HABITAT MANIPULATION AS A VIABLE CONSERVATION STRATEGY

Kevin T. Shoemaker, Glenn Johnson, and Kent A. Prior

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INTRODUCTION

Fifteen years ago, in a volume otherwise focused on snake ecology and behavior, Seigel and Collins (1993) saw fit to include a chapter on snake conservation (Dodd 1993). In his chapter, Dodd bemoaned the unquestioned acceptance of habitat manipulation practices such as conservation corridors and road-crossing structures: "there is an urgent need to evaluate what are rapidly becoming accepted ... management techniques." In an effort to provide managers, planners, and field practitioners with a framework for making informed habitat management decisions, we 1) review the use of habitat manipulation in snake conservation, 2) evaluate the extent to which habitat manipulation has been successful in achieving conservation goals, and 3) make recommendations regarding the use of habitat manipulation in future snake conservation endeavors. In so doing, we hope to highlight knowledge gaps and profitable applied research opportunities, the investigation of which should lead to improved conservation practice.

Habitat manipulation is often uncritically embraced as a practical management "fix." Its particular appeal may lie in the hope that habitat functions (e.g., the ability to support viable snake populations) might simply be restored through direct manipulation of habitat remnants: no net loss, everybody wins – ecological costs and benefits apparently optimized without harmful social or economic consequences. The recent conversion of Wisconsin farmland to support a population of the state-threatened Butler's Gartersnake (Thamnophis butleri), serves as a case in point (Wisconsin Department of Natural Resources 2007). However, the question remains: is habitat manipulation effective in improving the conservation status of snakes, or would scarce financial resources be better spent protecting existing habitat? Habitat manipulation projects may not function as managers intend; artificial or novel habitat elements may introduce threats that snakes are unequipped to detect, functioning as evolutionary traps (Kolbe and Janzen 2002; Schlaepfer et al. 2002). Even habitat manipulation projects that are ecologically benign can potentially drain resources from more effective conservation strategies.

We considered three broad categories of habitat manipulation: (1) manipulation of targeted habitat features (e.g., basking sites, hibernacula), (2) manipulation of the seral stage of natural communities (e.g., prescribed fire), and (3) manipulation of ecological landscapes (e.g., linear corridors). Published studies were identified by searching the ISI Web of Knowledge database and the online meta-search engine, Google Scholar for all references using the words "snake" or "reptile" along with terms such as "habitat management", "artificial hibernacula", or "prescribed fire" (the complete list of search terms is available upon request) and by searching the bibliographies of relevant publications. We also solicited the assistance of colleagues by: 1) posting requests on relevant electronic mailing lists, 2) contacting state-employed herpetologists and non-game wildlife specialists (USA), and 3) contacting university scientists currently conducting snake conservation research. Published studies that quantitatively evaluated the response of snakes to habitat manipulation were evaluated for overall strength of evidence (rigor of experimental design and strength of response), and key results from each study were compiled in a table. Due to variation in methodology and types of data reported, meta-analysis of rates of management success or factors influencing management success (Gates 2002) was deemed impractical.

We were able to locate 33 published studies relevant to our three broad categories of habitat manipulation (Table 1). The majority of studies (n = 22) investigated snake response to vegetation management (e.g., logging, prescribed fire). Several studies evaluated the use of herbivore-exclusion fencing and road-crossing structures in snake conservation. The response of snakes to manipulation of targeted habitat features (e.g., artificial hibernacula, retreat sites and basking sites) was not well-documented in the literature.

Manipulation of Targeted Habitat Features

Habitat management can target specific habitat needs of snakes, including basking, retreat, hibernation and aestivation, feeding, and nesting.

Basking Sites and Gestation Areas

Thermoregulation is closely associated with physiological function (e.g., shedding, digestion, locomotion, gestation) and serves as a fundamental driver of habitat selection for many snake populations (Reinert 1993; Shine and Madsen 1996; Weatherhead and Madsen, this volume). Open-canopy basking habitat is critically important for many snakes, especially large-bodied species (Stevenson 1985). Gravid females of many viviparous species spend the gestation season basking within open-canopy "gestation" habitat (Brown 1993; Parker and Prior 1999; see also Weatherhead and Madsen, and Shine and Bonnet, this volume), often forfeiting opportunities for feeding or other non-basking behaviors (Keenlyne and Beer 1973; Seigel and

Ford 1987; Seigel et al. 1987). Additionally, many snakes bask extensively upon emergence from hibernation. This behavior may be instrumental for the completion of spermatogenesis in some species (Gregory 1982).

Snakes often favor basking sites that provide low-cost access to a wide thermal gradient (Spellerberg 1975, 1988). For instance, Black Ratsnakes (Pantherophis [Elaphe] spiloides) apparently prefer forest/field ecotones for thermoregulation (Blouin-Demers and Weatherhead 2001). Although access to direct sunlight can be critical for thermoregulation, snakes often bask in or near some form of shaded cover or belowground retreat (Burger and Zappalorti 1988; Nilson et al. 1999). Rocky outcrops and talus slopes often provide abundant thermoregulation and retreat opportunities, and are consequently used by many snake species (e.g., Brown et al. 1982; Parker and Prior 1999).

Declines and even extirpations of snake populations may be linked to loss of basking habitat. Anecdotal records suggest that an endangered population of Massasaugas (Sistrurus catenatus) in New York has declined as basking habitat has reverted to a closed-canopy state after an 1892 fire (Johnson and Breisch 1993). One of us (KTS) recently assessed the case for habitat manipulation (canopy removal) at this site. Massasaugas generally selected the warmest available microhabitats for basking, but average temperatures at these sites were substantially lower (approximately 3 ºC) than selected basking sites at an open-canopy reference location (Shoemaker 2007). Habitat management to improve basking habitat is therefore likely to prevent the further decline of this endangered snake population.

Artificial basking habitat may consist of simple clear-cut patches or artificial tree-fall gaps within a forested matrix (Schmidt and Lenz 2001; Gregory 2007). Many reptiles are well-suited to take advantage of small canopy gaps (Vitt et al. 1998), and may even follow tiny sunflecks across a forest floor (Huey 1982). In addition, snakes are not known to be territorial, and individuals of many species bask communally (Gillingham 1987; Gregory et al. 1987). Efforts to create or improve basking habitat for snakes should therefore focus on quality and strategic location of basking sites rather than size of manipulated areas.

In some cases, vegetation removal may be insufficient to create optimal basking habitat. As noted above, habitat heterogeneity can be important for effective thermoregulation; homogenization of basking habitat is probably undesirable in most cases. Poorly-planned vegetation management may increase visibility of sedentary species that rely on crypsis as a predator-avoidance mechanism (e.g., Graves 1989). Potential costs of vegetation removal such as increased predation rate and decreased crypsis should be evaluated as part of any study of managed basking habitat.

Retreat sites

Retreat sites function primarily to shelter snakes from potential predators (Webb and Whiting 2005) and from extreme temperatures (Huey et al. 1989), and are used extensively by many species (Whiting et al. 1997; Whitaker and Shine 2003; Pearson et al. 2005; Sherbrooke 2006; Shine and Bonnet, this volume). In lieu of basking, some snakes access solar energy by selecting large flat rocks in open, sunny places (colloquially termed "snake rocks") as retreat sites (Huey et al. 1989; Webb and Shine 2000). Snakes also use retreat sites to protect themselves from desiccation (Clark 1970; Whiles and Grubaugh 1993), to lay eggs (Henderson et al. 1980), and to forage (Webb and Shine 2000; Russell et al. 2004; Shine and Bonnet, this volume). Because snakes spend much of their time stationary within retreat sites, selecting a proper site can improve fitness substantially (Webb and Shine 1998; Kearney 2002; Pringle et al. 2003; Webb et al. 2004).

Populations of the endangered skink, Adelaide Pygmy Bluetongue (Tiliqua adelaidensis), in Australia increased in size in response to establishment of artificial burrows (Milne and Bull 2000; Souter et al. 2004). However, similar examples are difficult to find in the snake literature (Table 1). Artificial retreat sites (Webb and Shine 2000) and selective removal of canopy vegetation from formerly-occupied retreat habitat (Webb et al. 2005) may improve the conservation status of the endangered Broad-headed Snake (Hoplocephalus bungaroides). The endangered Concho Watersnake (Nerodia paucimaculata) in Texas makes extensive use of retreat sites within rocky shoreline habitat, which can be in short supply during high water levels; creation of elevated rocky shoreline habitat may improve the conservation status of this snake (Whiting et al. 1997). Riprap (large stones and boulders used to stabilize waterways and prevent erosion) is used by snakes for basking and retreat in some locations (Herrington 1988; Perry et al. 1996; Wylie et al. 2002), suggesting that construction of rock piles may provide retreat habitat for many snakes, especially those adapted to talus slopes (Herrington 1988; Schmidt and Lenz 2001). Strategically placed brush or rock piles may similarly serve to create valuable retreat habitat for snakes (Frier and Zappalorti 1983; Seymour and King 2003).

Hibernation sites

Hibernacula are a special and particularly important type of retreat site for snakes in temperate climates. Winter kill and other hibernation-related losses represent some of the most important documented sources of mortality for snakes (Gregory 1982; Shine and Mason 2004), suggesting that hibernation habitat is a limiting resource for many temperate-zone populations. Choosing a proper hibernaculum is critical, as a poor choice is almost certainly fatal (Reinert 1993). A suitable hibernacula must 1) provide protection from freezing temperatures (Bailey 1949); 2) maintain relatively cool temperatures to reduce wasteful metabolic expenditures (Goris

1971); 3) provide protection from desiccation (Costanzo 1989); 4) provide protection from predation (Burger et al. 1992); 5) provide access to an adequate supply of oxygen (Gillingham and Carpenter 1978; Shine and Mason 2004); and, 6) remain free of molds and other pathogens (Goris 1971).

For communally-hibernating species, hibernation site improvement may be a relatively cheap, simple, and effective management strategy (Shine and Mason 2004). For example, the Red-sided Gartersnake (Thamnophis sirtalis parietalis) hibernates communally by the thousands within limestone caverns in central Canada. Observing high overwinter mortality at some hibernation sites, researchers suggested that levee banks could be erected to protect hibernacula against flooding, and that insulation of hibernacula may be used to protect snakes against freezing temperatures (Shine and Mason 2004).

Many snake species use human-made structures such as building foundations and sewer lines as hibernacula (Zappalorti and Reinert 1994; Seymour and King 2003), raising the intriguing possibility that artificial hibernacula could benefit wild snakes. In reality, attempts at creating artificial hibernacula often fail due to one or more critical violations of the criteria listed above (Bailey 1949; Goris 1971). Although failures documented in the literature generally involve captive snakes forced to use created hibernacula (see Goris 1971), wild snakes may also be threatened by poorly-designed structures.

Artificial snake hibernacula have promise as a management technique (Shine and Bonnet, this volume). Man-made hibernacula effectively decreased overwinter mortality from nearly 100% to approximately 10% at a commercial snake farm in Japan (Goris 1971). At this site, hibernacula were created by filling shallow holes with gravel for drainage, boulders to provide hibernation cavities, and packed soil for insulation (Goris 1971). Another design consisted of a drained, concrete-lined hole partially stacked with concrete blocks and covered with soil (used for a behavioral study). After a pump was installed to improve drainage at the study site (high mortality was observed in the first year of the study due to flooding) overwinter mortality fell to a relatively low 15% (Gillingham and Carpenter 1978). Artificial hibernacula similar to those described above were constructed for Northern Pinesnakes (Pituophis m. melanoleucus) in New Jersey. Many pine snakes, as well as individuals of other species, have been documented to use these structures (Zappalorti and Reinert 1994). The development of artificial hibernacula was not accompanied by population monitoring (Zappalorti and Reinert 1994), and the conservation success of these structures remains unclear.

The effectiveness of artificial hibernacula in snake conservation has not yet been demonstrated in the literature (Table 1). Until the effectiveness of this technique is firmly established, artificial hibernacula should generally be restricted to captive management studies and experimental field studies (Shine and Bonnet, this volume). We caution against the use of artificial hibernacula as quid-pro-quo for the destruction of known hibernacula.

Foraging sites

Improvements to foraging habitat may be an effective conservation strategy for prey-limited populations. In Australia, prey availability may be the primary determinant of population size for H. bungaroides, at least at the site-level (Shine et al. 1998). Artificial cover objects have been shown to elicit a positive response from Lesueur's Velvet Geckos (Oedura lesueurii) – the primary prey of the H. bungaroides – and may indirectly benefit broad-headed snakes by augmenting prey populations (Webb and Shine 2000). In central New York, plots cleared of woody vegetation in an effort to benefit S. catenatus showed higher Massasauga prey (small mammal) abundance and diversity following vegetation removal (Johnson 1995).

Manipulation of habitat structure may improve foraging success without changing prey density. In China, trimming tree branches improved foraging success for Shedao Island Pitvipers (Gloydius shedaoensis) by forcing birds to alight on branches strong enough to support snakes (Shine et al. 2002a). Mesocosm experiments with ratsnakes (Pantherophis) have shown that structural complexity of foraging habitat can influence foraging success; for this species, intermediate levels of habitat complexity (density of woody vegetation) maximized foraging success (Mullin et al. 1998).

Nesting habitat

Nesting ecology is poorly understood for most egg-laying snake taxa. Nesting habitat should supply embryos with the warmth necessary for proper development (see Weatherhead and Madsen, this volume), adequate moisture, and protection from predators, pathogens, and plant roots (Burger and Zappalorti 1991; Burger et al. 1992; Shine and Bonnet, this volume). Although nesting sites may be a limiting resource for many snake populations, the manipulation of nesting habitat is not common in snake conservation.

Some snake species use human-altered habitat for nesting. In a study of northern pine snakes in New Jersey, all observed nesting events occurred in areas recently disturbed by humans (Burger and Zappalorti 1988). Ratsnakes use man-made leaf piles and compost piles as nest sites (Weatherhead and Madsen, this volume). Rock walls are used for nesting by some species (Shine and Bonnet, this volume). Artificial nesting sites (carefully constructed rock piles) have been used by several snake species in France (Shine and Bonnet, this volume). European snakes (Natrix spp.) frequently nest in manure piles, where bacterial decomposition supplies supplemental warmth (Madsen 1984; Spellerberg 1988). In fact, northern populations of N. natrix may be dependent on the presence of manure piles for oviposition (Shine et al. 2002b). In

Germany, wildlife managers placed manure piles next to preferred N. tessellata (Dice Snake) foraging habitat to provide supplemental nesting habitat, but the success of this management intervention remains to be seen (Herzberg and Schmidt 2001).

Manipulation of habitat features as a viable conservation strategy

We found virtually no published studies evaluating manipulation of targeted habitat features in snake conservation; thus, the efficacy of these methods cannot be assumed. Manipulation of habitat features (especially hibernacula) should be accompanied by well-planned research and monitoring efforts. Nonetheless, small scale and specificity can make manipulation of targeted habitat features an attractive option compared with manipulation of entire communities.

Manipulating the seral stage of natural communities

Reversing vegetative succession

Many reptiles of forested regions depend on early-successional habitat. Nearly 75% of snake and lizard species in the southern United States require open-canopy habitats within their range, and more than half of these species are primarily associated with early-successional habitat (Trani 2002). In a Pennsylvania study, powerline right-of-ways (ROWs) maintained in an early-successional state supported a greater diversity and abundance of snakes than surrounding forested habitat (Yahner et al. 2001a,b; Yahner 2004). Some regions (e.g., the northeastern United States) are undergoing extensive reforestation as agricultural areas are abandoned (Motzkin and Foster 2002), with major implications for all early-successional species (Litvaitis 1993; Brawn et al. 2001). Natural vegetation succession can pose a threat to populations of snakes adapted to early-successional habitat (Johnson and Leopold 1998; Kingsbury 2002; Smith and Stephens 2003; Webb et al. 2005). Natural succession has been implicated in the presumptive loss of four native snake species and the decline of eight others from the Fitch Natural History Reservation in Kansas (Fitch 2006). Forest regrowth has also been implicated in the extirpation of several Asp Viper (Vipera aspis) populations in Switzerland (Jäggi and Baur 1999).

Before European colonization, a large portion of central North America consisted of grasslands (prairies) maintained by drought, fire, and grazing ungulates (Vickery et al. 1999). As prairies were converted to agriculture, however, prairie natives were often relegated to low-quality remnant habitat patches. Included among the native North American prairie fauna are several snake species including the Plains Hog-nosed Snake (Heterodon nasicus nasicus: Wright and Didiuk 1998) and the Eastern and Desert Massasauga (S. c. catenatus and S. c. edwardsii: Mackessy 2005), some of which are locally or nationally threatened. The coastal pine communities of the southeastern United States are also adapted to frequent natural disturbance (Ford et al. 1999; Greenberg 2000; Kilpatrick et al. 2004). Resident snake species of southeastern fire-adapted pine communities include the Eastern Indigo Snake (Drymarchon couperi), the Crowned snakes (Tantilla relicta and T. coronata), Short-tailed Snake (Stilosoma extenuatum), and the Pinesnake (P. melanoleucus: Greenberg 2000).

Conserving populations of early-successional reptiles may be accomplished by simulating or harnessing natural processes such as fire and grazing (Howe 1994). Prescribed fire has been used to maintain open-canopy habitat for the prairie-adapted Eastern Massasauga in several locations (Johnson and Leopold 1998; Wilson and Mauger 1999; Johnson et al. 2000). Evidence for success of prescribed fire in snake conservation is mixed (Table 1). A Kansas study suggested that prescribed burns and wildfire may increase long-term viability for Eastern Racers (Coluber constrictor) despite an apparent negative short term response (Cavitt 2000). In a Florida study, prescribed fire successfully altered herpetofaunal community composition to closely match that of a reference site with a "natural" fire-disturbance history. However, fire management appeared to elicit a negative response from the only snake included in this study, the Peninsular Crowned Snake (Litt et al. 2001). A similar study in Maryland documented a herpetofaunal community shift in response to fire, with some snake species (notably C. constrictor) responding positively and others (Storeria dekayi, Thamnophis sirtalis, Lampropeltis getula, and Carphophis amoenus) responding negatively (McLeod and Gates 1998).

In cases where prescribed burning is impractical, herbicide application or mechanical brush clearing may be used to discourage woody vegetation (Wigley et al. 2000). Herbicides can be particularly useful for clearing small areas of woody vegetation (Wigley et al. 2000), and as such may be an effective means of creating basking habitat for snakes (see Johnson and Breisch 1999). Herbicide application may be toxic or otherwise harmful to snake species and other non-target organisms, and must therefore be used only after expert consultation and thorough impact evaluation. The use of Round-Up® (Monsanto, Inc.) is especially discouraged because of reported detrimental effects on larval amphibians (Relyea 2005).

Mechanical brush clearing, using either hand-tools or heavy machinery, can be used to create or maintain early-successional habitat. In New York, Massasaugas responded favorably to mechanically-cleared treatment areas; 10% of aboveground radio-locations occurred in or around mechanically-cut treatments that constituted only 2.5% of the total core habitat at the study site (Johnson 1995). However, management success was apparently short-lived (Johnson and Breisch 1999).

The response of herpetofauna to commercial forestry operations has been fairly well studied (reviewed in Russell et al. 2004). Some snake populations may benefit from the mosaic of seral stages resulting from logging activities (Greenberg et al. 1994; Ross et al. 2000; Crosswhite et al. 2004; Shipman et al. 2004; Loehle et al. 2005). In a post-hoc analysis of Australian faunal survey records, researchers noted that three of seven snake species occurred more often on clearcut sites than on undisturbed forested sites; only one species occurred primarily on undisturbed forested sites (Kavanagh and Stanton 2005). In Pennsylvania, reduction in tree basal area due to logging was positively correlated with snake abundance (mostly T. sirtalis: Ross et al. 2000). Tropical heliothermic snakes may be attracted to canopy openings created by logging (Vitt et al. 1998; Fredericksen and Fredericksen 2002). Much remains to be learned about the response of snakes to logging and other forestry practices (Goldingay et al. 1996: Table 1).

The relative merits of prescribed fire, mechanical cutting, and herbicide application in achieving snake conservation goals cannot be addressed adequately using available evidence (Table 1). In a study of powerline ROWs in Pennsylvania, researchers found that snake abundance and diversity was generally higher in ROWs cleared with herbicides than those cleared by mechanical means (Yahner et al. 2001a). Combinations of fire, herbicide, and mechanical clearing may be more effective in achieving conservation goals than any of these management tools used alone. An Oklahoma study found that snakes were most abundant on plots that had been treated with herbicide and subsequently burned than on plots treated with herbicide alone (Jones et al. 2000). Whenever possible, pilot management studies should assess the relative effectiveness of alternative management options.

Prescribed fire and other forms of vegetation management may injure or kill snakes directly. Studies investigating the direct mortality of snakes after prescribed fires generally indicate that mortality rates are low enough to be of little concern at the population level (Erwin and Stasiak 1977; Floyd et al. 2002). For reasons that are unclear, shedding snakes may be most vulnerable to direct mortality (Means and Campbell 1980). Every attempt should be made to limit direct snake mortality related to high-impact management activities by conducting these activities during times and seasons when snakes are least likely to be active (Dalrymple 1984; Johnson et al. 2000).

Perhaps of greater conservation concern, vegetation management may indirectly increase mortality rates for target snake species. In a Kansas tallgrass prairie, researchers recorded increased predation of large-bodied snakes by raptors on fire-managed plots (Wilgers and Horne 2006). At the same Kansas study site, small earthworm-eating snakes tended to be healthier and more abundant on unburned plots than on regularly burned prairie plots (Wilgers and Horne 2006). Researchers in Australia showed that low-intensity fire may degrade Southwestern Carpet Python (<u>Morelia spilota imbricata</u>) habitat by eliminating favored retreat sites (Pearson et al. 2005). To minimize risks inherent to high-impact management activities such as prescribed fire, unmanaged plots should always be interspersed with managed plots as refugia from direct mortality, predation, and habitat degradation (Setser and Cavitt 2003).

Promoting vegetative succession: herbivore exclusion

Herbivore exclusion functions to jump-start vegetative succession. Just as the introduction of grazing mammals can be used to maintain early-successional habitat, the exclusion of grazing mammals can be used to improve the quality of habitat devoid of vegetative cover (Szaro et al. 1985; Leynaud and Bucher 2005). Some researchers have documented a positive response of snakes to herbivore-exclusion plots (Table 1). Exclusion of grazers from riparian areas has been correlated with increased snake abundance in Pennsylvania (Homyack and Giuliano 2002) and New Mexico (Szaro et al. 1985). Results of a similar domestic herbivore exclusion study in Argentina were inconclusive (Leynaud and Bucher 2005).

Manipulation of vegetation communities as a viable conservation strategy

According to most published accounts, snakes respond favorably to anthropogenic canopy disturbance (Table 1). However, none of the published studies we reviewed documented improved snake conservation status in response to habitat manipulation. Moreover, given the abundance of literature on the effects of prescribed fire on herpetofaunal communities (Russell et al. 1999), surprisingly few studies demonstrated a benefit to snakes. In general, long term population-level studies of the response of snake populations to prescribed fire and other large anthropogenic disturbances are sorely needed.

Habitat manipulation from a landscape perspective

The number, size, and distribution of habitat patches within a landscape can have important ecological consequences (Harris 1984; Turner et al. 2001; Haila 2002). Dispersal rates, mortality rates, and other ecological processes of direct relevance to population viability may be related to landscape composition and configuration (Turner 2005; Jenkins et al., this volume). To effectively manipulate habitat at a landscape scale, detailed site-specific knowledge is often required (Roe et al. 2003; Fischer et al. 2004; Roe and Georges 2007). Therefore, any review of this topic should be interpreted with some caution; management success at one site may not translate to success at other sites.

Dispersal habitat

Dispersing snakes typically experience higher mortality rates than snakes engaged in sedentary behaviors (Bonnet et al. 1999; Kingsbury and Attum this volume). This generalization may be especially relevant for snakes inhabiting areas of high road density (Andrews and Gibbons 2005; Roe et al. 2006). Carefully placed artificial hibernacula and other critical habitat elements may reduce the need for dispersal, thus limiting dispersal-related losses (Shine and Bonnet, this volume). However, dispersal movements play an important role in the life cycle and evolution of many snake species (Gregory et al. 1987; Roe et al. 2006), and should not necessarily be discouraged. For example, species that hibernate communally, such as the Red-sided Gartersnake (<u>T. sirtalis parietalis</u>) and the Timber Rattlesnake (<u>Crotalus horridus</u>), engage in semi-annual migrations to and from communal hibernacula. Such migrations are likely important in maintaining gene flow among den sites (Gregory 1982). Increasingly, conservation professionals are implementing measures to restore landscape connectivity such as road-crossing structures and dispersal corridors.

Anthropogenic development and associated habitat losses often result in isolation of populations formerly able to exchange genetic information. In such cases, wildlife managers may wish to create linear corridors (e.g., riparian buffer zones) to improve landscape connectivity (Harris 1984). Use of movement corridors has yet to be refined as a management strategy for snakes. For example, an Australian study showed that many reptiles were functionally isolated despite the existence of linear forest remnants (Driscoll 2004). In heavily forested regions, powerline ROWs and other linear features maintained in an early-successional state may serve as effective movement corridors for early-successional snake species.

In some cases, manipulation of matrix habitat may increase snake dispersal in the absence of habitat corridors. As noted above, snakes tend to prefer habitat that affords protective cover (Shine et al. 2004; Andrews and Gibbons 2005). As part of the restoration of the Guadiamar River in Spain following a damaging toxic discharge, researchers used artificial cover objects to successfully promote re-colonization by snakes and other reptiles through an otherwise unfavorable matrix (J.M. Pleguezuelos and R. Márquez, pers. comm.). Similarly, research in Indiana indicated that the use of partially-submerged brush/debris piles may facilitate colonization of artificial wetlands by the state-endangered copperbelly water snake (Lacki et al. 2005).

Road-crossing structures

Of all human-built structures, roads are perhaps the most harmful to snake populations. Countless snake populations are threatened by existing roads or by proposed road-construction projects (Weatherhead and Madsen, this volume). Roads can serve as a source of direct mortality or as a dispersal barrier (Forman and Alexander 1998). The ecology and behavior of snake species affects the type and magnitude of threat posed by roads (Andrews and Gibbons 2005). Although few studies have demonstrated a detrimental effect of roads on snake populations (e.g., Row et al. 2007), it is likely that many populations have already been severely impacted. After relatively few generations, highway construction apparently contributed to genetic differentiation among occupants of different ratsnake hibernacula (Prior et al. 1997). Recently, roads have been shown to effectively impede gene flow among Timber Rattlesnake den sites (R. Clark, pers. comm.; King, this volume).

Harmful road impacts can be mitigated by crossing structures, often consisting of a roadside barrier directing animals toward a culvert or overpass (Forman and Alexander 1998;

Dodd et al. 2004; Aresco 2005). Such structures have been shown to reduce road mortality (and presumably increase dispersal rates) for herpetofauna, especially turtles (Aresco 2005) and amphibians (Langton 1989). Road-crossing structures may be most beneficial in cases where snakes engage in cyclic mass-movements, or where roads cut through snake hotspots (Smith and Dodd 2003; Dodd et al. 2004; Aresco 2005). In Manitoba, Canada, road-crossing structures have reduced road mortality for Red-sided Gartersnakes traveling to and from communal hibernacula (Shine and Mason 2001; Shine and Bonnet, this volume). In cases where snakes are reluctant to use road-crossing structures, structures may be made more attractive to snakes; well-placed cover objects may facilitate the use of road-crossing structures by snakes and other vertebrates (Rodriguez et al. 1996). In one case, researchers used pheromones to entice migrating Red-sided Gartersnakes to use road-crossing culverts (Shine and Mason 2001).

Road-crossing structures carry no guarantee of conservation success. Culverts may flood, causing them to lose their value for terrestrial animals. Improperly designed crossing structures may strand animals in a highway median strip or lead them into unsuitable habitat (J. Brown, pers. comm.). Fence/culvert systems must be regularly maintained to ensure long-term effectiveness (Dodd et al. 2004). Finally, snakes simply do not make use of road-crossing structures in many cases (see Wright 2006). Unfortunately, such management failures are rarely documented and disseminated to the conservation community.

Because money is limited, road-crossing structures should be carefully placed where they will have maximum positive impact on snake populations. Behavioral experiments (e.g., Andrews and Gibbons 2005) can be paired with GIS simulations of snake movement patterns to aid managers in maximizing the positive impacts of road-crossing structures. Carefully-designed experiments and observational studies can identify factors (adjacent habitat types, diameter of culvert, length of culvert, temperature, light within culvert, etc.) influencing crossing structure use by snakes (Yanes et al. 1995; Rodriguez et al. 1996).

Managing land-cover diversity

Some snake species require multiple habitat-types within their range, either to fulfill basic needs or because of phenological shifts in habitat selection. For these species, habitat may be managed for land-cover diversity (Spellerberg 1988; Smith and Stephens 2003). Creating and maintaining land-cover diversity need not be expensive or time-consuming; a well-designed prescribed fire regime should result in a mosaic of seral stages, which can be favorable for reptile communities (Masters 1996; Litt et al. 2001; Smith and Stephens 2003). Maintaining a mosaic of patch types may also function to increase ecosystem resilience. An Australian study indicated that, although the diversity and abundance of reptiles (mostly lizards) was low on recently burned plots, these patches were likely to serve as fire-breaks, benefiting the integrity and resilience of the reptile community as a whole (Masters 1996).

Semi-aquatic snakes may benefit from created wetlands or the creation of a mosaic of wetland and upland habitats. In an Ohio study, snakes were frequently associated with mine-reclamation wetlands (Lacki et al. 1992). Constructed wetlands were used readily by the state-endangered Copper-bellied Watersnake (Nerodia erythrogaster neglecta) in Indiana (Lacki et al. 2005). In central California, wetlands were created on former agricultural land to benefit the Giant Gartersnake (T. gigas); although Giant Gartersnakes have used the created wetlands, improved conservation status has not yet been demonstrated (Wylie et al. 2002). In Germany, management of Natrix tessellata habitat featured the restoration of a mosaic of natural habitat features (such as inlets and fluvial islands) to a heavily disturbed riverine system. Anecdotal evidence suggests that this project has been successful (Lenz and Schmidt 2002), but scientific documentation of management success is not yet available.

Managing patch size

Island biogeography theory (MacArthur and Wilson 1967) continues to influence landscape ecologists and land-use planners. Within this conceptual framework, island (patch) size is generally considered a key determinant of species richness (Harris 1984). In a New Hampshire study, snake diversity and abundance was generally higher on large habitat patches (> 10 ha) than on small patches (< 1 ha); thus, increasing the size of existing patches may benefit snake communities more than the creation or preservation of isolated habitat patches (Kjoss and Litvaitis 2001). The Copper-bellied Watersnake may benefit from an increase in the number of habitat patches (shallow ponds and wetlands) rather than an increase in the size of existing patches. Because the Copperbellied Watersnake specializes on an ephemeral food resource (amphibians), increasing the number and heterogeneity of ponds theoretically increases the likelihood that at least one pond will contain high prey densities at any given time (Roe et al. 2004). Although it is clear that the size and arrangement of habitat patches influences habitat quality for snakes, further research is necessary to understand the conservation implications of alternative landscape configurations on snake populations and communities.

CONCLUSIONS AND FUTURE RESEARCH

Based on available literature, few (if any) studies have demonstrated that habitat manipulation has resulted in improved conservation status for a snake taxon or population. In fact, few studies explicitly measured the response of snake populations to habitat manipulation (Table 1); the response variable most commonly measured was the number of animals captured in pitfall traps, funnel traps, or under cover objects. In addition, the inference power of many of the studies we reviewed was compromised by pseudoreplication (Hurlbert 1984) and a lack of temporal or spatial controls. Admittedly, independent replicates of experimental treatments are difficult to achieve in habitat management studies; “replicate” plots can be spatially autocorrelated even when separated by hundreds or even thousands of meters. Pseudoreplication arises when experimental units treated as replicates are predisposed to respond to experimental treatments in similar ways. Pseudoreplication can increase the likelihood of a study reporting a significant response when management in reality had no effect (see Hurlbert 1984). Until the safety and effectiveness of habitat manipulation is firmly established in snake conservation, the success of habitat manipulation projects should be monitored experimentally – using proper controls and replication wherever possible.

Managers should exercise extreme caution when using habitat manipulation to mitigate the impacts of proposed development projects (e.g., “replacement” of a drained wetland with a created wetland; see Perry et al. 1996). Increasingly, artificial snake hibernacula and gestation sites are being incorporated into construction projects to ease permitting restrictions (Kelly and Hodge 1996). Highway departments and conservation agencies are erecting road-crossing structures to reduce the harmful effects of road-building projects on snakes and other wildlife. The results of this review indicate that such "mitigation" efforts, although perhaps beneficial, cannot be justified as quid pro quo for loss of natural habitat.

Moving towards evidence-based conservation

Responding to a paradigm-shift in the medical profession, many conservation professionals have called for a shift towards “evidence-based conservation” (Smallwood et al. 1999; Fazey et al. 2004; Sutherland et al. 2004). Essentially, the “evidence-based conservation” paradigm calls for the development of testable management hypotheses based on systematic review of published and "grey" literature (Smallwood et al. 1999). Well-designed monitoring programs provide raw evidence for or against alternative management hypotheses (Smallwood et al. 1999; Nichols and Williams 2006). Finally, timely publication and dissemination of all findings completes the cycle by making information available for future management efforts (Box 1).

Developing an evidence-based plan for habitat manipulation

The evidence-based conservation paradigm requires that key management questions (e.g., which of various management alternatives have historically been most successful in improving population viability for this snake species?) are evaluated through systematic review of published and unpublished literature before drafting a management plan (Gates 2002; Fazey et al. 2004; Sutherland et al. 2004). Where possible, meta-analysis should be used to gain a rigorous understanding of the information content and implications of previous research (Fazey et al. 2004; Sutherland et al. 2004). Admittedly, conducting systematic reviews can be difficult for land managers who may lack access to scientific databases or lack the necessary expertise. We strongly encourage collaboration in this effort between natural resource managers and academic or consulting ecologists. At the very least, systematic reviews would inform conservation professionals of promising new habitat manipulation techniques and specific areas in need of further research (Fazey et al. 2004; Sutherland et al. 2004).

In cases where the ecology, behavior, and management needs of a target species is undocumented, "expert" knowledge (generally the experience-based opinions of other wildlife management professionals) is regularly used in the drafting of management plans (Sutherland et al. 2004). As a rule, however, "expert" knowledge is not based on sound science and should be considered weak evidence (Smallwood et al. 1999; Sutherland et al. 2004). The use of anecdotal sources appears to be common in snake habitat management; for instance, expert opinion was used to justify the inclusion of rice fields as key Giant Gartersnake habitat in a USFWS Habitat Conservation Plan and region wide recovery plan although there was no documented evidence to support this decision (Smallwood et al. 1999). Ideally, managers faced with lack of information should conduct pilot experiments or observational studies (perhaps working with local academic or consulting ecologists) to generate the evidence needed to develop informed management hypotheses.

After reviewing available sources of information, management professionals should articulate one or more testable hypotheses related to their management goals. For example, the literature suggests that Coluber constrictor may avoid prescribed burn units immediately after fire, yet prefer the same habitat several months post-fire (see McLeod and Gates 1998; Cavitt 2000). Further literature review might suggest several plausible hypotheses to explain this phenomenon: 1) C. constrictor is responding to post-fire population cycles of primary prey; 2) C. constrictor requires more protective cover than is afforded immediately after fire; 3) C. constrictor requires a more heterogeneous thermal regime than is available immediately after fire; and, 4) C. constrictor is responding to a complex interaction of one or more of the above factors. To test these alternative hypotheses, a management plan for this species may be developed that monitors relationships among snake densities, prey densities, protective cover, and thermal regimes after a prescribed fire.

Although it is not yet standard procedure, habitat management plans for the conservation of at-risk snake populations should be subjected to external review before implementation (Smallwood et al. 1999). Just as peer-review underpins the integrity of academic publications, external review of management proposals ensures that the "best available evidence" is used in practice (Smallwood et al. 1999).

Monitoring the success of habitat manipulation

Well-designed monitoring efforts ultimately provide the evidence for or against alternative management hypotheses. To generate a baseline with which to gauge the effects of any subsequent management action (Smallwood et al. 1999), monitoring programs should generally be implemented several years before habitat manipulation is initiated (Gibbs et al. 1999; Renken et al. 2004). Note that exceptions can and should be made in cases where a population appears to be in immediate danger of extirpation (e.g., Daltry et al. 2001). With foresight, unfocused baseline monitoring can be replaced by data collection efforts targeting management hypotheses (Nichols and Williams 2006).

To assess the effects of management on snake population viability, monitoring protocols should be able to detect changes in population-level characteristics such as increased reproductive ability, reduced mortality rate, increased adult survival or increased population size (Seigel et al. 1998; Renken et al. 2004; Dorcas and Willson, this volume). Long-term capture-recapture studies can be a powerful means of evaluating trends in population-size, age-structure, coarse movement patterns, mortality rates, and more (White and Burnham 1999). For long-lived snake species, population-size indicators may have a prohibitively long response time (Dorcas and Willson, this volume). For such species, it may be more appropriate to focus on monitoring indicators of fertility or mortality.

Adaptive management

Probability of success for any habitat manipulation project is in part a function of site-specific criteria (Fazey et al. 2004). Management decisions should therefore be based on a combination of outside information (e.g., systematic literature reviews) and site-specific information gained as part of the adaptive management process (Fazey et al. 2004). In the adaptive management paradigm, subsequent management actions are informed by previous monitoring efforts in an iterative feedback process (Gibbs et al. 1999; see Box 1). Adaptive management is not a trial-and-error process, but a hypothesis-driven process – and therefore has a place within the "evidence-based conservation" framework. Unfortunately, adaptive management is often misused and rarely functions as intended (Gibbs et al. 1999).

Integrating habitat manipulation with experimental research will not only benefit conservation efforts, but will enhance our knowledge of population ecology and of the response of animal populations to environmental change. We challenge conservation biologists and natural resource managers to combine their skill sets, share their successes and mistakes, and to make evidence-based conservation for snakes a reality.

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LIST OF TABLES

	Location	Focal or dominant snake species	Total number of snakes included in study	Pre-manipulation monitoring	Post-manipulation monitoring	Long-term monitoring (≥ 3 yrs)	Treatments replicated (adequate #, no pseudoreplication)	Response of individual snakes to habitat manipulation	Change in abundance after manipulation	Change in fertility, mortality or other fitness indicator	Overall strength of evidence for (+) or against (-) manipulation
1) Manipulation of Targeted Habitat Features											
Artificial Basking/Gestation Sites											
Webb et al. (2005)	southeastern Australia	Hoplocephalus bungaroides	2	Y	Y	Y	Y	+++	N/A	N/A	+++
Artificial Hibernacula											
Zappalorti and Reinert (1994)	New Jersey, USA	Pituophis melanoleucus Other species	139	N	N	N	N	++	N/A	N/A	+
2) Manipulation of the Seral Stage of Natural Communities											
Prescribed Fire											
Jones et al. (2000)	Oklahoma, USA	Virginia striatula Other species	48	N	Y	N	Y?	+	N/A	N/A	+
McLeod and Gates (1998)	Maryland, USA	Carphophis amoenus Coluber constrictor Other species	156	N	Y	N	N	M	N/A	N/A	U
Wilgers and Horne (2006)	Kansas, USA	Diadophis punctatus Tropidoclonion lineatum Other species	U	N	Y	N	N?	M	N/A	-	U
Kilpatrick et al. (2004)	South Carolina, USA	Tantilla coronata Carphophis amoenus	U	N	Y	N	Y	U	N/A	N/A	U
Masters (1996)	Northern Territory, Australia	Ramphotyphlops endoterus Other species	24	N	Y	Y	N	U	U	N/A	U
Cavitt (2000)	Kansas, USA	Coluber constrictor Thamnophis sirtalis Other species	550	Y	Y	N	N	-	U	N/A	-

	Location	Focal or dominant snake species	Total number of snakes included in study	Pre-manipulation monitoring	Post-manipulation monitoring	Long-term monitoring (≥ 3 yrs)	Treatments replicated (adequate #, no pseudoreplication)	Response of individual snakes to habitat manipulation	Change in abundance after manipulation	Change in fertility, mortality or other fitness indicator	Overall strength of evidence for (+) or against (-) manipulation
Litt et al. (2001)	Florida, USA	Tantilla coronata	U	N	Y	N	Y?	-	N/A	N/A	-
Setser and Cavitt (2003)	Kansas, USA	Coluber constrictor Thamnophis sirtalis *Other species*	92	N	Y	N	N	- -	N/A	N/A	-
Mechanical Clearing											
Johnson and Leopold (1998), Johnson (1995)	New York, USA	Sistrurus c. catenatus	U	N	Y	Y	Y	+	N/A	N/A	+
Clearcutting/Site Preparation											
Enge and Marion (1986)	Florida, USA	Coluber constrictor Cemophora coccinea Other species	280	N	Y	N	N	++	U	N/A	+
Greenberg et al. (1994)	Florida, USA	Tantilla relicta Other species	U	N	Y	N	N	+	N/A	N/A	+
Kavanagh and Stanton (2005)	New South Wales, Australia	Demansia psammophis Many other species	U	N	Y	N	Y?	N/A	N/A	N/A	+
Crosswhite et al. (2004)	Arkansas, USA	Agkistrodon contortrix *Coluber constrictor*	66	N	Y	N	N	U / +	U / +	N/A	U
Perison et al. (1997)	South Carolina, USA	Diadophis punctatus Other species	21	N	Y	N	N	U / -	N/A	N/A	U
Renken et al. (2004)	Missouri, USA	Storeria occipitomaculata Virgina valerae	U	Y	Y	Y	Y	U	U	N/A	U
Russell et al. (2002)	South Carolina, USA	Carphophis amoenus Coluber constrictor	U	Y	Y	N	Y?	-	N/A	N/A	U
Group Selection Harvesting/ Salvage Logging											
Greenberg (2001) (natural canopy gaps)	North Carolina, USA	Carphophis amoenus Diadophis punctatus Other species	108	N	Y	N	Y?	+	N/A	N/A	+

	Location	Focal or dominant snake species	Total number of snakes included in study	Pre-manipulation monitoring	Post-manipulation monitoring	Long-term monitoring (≥ 3 yrs)	Treatments replicated (adequate #, no pseudoreplication)	Response of individual snakes to habitat manipulation	Change in abundance after manipulation	Change in fertility, mortality or other fitness indicator	Overall strength of evidence for (+) or against (-) manipulation
McLeod and Gates (1998)	Maryland, USA	Elaphe obsoleta other species	226	N	Y	N	N	++	N/A	N/A	+
Ross et al. (2000)	Pennsylvania, USA	Thamnophis sirtalis Diadophis punctatus Other species	347	N	Y	N	Y?	+	N/A	N/A	+
Cromer et al. (2002)	South Carolina, USA	Diadophis punctatus Nerodia erythrogaster Storeria dekayi	387	N	Y	N	Y?	+	N/A	N/A	U
Goldingay et al. (1996)	New South Wales, AU	Various species	13	N	Y	N	Y	U	U	N/A	U
Right-of-Way Management											
Yahner et al. (2001a)	Pennsylvania, USA	Storeria occipitomaculata Diadophis punctatus Other species	50	N	Y	N	N	+++	N/A	N/A	+
Herbivore Exclusion/ Restoration of Riparian Habitat											
Homyack and Giuliano (2002)	Pennsylvania, USA	Nerodia sipedon Regina septemvittata Thamnophis sirtalis	~500	N	Y	N	Y?	++	N/A	N/A	+
Szaro et al. (1985)	New Mexico, USA	Thamnophis elegans vagrans	~25	N	Y	N	N	++	N/A	N/A	+
Leynaud and Bucher (2005)	Salta, Argentina	Bothrops neuwiedii Phimophis vittatus Other species	153	N	Y	N	N	U	N/A	N/A	U
Bowers et al. (2000)	South Carolina, USA	Nerodia fasciata Storeria occipitomaculata Other species	626	N	Y	N	N	U	N/A	N/A	U

3) Alteration of Ecological Landscapes

Road Crossing Structures

	Location	Focal or dominant snake species	Total number of snakes included in study	Pre-manipulation monitoring	Post-manipulation monitoring	Long-term monitoring (≥ 3 yrs)	Treatments replicated (adequate #, no pseudoreplication)	Response of individual snakes to habitat manipulation	Change in abundance after manipulation	Change in fertility, mortality or other fitness indicator	Overall strength of evidence for (+) or against (-) manipulation
Dodd et al. (Dodd et al. 2004); Smith and Dodd (2003)	Florida, USA	<u>Elaphe obsoleta</u> Other species	772	Y	Y	N	N/A	U	N/A	+++	++
Shine and Mason (2001)	Manitoba, Canada	<u>Thamnophis sirtalis parietalis</u>	U	N	N	N	N/A	(+) ?	N/A	(+) ?	+
Hwy 69 reports*	Ontario, Canada	<u>Sistrurus c. catenatus</u>	U	Y	Y	Y	N/A	- -	N/A	N/A	U
Aresco (2005)	Florida, USA	<u>Nerodia fasciata</u> <u>Coluber constrictor</u> Other species	363	Y	Y	N	N/A	U	N/A	U	U
Rodriguez et al. (1996)	central Spain	<u>Elaphe scularis</u> <u>Malpolon monspessulanus</u> <u>Vipera latasii</u>	U	N	Y	N	Y	(+)?	N/A	N/A	U

N/A = Study not designed to provide this information U = unclear M = mixed

TEXT BOX

An evidence-based approach to snake habitat manipulation. Step 1: Once a potential habitat-related problem is recognized, review all information relevant to habitat and management needs of target species and potential consequences of alternative management regimes; Step 2: Establish plausible management hypotheses (e.g., prescribed fire will result in increased mammal densities, leading to increased snake densities); Step 3: Develop plan for habitat manipulation that explicitly addresses management hypotheses (e.g., replicate management treatments, use appropriate controls, and monitor response variables) and submit plan to external review; Step 4: Implement a monitoring program before initiation of any habitat manipulation. Note - This is an on-going process which continues throughout initial and any subsequent habitat manipulations; Step 5: Implement management plan; Step 6: Evaluate the weight of evidence supporting each alternative management hypothesis. Document and disseminate all important findings. Adaptive Management (repeat Steps 1-6): Revise management hypotheses as necessary based on findings and further review of outside sources of information.