Problematizing Beaver Habitat Identification Models for Reintroduction Application in the Western United States

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ABSTRACT

Due to the beaver's former role as a ubiquitous keystone species, there are increasing efforts in the American West to assist beaver in recolonization. Many interested in reintroduction are using two methods to identify optimal habitat: habitat suitability indexes/models (HSI), and historic occupation. This study details some of the problems inherent in HSIs applied to beaver habitat. The paper then interrogates historical occupation as a relocation tool, and finds that while more logically consistent, this method of habitat identification is also problematic. Historic range does not integrate past or present causes of extirpation and absence. I argue that, specifically in the case of beaver relocation but potentially for other species as well, causes of mortality are as important as are environmental amenities in identifying appropriate habitat.

Key words: *habitat suitability index, beaver, Oregon*

Introduction

Though the public is generally unaware of it, many land-use managers in Oregon and in other western states are in the early stages of a potentially revolutionary movement (see Buckley et al. 2011, Wild 2011, Carpendo 2011). These groups are preparing to engage in a working partnership with a nonhuman species in an effort that could substantially change stream hydrologies across the entire state.

Beaver were once a keystone species across most of North America, ranging from coast to coast and from the Sonora Desert to the Arctic steppes, in numbers estimated to have been between sixty million and four hundred million. Through their dams, beaver provide numerous ecosystem services. They create less-flashy hydrologies by slowing high stream-flow events and, through aquifer recharge and cooled secondary upwelling, extend stream flows into dry seasons, often at the lower temperatures preferred by many fish species.

Beaver ponds specifically provide several functions. Hydrologically, they reconnect channels with riparian areas on valley floors (Westbrook et al. 2006). Well-watered riparian zones often host willow and aspen that shade the stream, stabilize banks, and provide habitat. The ponds themselves provide vital habitat. Ponds work to protect young fishes such as endangered coho salmon, from being flushed to sea too soon (Pollack and others 2007, 2004, 2003). Fish biologists in Oregon are particularly interested in enrolling beaver for this benefit. Indeed, my analysis of the Oregon Conservation Strategy (ODFW 2006) finds that beaver ponds would benefit eleven of the sixty-two birds, two of the five reptiles, seventeen of the eighteen amphibians, and twenty of the thirty fish species listed for special treatment. Ponds also accumulate and sequester significant amounts of sediment (Pollack et al. 2007), to the extent that they often slowly change to wet marshes, themselves vital habitat and significant carbon sinks (Naiman et al. 1986; Naiman, Johnston, and Kelley 1988; Gurnell 1998; and Rosell et al. 2005).

Finally, winter climate is changing across many Western states. Winters are becoming wetter and warmer. As a result, snow packs that formerly melted slowly and fed summer stream flows are diminishing (Chang and Jones 2010). Beaver ponds, which store about six acre-feet and are built about one hundred meters apart in appropriate habitat, could bank significant amounts of water, thus evening seasonal stream flows (Müller-Schwarze and Sun 2003, Baker and Hill 2003).

Given the dawning awareness of the potential benefit of increasing beaver presence in Western streams, several Oregon government and public organizations are becoming interested in assisting beaver re-colonization (e.g., The Beaver Workgroup, the Beaver Advocacy Council, the Willowa-Whitman National Forest). The term recolonization is used here to reflect historical ecologies. While the current population of beaver in Oregon is no more than a few tens of thousands, Oregon was home to at least one million beaver prior to intense commercial trapping between 1780 and 1850. That coho salmon (Pollock et al. 2004) and other species do so well in habitat created by beaver suggests a significant degree of co-adaptation. Any expansion of beaver populations is a gesture toward what was normal prior to Euro-American colonization.

One major problem faced by people aiming to assist beaver recolonization is determining where to release beaver. At this point, in Oregon and elsewhere across North America, there are two primary strategies used in identifying potential and optimal habitat: Habitat Suitability Indices or Models (HSIs) and historic presence. However, both of these are problematic, more for what they omit than for what they include.

Given the extent of Euro-American landscape alteration, and anticipated changes in boundary conditions and inter-species relations due to climate change, understanding where to relocate populations has become an ever-more-current issue. Though HSIs are not new, designers have recently been able to couple habitat requirements with geographic information science to model and identify potential and optimal habitat on the scale of watersheds and even entire Western states. This new technology stands in contrast to the older technique of ascertaining a pre-disturbance population range and then seeking to reestablish that population.

Habitat Suitability Indices

By the mid-1990s HSIs had become one of the most important and widely used tools in ecological assessment, conservation planning, and wildlife management (Brooks 1997, Grey et al. 1996). Burgman et al. (2001) trace the use of HSIs in the United States to development by the United States Fish and Wildlife Service (USFWS) beginning in 1980. The logic underlying HSIs is straightforward: identify a species *preferenda*, the environmental attributes necessary or favorable for a population's success; and then identify where on the landscape that suite of requirements and preferences are available. Using GIScience, various geo-referenced data sets can be overlain to map areas of ranked preference or potential viability.

However, HSIs have been critiqued nearly from their inception. In the USFWS's original publication and in the subsequent "Standards for the development of habitat suitability index models" published the next year, the Service was already critical of suitability indices. The study notes that errors arise from simplifications concerning "temporal variability, spatial variability, and systematic and random measurement errors" (Burgman et al. 2001, 71). Those errors are often retained because once models are developed, there is typically little empirical study between the variables identified by the models and the success of populations in study areas (Brooks 1997). In the successive "Standards" publication (1981), the USFWS was further critical of a lack of empirical study in support of variables chosen for inclusion is HSIs. Rather, expert opinion was the most common source for variables.

The report notes that those opinions are often inconsistent (Burgman et al. 2001, Crance 1987).

In the years that followed, the inconsistency among HSIs has caused several authors to question their usefulness (Cole and Smith 1983; Van Horne and Wiens 1991). Roloff and Kernohan (1999) evaluated the quality of fifty-eight HSI models and found all "deficient," most commonly because they failed to integrate the variability of habitat requirements, sampled insufficient ranges of habitat variables, and used inappropriate temporal scales in sampling and spatial scales in applying their models.

Several authors have suggested measures to improve the reliability of HSIs. Many identify a disconnect between modeling and empirical application as problematic. Brooks (1997) recommends a more-recursive but also more-expensive and -time-extensive model. The author outlines four phases of model development led by "development" in which habitat variables are identified through observation, expert opinion, and/or literature reviews. Brooks adds that models should then be calibrated against actual test sites until excellent and poor conditions are accurately predicted. The model should then be verified through the accuracy of its suitability prediction in several additional sites. Finally, models should be validated through the actual success of populations in recommended habitats. While this protocol seems sound, few reintroduction projects have the resources to fulfill its requirements.

More recently Cianfrani et al. (2010) used ongoing recolonization by Eurasian otter (*Lutra lutra*) in southern Italy to test modeling practices. Through statistical analysis beyond the focus of this paper, the group found that variable selection in HSI development is often directly related to increased randomness in model predictions. More importantly, the authors found that the inclusion of data about population preferences drawn from absence "may prevent the models from correctly identifying areas suitable for a species spread" (421), which is to say there may be suitable habitat, but for non-local reasons the species is absent. This finding was supported by statistical analysis of field observations. In the application of models, those based only on preferences for which presence stands as a proxy were far more reliable than those that inferred that absence indicated the inappropriateness of habitat. This point is especially important with regard to beavers, as many HSIs do use absence as proxy for environmental inappropriateness and presence as validation for habitat variable preference. Using absence in this way is problematic because to do so builds upon the assumption that the subject animal is absent due to preference, rather than to past and ongoing predation by non-humans and humans. In other words, they ignore anthropogenic causes of death or extirpation.

Historical presence

In addition to HSIs, some projects use simple historical presence to indicate viable release sites. Of the two such projects included here, both rely upon validation of historical presence through contemporary field checking to ascertain current habitat viability. Conditions such as availability of forage and construction material are checked, and often, if the physical conditions are not favorable, revegetation efforts, such as willow planting, are made prior to release. In both studies, participants rely primarily upon living memory. Field work by the author suggests that in some cases in which extirpation predates living memory, historical presence may still be ascertained by walking incised streams and examining banks for evidence of dams that were buried by the sediment trapping by successive dams. These were especially evident in surveys conducted by the author in the Madison and Gravelly Ranges in western Montana. In California, where state law requires proof of former inhabitance before reintroduction is allowed, anthropologists have examined local native languages to determine whether they had a word for beaver. While perhaps indicative of historical presence, such information is not useful in selecting precise release sites, and boundary and biotic conditions may have since so changed as to make repopulation difficult.

As suggested earlier, both of these strategies for identifying release sites for recolonization are problematic. Among HSIs, the degree of disagreement between models is notable, and the use of absence as a proxy for preference is untenable for populations under predation pressure. The historical presence paradigm similarly overlooks the cause of extirpation and so may only recreate the previous local extinction by placing populations in sites where they will be killed.

Analysis: Beaver HSI Inconsistency

Here I review the results of five beaver HSIs, one study on pool morphology that inadvertently serves as a review of habitat suitability, and two relocation programs employing living memory of beaver presence. It is important to note that the HSI studies represent a wide range in terms of statistical sophistication. A comparison of those techniques is beyond the scope and interest of the current study. Rather, the focus here is on the significant and problematic variability in the results of these studies.

Table 1. Overview of HSIs.

Author	Place	Spatial correlation		Natural history		Presence/ Absence
Howard and Larson (1985)	Massachusetts	Regression		Extended observation		
Retzer et al. (1956)	Colorado			Extended observation		
Beiber and Barrett (1987)	CA/Nevada	Stepwise regression				Yes
McComb et al. (1990)	E. Oregon	Various tests/decision tree				Yes
Suzuki and McComb (1998)	W. Oregon	Discriminant function				Yes
Barnes and Mallik (1997)	Ontario	Various tests				Modified*
Jones (2008)	W. Oregon	Discriminant analysis				Modified*
Stack (1988)	W. Oregon					Modified*

I briefly review some of the details of these studies before discussing inter-model variability. The first of the two historical presence models was authored by Howard and Larson (1985). The team used twenty-eight years of observation to test two regression models' ability to identify observed habitat amenities. In that case, beaver hunting and trapping had been illegal in the study area for the previous forty-nine years. They found that watershed size, stream width, and gradient best explained beaver presence, while vegetation variables had little predictive ability. Retzer et al. (1956) focused particularly upon the effect of stream gradient on beaver presence. Among models relying upon presence/absence observations, Beiber and Barrett (1987) used stepwise logical regression to identify the optimal level and the strength of relationship between environmental attributes and beaver presence in a portion of the Truckee River drainage (approximately 600 mi^2). They concluded that "increasing stream width and depth and decreasing gradient had the strongest positive effects on habitat use; food availability variables added little explanatory power" (794). McComb et al. (1990) used presence and absence as a proxy for preference and found that dams were more likely in wider and shallower streams; that shallow bank slopes are favored; and that greater tree canopy cover, particularly with thinleaf alder, was also an important predictor. Suzuki and McComb (1998), using a presence/absence paradigm, found that beaver built dams only on first- to third-order streams with wide valley floors, low stream gradients, high grass/sedge cover, and low red alder and shrub cover. Barnes and Mallik (1997) were particularly interested in the role of vegetation. They tested McComb's model and found its predictive power was weak. They also found that in their study area in Ontario specifically, "beaver relied on both physical (upstream watershed area and stream cross-sectional area) and vegetation (shoreline concentrations of woody plants with diameters 1.5–4.4 cm) factors in choosing dam sites" (1371). Some of this variation is undoubtedly a function of the specific landscapes studied.

On the Umpqua River in southwestern Oregon, Jackson used extensive fish habitat surveys that included descriptions of beaver presence to develop an HSI. He identified 300 reaches with beaver and compared the environment above and below dam sites, testing for correlation with twenty variables. He found that four were significantly predictive: stream gradient and width, forest canopy closure, and availability of small hardwood or mixed trees.

Jones makes a very honest statement in his introduction: "We chose to focus on the Nehalem basin…[because] we were unable to identify significant associations of beaver activity with channel or riparian features when using the full set of sites from all coastal streams" (1). Thus, any predictive results would be limited to that watershed and explicitly not apply to other streams. The resultant model found that, in that stream, beaver preferred streams with smaller watersheds, low stream gradient, wide valley floors, "and abundant hardwood trees in the riparian zone" (3).

The Stack (1988) study is not explicitly focused on beaver. Rather, it examines stream pool morphology controls in Oregon's central Coast Range. However, in his data, Stack records physical conditions for nineteen streams: three in which beaver are associated with nearly all pools, two with some beaver presence, and fourteen with no beaver presence. While the data on beaver habitat suitability is unintentional, it is also revealing in that, except for one indicator, there is no clear correlation between any environmental amenity and beaver abundance, presence, and absence.

HSIs Compared

Stream gradient is the most commonly included habitat characteristic among HSIs for beaver. As Table 2 indicates, there is disagreement regarding optimal and allowable gradient. Barnes and Mallik find that optimal gradient is 1.1%, while Howard and Larson identify 2.65% as optimal and Retzer et al. identify any gradient below 6% as good and up to 13% tenable. Jackson found that nearly all dams were on reaches with gradients of less than 10%, but most dams were on reaches with less than 5% gradient. In contrast McComb et al. find absence in streams averaging 6.4%. Similarly, Suzuki and McComb find gradients averaging 3.9% as too steep. Several of the models identify increasing gradient as a limiting factor, yet Barnes and Mallik find low gradient to be prohibitive. Finally, Stack finds no linear correlation: low presence is associated with shallow gradient, but absence is associated with higher gradients—and the range for presence exceeds the mean for low presence and for absence.

Table 2. Stream gradient—percent.

Beaver presence	Active	(Range)	Low	Absent
Stack	2.8	0.5–5.3	1	3.1
Howard and Larson	2.7	0.5–4.7		
Beiber and Barrett	1.2	0–2		>2
McComb et al.	2.2			6.4
Suzuki and McComb	2.2			3.9
Retzer et al.	0–6		7–14	>14

Stream width is the second-most-frequently included parameter, and again there is disagreement, with optimal widths varying from 1.0 to 8.1 meters (see Table 3). Barnes and Mallik found that relatively narrow streams were most often occupied, whereas Beiber and Barrett found that larger streams are preferred. Two models (McComb et al. and Suzuki and McComb) find the difference between presence and absence is 0.7 meters or less. Stack found that the difference between present and absent is small, and again the ranges of each category overlap.

Table 3. Stream width—meters.

Presence	Active	(Range)	Low	Absent
Stack	7.7	5.4–10.1	9.3	6.0
Howard and Larson	2.9	1.5– 4.2		
Beiber and Barrett	8.1		5.9	4.9
McComb et al.	3.9			3.3
Suzuki and McComb	4.1			4.8

Stream depth was included in four HSIs and shows similar variability. Average depths for beaver presence range from 0.05 to 2.4 meters. Average depths for beaver absence varied from 0.13 to 1.9. Suzuki and McComb found no difference in average depth for presence and absence; and while two of the HSIs correlate absence with decreasing depth, McComb et al. find the opposite. Interestingly, Stack shows a clear linear correlation. This is potentially the result of that author's focus on pool morphology and unique method (Stack 1988, 30).

Table 4. Bank slope—percent.

Beiber and Barrett	Active	1.2
	Signs	1.4
	Absent	1.8
Barnes	Active	6.4
	Signs	5.6
	Absent	4.6
McComb	Present	11.1
	Absent	21.1
Suzuki and McComb	Present	31.8
	Absent	45.6

Bank slope was also included in four HSIs. Mean bank slopes correlated with beaver presence varied from 1.22 to 31.8% (see Table 5). Absent was correlated with bank slopes varying from 1.8 to 45.6%. Though each study consistently correlated steeper slopes with increasing absence, no model identifies preferable slope that overlaps another model; i.e., the ranges are mutually exclusive. Bank slope may be related to valley floor width in many stream reaches. The two HSIs that included this parameter both found that wider valley floors are associated with beaver presence. McComb et al. (1990) found beaver present where valleys had a mean width of 13.5 meters, but absent where floors were 12 meters in width. Suzuki and McComb's (1998) results conflict, finding active colonies where mean valley width was 32.8 meters, and streams without beaver had a mean valley width of 22.7 meters. This result is consistent with beavers' need for an accessible riparian zone.

Several studies included watershed size, but again as the table suggests, there is very little consistency in absolute terms, though the HSIs do agree that beaver presence is correlated with smaller watersheds. This may be a function of stream power. However, Pollack has recently observed that dam permanence is more a function of beaver building dams to bank-full heights, which allows flood waters to flow along paths outside the channel, thus putting less pressure on the dams themselves (2012).

Table 5. Drainage area—in ha.

Author		**Mean**	**Range**
Stack	Abundant	6.7	
	Low	13.8	
	Absent	6.2	
Howard and Larson	Mean	133	±169
Barnes	Active	521.1	
	Signs	948.8	
	Absent	6247.3	

Many authors include vegetative cover in their studies; however, as Table 6 indicates, the methods are inconsistent and results highly variable. Howard and Larson found that preferable canopy cover varied between 0 and 45%, while Jackson found canopy closure of 25 to 50% optimal, and Allen estimated that a 40 to 60% canopy cover was optimal. Beiber and Barrett found little statistical correlation between vegetation and beaver presence. Focusing on stem diameter, Jackson found that hardwoods whose trunks where between 15 and 30 cm (6 to 12 inches) were important; however, Barnes found that beaver most frequently used stems ranging from 1.5 to 4.4 cm, though woody species utilization was nonspecific. Wild (2011) explicitly excluded vegetation from her GIS-based model because vegetation cover data was of insufficient resolution, and because she felt that beaver could persist in all but barren landscapes (2012).

Table 6. Vegetative cover—various measures.

Author	Mean	Range
Howard and Larson		
Cover within 100m	17.5	± 27.5
Jackson		
Canopy closure		25–50%
Stem diameter—chest		15–30 cm
Beiber and Barrett	*Little correlation*	
Barnes		
Vegetative diameter		1.5–4.4 cm

Historical Knowledge

Two relocation projects on the Umpqua River in Oregon's southwestern Cascade Range allow a partial comparison of the efficacy of HSIs and historical knowledge as habitat identification strategies. One project, conducted by the Beaver Advocacy Council, a nonprofit group of private citizens, relied upon living memory and observation to select their release sites. The BAC released twelve radio-tagged adults and three juveniles at sites on five streams. The group followed relocation protocols developed by Tippie (2010), taking care to catch entire family groups when possible and release them together (Petrowsi and Houston 2011). Of those relocations, six adults remained within 100 meters of the release site; and of those six, five survived through the end of the study. The remaining six adults were lost either to predation or to a loss of their radio transmitter.

The second project conducted by the Oregon Department of Fish and Wildlife (ODFW) used an HSI still under development. In that study, ODFW officers released thirty-four beaver with radio beacons attached to their tails at thirteen sites on three tributaries of the upper Umpqua. Very few beaver remained at their release site, indicating initial problems with the HSI. Of the released beaver, seventeen are known to have died: nine by predation, four by vehicle collision, and four through other accidents. Of the remaining, ten transmitters have either fallen off (probably due to necrosis—attachment techniques have since improved) or are no longer being tracked. Only seven adults are still being tracked; thus, mortality is between fifty and seventy-nine percent (Jackson 2011). In both cases, active mortality was a significant factor in relocation success and failure.

This comparative analysis highlights two specific issues with applying HSIs to beaver recolonization. The models display problematic variance and contradiction in the preferenda observed. This is explained in part by beaver's ability to generalize environmentally (see Naiman et al. 1986; Naiman, Johnston, and Kelley 1988; Pollack et al. 1995; Baker and Hill 2003; Pollock et al. 2003; and Rosell et al. 2005). As a species, they are very adaptive, able to construct dams from many hard and softwood species, but also observed to have used such unlikely vegetation as creosote branches and blackberry canes. As a keystone species, once dam/pond complexes are established, beaver begin to "cultivate" plants that are useful—plants that have co-adapted—to beaver. In short, beaver are able to inhabit a wide range of environmental gradients.

The second issue relates directly to issues regarding presence and absence. Performing statistical analysis in order to correlate *preferenda* through population success assumes that absence is the result of beaver preference. That assumption is highly problematic. Though wildlife managers often suggest that, at least in Oregon, beaver currently occupy all appropriate habitat, there are many forces working against beaver recolonization. Though an in-depth discussion is beyond the scope of this article—I address this in a subsequent piece on mapping beaver absence—a brief address is illustrative. Euro-Americans have a long history of killing beaver in North America. There are several motivations behind that process. Though difficult to study, there is a subculture that valorizes shooting beaver recreationally. Anecdotal evidence suggests the toll from this practice is significant. Trapping also suppresses populations, though to a lesser degree, it would seem. In Oregon, between 1993 and 2010, an average of 3,459 beaver were killed annually by an average of 196 trappers (data provided by ODFW). However, trapping regulation applies in only about one-quarter of Oregon's territory. Across the remaining three-quarters of Oregon (private and leased-public lands), Oregon Statute ORS 610.002 classifies beaver as predators and, as such, allows unregulated "removal." A recent statewide poll of landowners found that twenty-four percent did not want beaver on their own or on their neighbors' property and that many had either killed beaver or had them killed (Needham and Morzillo 2011). Landowners and managers are motivated to kill beaver because they can cause damage to roads that cross streams and to trees, and they can flood pastures, typically within forty to seventy meters of streams.

Though inadvertent, Stack's study provides empirical evidence that supports this argument (1988). Stack correlated pool presence with logging recency. Among the eighteen streams included, beaver were so abundant in three of them as to account for nearly all identified pools. As Table 7 indicates, of those three streams, two were unlogged over the previous decade; and of those, one had not been logged over the past fifty years and the other had lost only 0.6% of its forest. In the third of the beaver streams, 5.4% had been logged in the past ten years, and 31.5% was logged eleven to twenty-five years prior to the study. However the effect of that logging might have been buffered by the size of the watershed—at 14.8 square kilometers, this was the second-largest watershed in the study. In the beaver-absent streams, the mean percentage of area logged in the previous ten years was nearly four times higher. Of those fourteen streams, nine had been heavily logged (8.5–65.6% of area) in the past twenty-five years. The remaining five beaver-absent streams had not been significantly logged over the past fifty years. However, of those five streams, one has a high stream power index and its bed is over 50% bedrock—nearly impossible conditions for beaver dam longevity. The remaining four streams are among the smallest in the study, averaging 7.2 cm in depth (range 5.8–9.1 cm) compared to an average of 29 cm for beaver streams, and so may be too small to allow easy recolonization.

Table 7. Drainage harvested—percent.

Past 10 years	**Mean**	**Range**
Abundant	1.8	0–5.4
Low	1.6	0–3.1
Absent	6.3	0–34.4
11–25 years prior		**Range**
Abundant	10.7	0–31.5
Low	12.9	12.5–13.5
Absent	11.9	0–31.2

Beaver predation among Oregon's timber lands was further corroborated by the spokesperson for JWTR Timber, which owns 950 square miles of forestland, approximately sixteen percent of Klamath County, and much of the county's forested area. At a Beaver Management Project Meeting held in Chiloquin by the Klamath Watershed Partnership in July, 2011, the spokesman stated that they have had only two beaver on their land (time period was unspecified), that they have fewer beaver than in surrounding National Forest lands, and that he did not know why there were not more. He also stated that people were removing beaver without explicit permission of JWTR, confirming that the firm was aware of the trapping and because they have made no move to stop it, tacitly approve of the removals. Clearly, unregulated human predation upon beaver in Oregon is significant, yet none of the HSIs identified here included this vital dis-amenity. Jones, however, does note that fish habitat surveys need to include information on both the biology and *harvest* of beavers (my emphasis 2008, 4).

Humans are not the only species that kill beaver. Bear, wolves, coyotes, and cougar/mountain lion are all natural predators of beaver, and in the Western U.S. the populations of each have been rebounding over the past few decades. These predators are particularly relevant to relocation efforts because beaver are most vulnerable to predation at times and in places when they do not have pooled water in which they can cover reasonably safely. In small streams this requires a natural pool, or a pool created by a beaver dam. Thus, the presence of human and nonhuman predators may have as much or more to do with beaver absence than any of the environmental attributes identified in HSIs.

Conclusion

Given the increasing ability of GIScience, statistical analysis of beaver habitat preferences seems attractive. Carpendo (2011) uses an HSI in combination with GIScience to identify low, marginal, and good beaver habitat for the approximately 3,200-square-mile Big Hole Watershed in Montana. Wild (2011) uses an HSI and GIScience to map biodiversity hotspots vulnerable to anticipated environmental shifts related to climate change where beaver could be reintroduced to effectively increase the resilience of those communities—for the entire state of New Mexico. The extent of coverage through automation of the selection of habitat is impressive.

This study questions the utility of that technique. Clearly there is considerable disagreement, and even contradiction, regarding habitat preferences. Historical presence and natural history studies can provide a useful adjunct in relocation site selection.

As importantly, because the HSIs used for beaver relocation fail to include causes (human and other) of mortality and extirpation, their results are likely to continue to disappoint.

Other HSIs have included minimization of human contact as a habitat quality. I have begun to develop a GIScience-based habitat suitability model that will include several probabilistic mortality surfaces that go beyond human presence to include qualities such as land tenure and management regimes.

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