their foraging closer to shore on the island where black bear (*Ursus americanus*) predation of beaver was highest. Therefore, as the cost of provisioning and the risk of predation increase with distance from the water's edge, there should be a distance beyond which it is not profitable for beavers to forage.

2.1 Published data selection

Beaver foraging is easily documented because beavers leave clear evidence of their foraging activities in the form of cut branches and tree stumps. Thus, data on beaver foraging intensity versus distance from the water's edge is available from a variety of published papers testing energy maximization models of central-place foragers (Jenkins 1980; Pinkowski 1983; Belovsky 1984; Basey et al. 1988; Fryxell 1992; Gallant et al. 2004), investigating competition between species of herbivores (Nietvelt 2001; Hood and Bayley 2008b), or studying the influence of beaver foraging on the structure, composition and succession of woody plant communities in riparian areas (Barnes and Dibble 1988; Donkor and Fryxell 1999, 2000; Barnes and Mallik 2001; Martell et al. 2006; Voelker and Dooley 2008).

As our goal is to determine how far beavers venture to harvest the majority (i.e., 95%) of their woody vegetation, only those studies in which researchers determined maximum foraging distance, and (or) recorded cut stems from the water's edge to at least that distance, have been considered. Among these studies, only those that reported all tree species cut, or species that compose at least 70% of all stems cut (Northcott 1971; Jenkins 1980; Martell et al. 2006) were retained to determine the minimum land width that provides the majority of the beavers' forage, regardless of beaver preferences or species availability. For two studies in which the data were

reported only for *Populus* spp., we included only the site where aspens were the dominant tree species around the beaver colony (Little Valley, Nevada, in Basey et al. 1988), and we ignored aspen stands that had a breadth less than 30 m in the direction perpendicular to the shoreline, which would force a distance limit on beaver foraging for aspen (two out of four sites in Nietvelt 2001).

The 16 papers that met the above criteria are listed in Table 1; the first 10 reported foraging intensity versus distance, the last six reported only maximum foraging distance. We further ascertained that the foraging ranges reported were not likely to be influenced by human disturbances. Most studies were carried out in national, provincial, or state parks (Belovsky 1984; Müller-Schwarze et al. 1994; Donkor and Fryxell 1999, 2000; Gallant et al. 2004; Hood and Bayley 2008b), or other protected areas (Jenkins 1980; Barnes and Dibble 1988; Voelker and Dooley 2008). In other cases, study sites were chosen far from human activities that might otherwise influence beaver foraging ranges (e.g., trapping or roads: Barnes and Mallik 2001; cutblocks, pipelines, or oil wells: Martell et al. 2006).

2.2 Data analysis

Figure 1 summarizes beaver foraging data versus distance from the shoreline of water bodies, most often beaver ponds, for active or recently abandoned beaver colonies (the 10 first studies in Table 1). The basic measurement is the number of stems cut, often with a threshold minimum diameter for counting in the range of 0.5 to 5.0 cm if specified. However the data are sometimes reported in other units, such as basal area cut (Martell et al. 2006) or percent availability (stems cut/total stems in the sampling plots: Basey et al. 1988; Nietvelt 2001). To be able to compare all data sets, they were recomputed as cumulative percentage of total amount foraged and plotted versus distance from water (Fig. 1). When data were published only as graphs, the graphs were scanned and imported into graphics software (FreeHand MX, Macromedia Inc.) to facilitate the reading of data points. In some studies, only combined data for several beaver colonies were published, but whenever a data set was reported for each individual colony or site, it was plotted separately in Fig. 1.

2.3 Results

The data show that in all cases but one, beavers obtained 95% of their forage within 50 m of the shoreline at the most (Fig. 1). This distance is further confirmed by the other studies that report only the maximum foraging distance, ranging from 20 to 60 m (last six studies in Table 1). The single exception is the Blue Heron Cove (BHC) location of Jenkins (1980) where only 50% of the stems cut were found within 60 m of the shoreline (Fig. 1) and 90% of foraging was achieved at 100 m from the water's edge. However, the data reported for BHC are for only one of several foraging sites around the beaver pond. Foraging at the other sites was concentrated closer to the shoreline (Jenkins 1975), indicating that if data were reported for the entirety of the beaver pond, the relationship between number of stems cut and distance from water would be more similar to that of other colonies in Fig. 1. For this reason, Jenkins' data for BHC have not been used in the estimation of beavers' foraging distance.

The fact that beavers obtain 95% of their forage within

50 m from the shoreline (Fig. 1) does not mean that beavers will not travel beyond 50 m: home range studies by telemetry suggest that beavers will roam farther than 100 m from the water's edge (Wheatley 1994) and aspen, the favourite food of beavers, has been reported cut as far as 200 m from the water (Smith et al. 1994; Müller-Schwarze and Sun 2003). Nevertheless, proportionately little foraging of woody vegetation seems to take place at these greater distances.

In some locations beavers found 80% to 100% of their forage within 20 m of the shoreline, whereas in other locations they travelled 40 or 50 m to get that quantity of woody stems (Fig. 1). This variability among study sites can be attributed to the fact that the distance at which beavers will forage depends on the food species available (palatability, nutritional value), the size of stems and their distribution along the transect, all of which, in turn, depend on the length of time a particular site has been occupied by beavers. The longer a beaver colony has been active, the more foraging has taken place, and beavers have to go further from the water to provision, and (or) switch to different, less palatable species (Müller-Schwarze and Sun 2003). This trend with colony age is confirmed by feeding experiments in captivity which show that as stem density per unit area decreases, beavers forage further away from the water (Fryxell 1992). The fact that older colonies, or beaver families that resettle a previously occupied site, must forage farther is due not only to depletion of woody vegetation but also to the decreased palatability of regrowth or juvenile forms of trees that are enriched in defensive chemicals, at least in the cases of aspen (*Populus tremuloides*) and cottonwood (*P. fremontii* and *P. angustifolia*; Basey et al. 1988, 1990; Martinsen et al. 1998).

All studies considered represent 106 beaver colonies or ponds from locations ranging from the forests of the Sierra Nevada (Basey et al. 1988) and the Canadian Rockies (Nietvelt 2001) north to the Mackenzie River delta arctic taiga (Aleksiuk 1970) in the west, and from the boreal forest of Newfoundland (Northcott 1971) to southern Ohio (Voelker and Dooley 2008) in the east. Given the wide variety of ecological conditions such as climate, vegetation, predators, competitors, and beaver colonization history, it is noteworthy that 99% of these colonies did not forage significantly beyond 50 m from the water's edge, including those that inhabited the site for a relatively long period (e.g., for more than 5 years; Donkor and Fryxell 1999, 2000; Hood and Bayley 2008b). The data reviewed here therefore indicate that 50 m is the approximate distance beyond which regular, frequent foraging is not profitable for beavers. If resources become insufficient within this distance, beavers do not survive or abandon the site and do not recolonize it until it has recovered enough to support a new colony (Fryxell 2001; Wright et al. 2004). The sequence of colonization, abandonment and reoccupation by beavers has been documented in many locations (Müller-Schwarze and Sun 2003; Martell et al. 2006 and references therein). We now turn our attention to identifying other riparian obligate animals and assessing the extent to which a 50 m riparian width may also satisfy the terrestrial habitat needs of these species.

3. Riparian obligate animals

We reviewed the literature for information on the terrestrial

Table 1. Summary of published beaver (*Castor canadensis*) foraging studies that have measured terrestrial foraging distance from the shoreline. Only studies where all or the majority of species cut by beaver were reported are listed. The first 10 studies report foraging intensity versus distance from the water's edge (see Fig. 1). The last six studies report maximum foraging distance only.

Author	Location	Maximum foraging distance (m)	No. of colonies or ponds (No. of transects)	Age of colony or dam	Vegetation measured (dominant species at site in parentheses)
Hood and Bayley 2008b	Inside Elk Island National Park, East-central Alberta	66	5	at least 5 years	All species (trembling aspen – <i>Populus tremuloides</i>)
Voelker and Dooley 2008	Outside park The Wilds conservation, research and recreation facility, Southeastern Ohio	73 40 20	5 (total: 106) 1 (4) 2 (5)	at least 5 years active recently abandoned	All species (sweetgum – <i>Liquidambar styraciflua</i> , autumn olive – <i>Elaeagnus umbellata</i>)
Martell et al. 2006; Martell 2004	Mid-boreal mixed wood forest sites, Northeastern Alberta	50	6 (36)	1, 1, 5, 9, 24 and 35 years respectively	Poplar species , which compose 97% of beaver consumption (trembling aspen – <i>Populus tremuloides</i>)
Gallant et al. 2004	Kouchibouguac National Park, New Brunswick	90	25 (transects every 50 m around each pond)	active, well established, with maintained dams	All species (trembling aspen – <i>Populus tremuloides</i> , red maple – <i>Acer rubrum</i> , speckled alder – <i>Alnus rugosa</i> , conifers, grey birch – <i>Betula populifolia</i>)
Barnes and Mallik 2001	Swanson River drainage, Chapeau Crown Game Preserve, Northern Ontario	40	8 (24)	less than 5 years	All species (conifers, alder – <i>Alnus</i> spp., white birch – <i>Betula papyrifera</i> , trembling aspen – <i>Populus tremuloides</i>)
Nietvelt 2001	Bow River Valley Kananaskis Valley, near Banff National Park, Alberta	38 46	1 (16) 1 (10)	active active	Aspen - assumed to be the majority of cut stems in "homogenous stand" (trembling aspen – <i>Populus tremuloides</i>)
Donkor and Fryxell 1999	Southern Algonquin Park, Ontario	60	15 (6 to 11 transects each)	8–10 years	All species (poplars – <i>Populus</i> spp., white birch – <i>Betula papyrifera</i> , red maple – <i>Acer rubrum</i> , conifers)
Basey et al. 1988	Frankton Creek, near Little Valley, Toiyabe National Forest, Nevada	18	1 (5)	less than 2 years	Aspen - assumed to be the majority of cut stems in "aspen stand" (trembling aspen – <i>Populus tremuloides</i>)
Pinkowski 1983	Swale of prairie cordgrass (<i>Spartina pectinata</i>) near Mandaree, McKenzie County, North Dakota	55	1 (7)	less than 1 year	All species (trembling aspen – <i>Populus tremuloides</i> , green ash – <i>Fraxinus pennsylvanica</i>)
Jenkins 1980; Jenkins 1975	West shore of Taplin Road Pond Southwest shore of East Fever Brook	30 30	1 (9) 1 (9)	12–15 years active	Maple – <i>Acer</i> spp. and cherry – <i>Prunus</i> spp.: 81% of total cut Maple – <i>Acer</i> sp., oak – <i>Quercus</i> spp., and birch – <i>Betula populifolia</i> : 72% of total cut
Müller-Schwarze et al. 1994	West shore of Blue Heron Cove; All sites in the Quabbin Reservation, Central Massachusetts	100	1 (5)	12–15 years	Maple – <i>Acer</i> spp., oak – <i>Quercus</i> spp., birch – <i>Betula populifolia</i> and witch-hazel – <i>Hamamelis virginiana</i> : 91% of total cut
Johnston and Naiman 1990	Allegany State Park, New York Amity Creek, near Duluth, Minnesota	60 35 55	7 (sampled 60 m width along entire shoreline) 1 (9) 1 (6)	not stated recolonized recently after abandoned 6 years 5 years	All species (mixed woods, species composition not described) All species (trembling aspen – <i>Populus tremuloides</i>)

Fig. 2 (concluded).

Author	Location	Maximum foraging distance (m)	No. of colonies or ponds (No. of transects)	Age of colony or dam	Vegetation measured (dominant species at site in parentheses)
Barnes and Dibble 1988	Tiffany Bottoms, Lower Chipewewa River, Wisconsin State Natural Area	45	6 (2–3 per site)	1 year	All species (ash – <i>Fraxinus</i> spp., silver maple – <i>Acer saccharinum</i> , American elm – <i>Ulmus americana</i> , river birch – <i>Betula nigra</i>)
Belovsky 1984	Isle Royale National Park, Michigan	48	1 (transects every 100 m around entire pond)	active	All species (yellow birch – <i>Betula alleghaniensis</i> , eastern white cedar – <i>Thuja occidentalis</i> , spruce – <i>Picea</i> sp.)
Northcott 1971	Grand Falls area and New World Island, Newfoundland	42	10 (every 30 m around each pond)	not stated	Alder – <i>Alnus crispa</i> and <i>Alnus rugosa</i> , at least 83% of total cut (conifers, alder – <i>Alnus</i> spp.)
Aleksiuk 1970	Mackenzie River delta, Northwest Territories	20	6 (12)	active	All species (white spruce – <i>Picea glauca</i> , willow – <i>Salix</i> spp., alder – <i>Alnus crispa</i> , balsam poplar – <i>Populus balsamifera</i>)

habitat use of invertebrates, amphibians, reptiles, mammals, and birds that can be considered riparian obligates (see Section 1.2). We sought published data on home range expressed as linear distance from the water's edge, which is rarely available to the extent and detail of beaver foraging studies because area or linear range parallel to the watercourse is more commonly reported, or the data is averaged over the entire riparian width studied. Moreover, methods vary considerably between studies and data are not directly comparable as is the case for the beaver. We focused on estimating the maximum home range size from the water's edge (rather than averages for groups of species) to evaluate the likelihood that a riparian width of 50 m is sufficient terrestrial habitat for the riparian obligate species considered. These estimates, discussed in the following, have been summarized in Fig. 2. For some species (e.g., crayfish, star-nosed mole) we rely on anecdotal information because data on the animal's abundance versus distance from water is lacking. In an effort to have more data, a few studies from outside North America were included in this review. Because home range (or "core habitat") is most often determined by inventory, capture, or radio-tracking, it may include some dispersal movement and thus be an over-estimation of the distance from water that is indispensable for an individual's survival. As in the case of the beaver, we aim at identifying "natural" terrestrial ranges and thus avoided study sites where this range is likely to be constrained by recent or ongoing land uses (e.g., clear cuts, agriculture, urban areas).

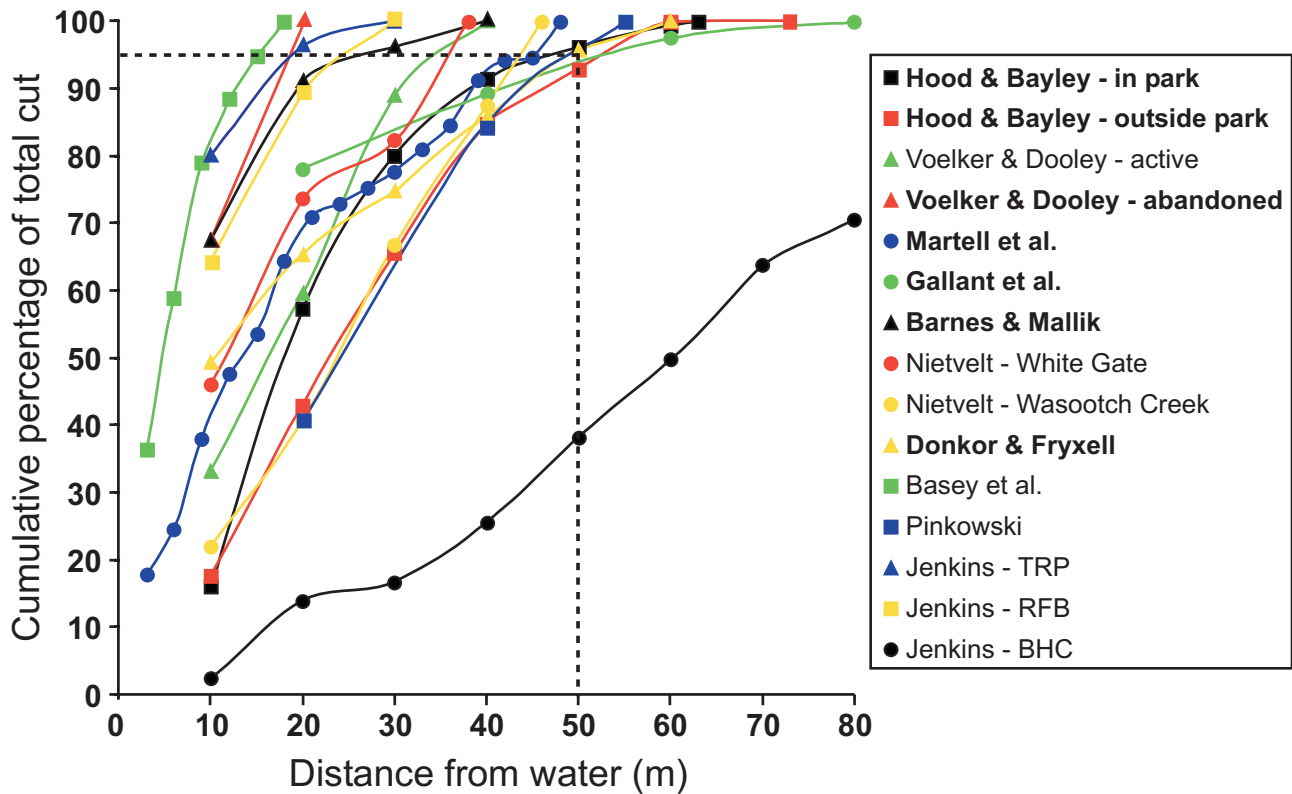
3.1 Invertebrates

Among aquatic invertebrates, emergent insects (i.e., those that have larval stages in water but emerge from it as adults) can be considered riparian obligates. These flying adults use the riparian area for roosting, feeding and (or) mating (Malmqvist 2002; Briers and Gee 2004). These emergent insects are an important biological link between aquatic and terrestrial ecosystems, being a major source of prey for fish, amphibians, reptiles and semi-aquatic mammals (e.g., water shrews) as larvae, and for terrestrial consumers such as birds, bats, spiders and small mammals as adults (Malmqvist 2002; Baxter et al. 2005).

In general, the abundance of emergent insects decreases exponentially with distance from the water's edge (Petersen et al. 1999; Briers and Gee 2004; Baxter et al. 2005). Studies of such lateral distributions show that in most locations the majority of emergent insects are found within 50 m of the water's edge, and commonly within 10 m (Petersen et al. 2004 and references therein; Winterbourn 2005; Finn and Poff 2008), particularly for mayflies (Ephemeroptera), stoneflies (Plecoptera), and caddisflies (Trichoptera) which represent the bulk of the available data. There is evidence that in the case of chironomid midges (Gratton et al. 2008) and mosquitoes (Culicidae; Barker et al. 2009 and references therein), blood-feeders such as black flies (Simuliidae; Finn and Poff 2008), some individuals range somewhat further from the water's edge. Dragonflies and damselflies (Odonata) seem to range further than the other emergent insects although seldom beyond 200 m from the water's edge (Bried and Ervin 2006 and references therein; Rouquette and Thompson 2007).

Although the limited data suggests that a 50 m riparian buffer may not be sufficient for some species of dragonflies,

Fig. 1. Cumulative percentage of total woody vegetation cut by beaver versus distance from the shoreline (e.g., beaver pond). The data used to calculate percent of total forage is generally number of stems cut. Exceptions are Martell et al. (2006): basal area cut; Nietvelt (2001) and Basey et al. (1988): percent stems available (cut stems / all stems). The legend items in bold represent data sets combining several beaver colonies (see Table 1). The dashed lines indicate the maximum distance needed to obtain at least 95% of the total forage for 73 beaver colonies (excepting Blue Heron Cove (BHC), Jenkins 1980).



mosquitoes, black flies, and midges, the larger movement distances may be partly related to dispersal rather than represent terrestrial habitat needs of individuals. This is because measurements of emergent insects distribution versus distance from the water's edge cannot distinguish easily between active dispersal (flight), passive dispersal (wind) and home range for life history needs (e.g., mating, feeding; Bilton et al. 2001; Malmqvist 2002; Briers and Gee 2004).

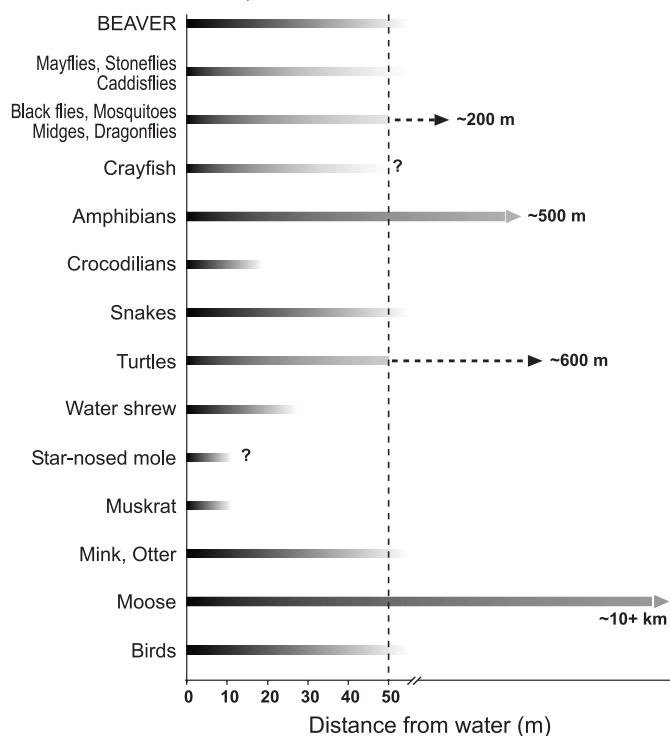
Another group of invertebrates to be considered in the context of riparian obligate species is American crayfish (Cambaridae and Astacidae) which are associated with aquatic or semi-aquatic habitats as they need free water for reproduction. Exceptions are crayfish associated with perched water tables or poorly drained soils in upland areas that have been documented recently (*Distocambarus youngineri* and *D. crockeri*; Eversole and Welch 2010). These species do not depend on streams for reproduction and can be considered terrestrial (Welch and Eversole 2006), not riparian obligates. Many species of crayfish live exclusively in water and rarely burrow (tertiary burrowers), whereas others inhabit seasonally flooded areas and are restricted to burrows only during dry periods (secondary burrowers; Welch and Eversole 2006). In particular, Astacidae are less adept at burrowing and appear to do so only in streambeds and banks (Cordeiro 2010). As such, these crayfish inhabit the aquatic and semi-aquatic habitat mostly included in the watercourse at high water mark. Primary burrowers are likely to range further from the water's edge as they tolerate more xeric conditions,

living in burrows and migrating to free water only for breeding (Cordeiro 2010). We could not find data on burrow distance from water, but the tendency of primary burrowers to seek shallow water tables that can be reached by burrowing suggests that they will stay in proximity of the watercourse and that a 50 m riparian area should satisfy their needs in the majority of cases.

3.2 Amphibians

Amphibians are, by definition, riparian obligates as they use water bodies for breeding, but live on land for at least part of their adult life. Notable exceptions are the woodland salamanders (*Plethodon* spp.), which have no aquatic larval stage and inhabit moist forest floor throughout their life history (Wells 2007). Movements of adult amphibians directly related to basic needs (i.e., feeding, mating, or hiding but not dispersal) involve short distances on the order of a few metres in many cases, but their seasonal ranging behaviour (e.g., to reach hibernation sites) in response to temperature and humidity changes may involve much longer distances (Pauley et al. 2000; Olson et al. 2007; Wells 2007). Semlitsch and Bodie (2003) reviewed the use of terrestrial habitat by amphibians in terms of movement distance from the water's edge. Among the 39 North American studies for which they list minimum and maximum distances (not only a mean or mode), seven report maximum ranges less than 50 m, 17 report minimum ranges below 50 m, and most maximum values are 500 m or less. Wide variations occur

Fig. 2. Estimate of riparian habitat width used by riparian obligate wildlife (Section 3). Dashed arrows show range beyond 50 m from the water's edge used only by some individuals of the species considered (some emergent insects and turtles). Solid bars with arrow head show that many individuals of some of the species considered use habitat beyond 50 m (amphibians and moose). A question mark indicates that the distance from water is inferred from life history of the species but that no values could be found in the literature (crayfish and star-nosed mole).



not only between species but between individuals of a single species. This is not surprising as amphibian movements cannot be easily generalized, study results being particularly sensitive to the sampling scheme and influenced by local environmental characteristics (Cushman 2006). For example Goates et al. (2007) observed occasional movements of boreal toads (*Anaxyrus boreas*) beyond 100 m from the water's edge in aspen-mixed conifers forests of Utah, particularly during more humid months and years. For the same species, Browne and Paszkowski (2010) observed individual distances travelled to hibernacula from 13 m to as far as 1936 m in north-central Alberta. These distances were all within 100 m of the water's edge in the least human-impacted study site (Elk Island National Park) whereas the longer distances were recorded in land modified by forestry or agriculture, presumably because of less desirable cover types close to water (Browne and Paszkowski 2010). As another example, stream-breeding salamanders such as dusky salamanders (*Desmognathus* spp.) or torrent salamanders (*Rhyacotriton* spp.) were found to decrease sharply in abundance within 40 m of the water's edge (Vesely and McComb 2002; Perkins and Hunter 2006; Crawford and Semlitsch 2007). Crawford and Semlitsch (2008) confirm these findings in forests older than 40 years but did not observe stream-breeding salamanders beyond 10 m from the water's edge in younger even-

aged stands, presumably because of the diminished leaf litter depth and moisture.

In conclusion, it appears that a 50 m buffer is sufficient to encompass the core habitat of some but not all amphibians. The examples above show that distances travelled by amphibians depend on the local vegetation and microclimate and suggest that maintaining continuous intact native vegetation (including old growth) along watercourses is essential and may reduce the distance individuals must travel to fulfill their terrestrial habitat needs.

3.3 Reptiles

Among reptiles, turtles, crocodilians and some snakes are semi-aquatic. The majority of turtles live in water but nest on land (Pauley et al. 2000). Exceptions are box turtles (*Terrapene* spp.) and gopher tortoises (*Gopherus* spp.), which are terrestrial (Conant 1975), and thus not riparian obligates. In a review of data relating to the terrestrial movement of aquatic turtles, Bodie (2001) calculated average distances from water to nests varying from 2.3 to 50 m depending on the species. Many turtles prefer to lay eggs in sand and will use sandy beaches and bars at the water's edge (Bodie 2001) but can go much further to find adequate nesting sites if necessary. Distances from the water travelled for seasonal migrations and over-wintering vary greatly between individuals of the same species and to include 95% of individuals, Bodie (2001) recommended riparian buffers of 150 m. In a review of aquatic turtle movements, Semlitsch and Bodie (2003) list 42 studies reporting minimum and maximum ranges for various species. Thirty seven of these studies report minimum values less than 50 m, indicating that for most species 50 m is sufficient for at least some of the individuals observed.

By all accounts, crocodilians stay in the water or on the shoreline at all times, with the exception of females which go a little further on land for nesting (Newsom et al. 1987; Webb et al. 2009). Observations of nests have been well within 50 m (0 to 17 m) from the water's edge for all three North American species: American alligator (*Alligator mississippiensis*; Goodwin and Marion 1978) American crocodile (*Crocodylus acutus*; Platt and Thorbjarnarson 2000), and caiman (*Caiman crocodilus*; Allsteadt 1994).

Among snakes, cottonmouths (*Agkistrodon piscivorus*), crayfish snakes (*Regina* spp.), ribbonsnakes (*Thamnophis* spp.), and watersnakes (*Nerodia* spp.) rely on the aquatic environment for feeding. Published information suggests that these species stay in proximity of the water body, particularly queen snakes (*Regina sempervittata*) and eastern ribbonsnakes (*Thamnophis sauritus*) which were mostly observed within 5 m from the water's edge (Smith 1999; Bell et al. 2007). Cottonmouths and watersnakes appear to range further, but seldom beyond 50 m from streams or wetlands (Tiebout and Cary 1987; Whiting et al. 1997; Roe et al. 2003; Roth 2005; Roth and Greene 2006; Rose et al. 2010).

3.4 Mammals

Besides the beaver, the mammalian riparian obligates considered here are the most widely distributed in North America: water shrews (*Sorex* spp.), star-nosed mole (*Condylura cristata*), muskrat (*Ondatra zibethicus*), mink (*Neovison*), otter (*Lontra canadensis*), and moose (*Alces americanus*). Ex-

cept for moose, all these species rely on the aquatic environment for the majority of their food.

The American water shrew (*S. palustris*), which feeds on aquatic invertebrates, has been captured mostly within 5 m of streams by Lehmkuhl et al. (2008) and most captures of the marsh shrew (*S. bendirii*) occurred within 25 m of the water's edge (Anthony et al. 2003 and references therein). These indications that the home range of water shrews does not exceed 50 m from water are supported by observations of the European species (*Neomys fodiens*) whose terrestrial activities are confined mostly to the water's edge (Churchfield 1998 and references therein) with a mean range of 6 to 7 m from water reported by Rychlik (2000).

No data could be found on the width of the riparian zone used by the star-nosed mole, which concentrates its activities along waterways (McShea 1986). Because this mole feeds mostly in water and burrows in stream banks with entrances at or below the water line (Forsyth 2006) it is safe to assume that its habitat requirements are usually well within 50 m of the water's edge.

The muskrat is one of the most aquatic of riparian mammals: its dens are in stream banks if not in the wetland itself and it feeds almost exclusively on water plants and small aquatic or semi-aquatic animals (Allen and Hoffman 1984; Hammerson and Cannings 2010a). Muskrats on land are usually observed within a few metres from the water's edge (Allen and Hoffman 1984; Spackman and Hughes 1995; Anthony et al. 2003). MacArthur (1980) reported that 61% of observations of muskrat activity were within 25 m of a lodge or burrow. Other studies suggest that muskrats do not forage further than 11 m from their home site and that home ranges are generally less than 100 m in diameter (Hammerson and Cannings 2010a). These distances include aquatic habitat, not only terrestrial riparian area, indicating a terrestrial range, if any, that is well within 50 m.

Minks and river otters are mostly observed travelling along stream banks within a few metres of the shore (Spackman and Hughes 1995), consistent with the fact that they both feed mostly on aquatic animals (Anthony et al. 2003). Because of the linearity of their home range, its dimension is often expressed as length of watercourse occupied and thus little information on movement distances perpendicular to the shoreline is available. Limited data indicate that most mink activities took place within 30 m of the water and that their dens were at most 10, 70, or 100 m from the water depending on the study; in coastal habitat, 87% of mink dens were found within 50 m of the water (Allen 1986 and references therein). Similarly, river otters have been reported to stay within 20 m of the shoreline when foraging along marine coastlines (Larsen 1983 in Buskirk and Zielinski 2003). Even though some otter dens are found several hundreds of metres from water (Gorman et al. 2006), these animals often use beaver lodges or burrows for dens (LeBlanc et al. 2007), thus staying close to water.

Finally, the American moose is considered a riparian obligate here because it is often found in shallow-water and palustrine habitats during the warm season. Moose seek wetlands as a refuge from predators, to avoid heat stress and to eat aquatic plants, particularly to satisfy their salt requirements (Snaith and Beazley 2004; Forsyth 2006; Hammerson and Cannings 2010b). Moose also depend on upland forest

for wintering and feeding and, with home ranges of tens to hundreds of square kilometres (Snaith and Beazley 2004; Hammerson and Cannings 2010b), a 50 m riparian area cannot provide all of the moose habitat requirements, but an area of this width is likely to facilitate movement to and from uplands and along watercourses.

3.5 Birds

There is a wide variety of freshwater-dependent birds, most of them relying on wetlands or open water bodies for feeding. Some nest in shallow water (e.g., loons, bitterns) or build floating nests (e.g., grebes) and hardly use the riparian area. Swans, geese, ducks and mergansers that build nests on the ground usually prefer to do so near the water's edge. Notable exceptions are cavity-nesting ducks such as wood duck (*Aix sponsa*), goldeneye and bufflehead (*Bucephala* spp.) or common merganser (*Mergus merganser*) that can nest more than one km away from water if necessary (Terres 1980; Sousa and Farmer 1983). However, these ducks favour nesting sites close to water, and an unharvested riparian area should provide suitable cavity trees and reduce the need to nest far from the water's edge. This is also true for the tree nesters such as herons, egrets, ospreys, Bonaparte's gull (*Chroicocephalus philadelphia*) or solitary sandpiper (*Tringa solitaria*).

Among bank-dwellers the belted kingfisher (*Megaceryle alcyon*), which needs perches overhanging water to fish, can also be considered a riparian obligate. On the other hand, bank swallows (*Riparia riparia*), which favour riparian habitat as the scientific name testifies, are not riparian obligates because they can live away from water if they find suitable nesting sites (e.g., the walls of human-made quarries or embankments rather than river banks; Terres 1980). Freshwater-dependent passerine birds usually nest very close to the shore or in wetlands such as marsh wren (*Cistothorus palustris*), swamp sparrow (*Melospiza georgiana*), rusty blackbird (*Euphagus carolinus*), waterthrushes (*Seiurus* spp.), or American dipper (*Cinclus mexicanus*), to name a few (Terres 1980).

The majority of bird studies in riparian areas have been concerned with mitigating the effects of timber harvest on bird communities (see review by Marczak et al. 2010). These papers report average population densities in different riparian buffer widths, usually soon after clear-cutting, which may not be an accurate representation of the natural terrestrial range of birds from the water's edge. Minimum widths proposed to retain preharvest bird assemblages vary from 45 to 70 m (Darveau et al. 1995; Hagar 1999; Pearson and Manuwal 2001) to more than 100 m (Shirley and Smith 2005) or even 200 m (Hannon et al. 2002). In the case of unharvested natural forests, Spackman and Hughes (1995) found that 150 m included 90% of the bird species recorded within 200 m of streams. All these studies have been concerned with retaining forest interior as well as other species and are probably an over-estimate of riparian obligates' terrestrial ranges. In fact, when ignoring some forest interior species (Hagar 1999) or focusing on "riparian specialists" (Shirley and Smith 2005), buffer widths in the range of 20 to 40 m were found sufficient to retain preharvest bird abundances. Whitaker and Montevecchi (1999) reported that spotted sandpiper (*Actitis macularius*), northern waterthrush (*Seiurus noveboracensis*), belted kingfisher and rusty blackbird were

rarely observed away from water but were travelling long distances along the shoreline. These observations suggest that an undisturbed 50 m riparian area may provide sufficient habitat for riparian obligate birds.

4. Discussion and conclusions

As an ecosystem engineer, the North American beaver has a profound influence on the shape and function of riparian ecosystems. Therefore, riparian conservation measures for North American watercourses should include the terrestrial habitat needs of beavers. Published data on beaver foraging on land shows that 95% of the woody vegetation harvested by beavers is found within 50 m of the water's edge. We propose that a riparian buffer of that width, measured from the high water mark of the watercourse, should be left intact (e.g., native vegetation, no timber harvest) to maintain the beavers' terrestrial habitat.

The fact that beaver activities may change the location of the water–land boundary adds complexity to the delineation of the riparian buffer. However, this boundary is not necessarily modified by beaver colonization. First, in low relief areas with abundant lakes and wetlands, beavers find sufficient still waters and do not build dams or only small ones (Müller-Schwarze and Sun 2003; P. Stoffyn-Egli, personal observations, 2005, 2008). Second, the beaver dam does not necessarily bring the water level above that of the high water mark: beaver dams are semi-permeable structures only partially obstructing water flow, and overflowing during high water discharge periods (Müller-Schwarze and Sun 2003). Third, beavers reoccupy past sites in which case the water–land boundary may not change much from the time of previous occupation, particularly when the old dam has not failed in the interval between occupations.

In regions where beaver populations are still recovering from low numbers or extirpation, an increasing number of beaver impoundments are to be expected and are beneficial as far as restoring wetland habitat and ecosystem functions (Hood and Bayley 2008a). The resulting need to modify buffer location owing to beaver activities is not different from relocations in response to riverbank erosion, river meander migration or infilling and plant growth in abandoned channels. Watercourses are dynamic, evolving systems where management must adapt to inherent changes, regardless of whether they are caused by beavers or other natural processes. Ease of adaptation depends on the land use. In the case of forestry, harvesting takes place at intervals of many decades. At each harvest, the buffer can be easily adjusted, by leaving a “new” buffer strip along a beaver pond that inundated the previous strip. On the other hand, if residences have been built along the buffer, moving this buffer inland to accommodate a beaver pond may not be possible. Terrain slope can be used to predict the likelihood and extent of riparian area flooding by beavers or other natural events, so as to avoid permanent development in flood-prone areas.

The fact that the beaver can modify the vegetation in the 50 m riparian width to the point of exhausting the resources it needs is another aspect of the inherent time variability of riparian systems and is not in contradiction with a buffer width based on the beaver's terrestrial habitat needs. It is well documented that beavers recolonize a previously occu-

ried area when woody vegetation has at least partially recovered (Fryxell 2001; Müller-Schwarze and Sun 2003; Martell et al. 2006). Through these cycles of colonization, abandonment, and recolonization the beaver introduces variability in the landscape (Naiman et al. 1988; Wright et al. 2004; Martell et al. 2006). Beaver-induced disturbances create habitat patches of value to other riparian species even when beavers have temporarily left the area.

A review of data on the terrestrial habitat needs of strictly riparian obligate species of invertebrates, amphibians, reptiles, mammals, and birds, indicates that a 50 m riparian area bordering streams, rivers, lakes, and wetlands will fulfil the habitat needs of many of these species (Fig. 2). Therefore, the conservation value of a 50 m riparian buffer goes far beyond the protection of beaver populations and is applicable to the entirety of the watercourse, not only the reaches adequate for beaver colonization. As such, the beaver may be considered an “umbrella species” for conservation purposes (Beazley and Cardinal 2004; Roberge and Angelstam 2004). Moreover, 50 m is approximately the width performing most of the riparian functions ensuring the ecological health of the watercourse, estimated to be on the order of one site-potential tree height (FEMAT 1993; Naiman et al. 2000a). This width encompasses most of the microclimatic gradients characteristic of the riparian ecotone (Brososke et al. 1997; Olson et al. 2007 and references therein) and the related vegetation changes (Spackman and Hughes 1995; Harper and MacDonald 2001). In other words, a 50 m distance from the water's edge corresponds approximately to the upland limit of the riparian ecotone.

The findings of this study provide the foundation for proposing that 50 m is the minimum width for supporting water-dependent species that need terrestrial habitat immediately adjacent to fresh water for their survival, with the exception of moose and wide-ranging amphibians (Fig. 2). In the case of some aquatic insects and turtles, 50 m is adequate for a significant proportion of individuals, but not all. However, these conclusions are based on terrestrial home range information that is scant, incomplete or inferred from other evidence for a number of species. More studies on the terrestrial habitat use of riparian obligates in terms of distance and distribution from the water's edge are needed to further validate these conclusions. The 50 m estimate is the minimum distance for the survival of the species considered, but not necessarily for maintaining the number of individuals that an undisturbed riparian–upland continuum might support. For example, toads, turtles, minks, otters and birds sometimes hibernate, nest or den further than 50 m from water and a 50 m buffer may be insufficient for these individuals. Similarly, some individual snakes, turtles, and alligators travel to isolated wetlands farther than 50 m from watercourses (Roe et al. 2003; Roe and Georges 2007; Subalusky et al. 2009) and may not survive if not able to do so. On the other hand, an undisturbed 50 m buffer, particularly if continuous along the watercourse, may provide more hibernating, nesting, and denning opportunities near water than current narrower buffers allowing some timber harvest, and thus eliminate the need to travel beyond 50 m for these individuals. A continuous buffer may also in part compensate for the loss of overland dispersal pathways, and concurrent pop-

ulation isolation, caused by anthropogenic landscape changes and fragmentation.

It should be noted that the ecological integrity of even an undisturbed 50 m buffer may be jeopardized by adjacent high-impact human activities (forestry, agriculture, industry, roads, residences), which can cause detrimental edge effects such as microclimate changes or wind-throws (Brosfokske et al. 1997; Reid and Hilton 1998; Mascarúa López et al. 2006; Olson et al. 2007). In such cases, a transition zone between the 50 m riparian reserve and full-fledged land use should be implemented to mitigate edge effects (Reid and Hilton 1998; Palik et al. 2000; Semlitsch and Bodie 2003). The width of this transition zone depends on the type of human activity and the negative effect to be mitigated. In the case of forestry for example, partial timber harvest may require only a transition zone where fewer trees are harvested (Palik et al. 2000), whereas for clear-cutting, a transition zone three to four tree-heights wide may be necessary to prevent increased wind-throw in the buffer zone (Reid and Hilton 1998). When edge effects on microclimate and vegetation structure are considered, it appears that a forested transition zone of at least 40 m is necessary to protect the riparian buffer from these effects. (Brosfokske et al. 1997; Hannon et al. 2002; Mascarúa López et al. 2006). In the case of agriculture, vegetated strips (grasses, forbs, shrubs, and (or) trees) of various widths (a few meters to a few tens of meters) have been proposed and used to mitigate fertilizer use and erosion impacts on the riparian area (NRC 2002; Naiman et al. 2005). Although there is no consensus on the composition and width of such transition zones, the guiding principle is that they establish a gradient of impact of land uses, the impact decreasing toward the riparian buffer edge. These zones also have habitat and connectivity value for many species besides riparian obligates.

A buffer width of 50 m is insufficient, however, for moose and wide-ranging species of amphibians (Fig. 2) that need upland habitat as well as riparian and aquatic habitat to complete their life history, and the intervening land to move from one to the other. In contrast with flying riparian obligates, wide-ranging amphibians cannot bypass the riparian area during their migration between aquatic and upland ecosystems, and need adequate temperature and humidity on the way (Olson et al. 2007). This conclusion is in agreement with that of Marczak et al. (2010) who found that current buffer regulations do not appear sufficient to maintain amphibians to the levels of undisturbed sites. As an alternative to much wider buffers, often impractical to implement, we propose a *continuous* 50 m riparian buffer *connected* as much as possible to blocks of upland reserves necessary for the conservation of upland species, particularly forest interior species (Whitaker and Montevecchi 1999; Potvin and Bertrand 2004). Such habitat connectivity at the watershed scale will not only conserve species particularly threatened by habitat fragmentation such as moose and wide-ranging amphibians (Snaith and Beazley 2004; Cushman 2006), but also provide travel and dispersal corridors for upland species as well as riparian species (Whitaker and Montevecchi 1999; NRC 2002; Anthony et al. 2003). Moreover, upland reserves judiciously placed near headwater streams can act as connectivity corridors between watersheds.

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