Blanding's Turtle (*Emydoidea blandingii*): A Technical Conservation Assessment

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Rocky Mountain Region,
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Authors' Biographies

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Blanding's turtle (*Emydoidea blandingii*). © Janet Hostetter, used with permission.

List of Errata

Summary of Key Components for Conservation of Blanding's Turtle

Blanding's turtles (*Emydoidea blandingii*) are secure in Nebraska, and they range from being vulnerable to threatened, or endangered throughout most of the rest of their distribution. In Region 2, they have not been reported from Kansas, they are extremely rare in South Dakota, and they occupy wetlands in the northern half of Nebraska. The largest population known within the range of Blanding's turtles is at Valentine National Wildlife Refuge, Nebraska.

The core habitat of Blanding's turtles has an aquatic component that consists of a permanent wetland and a suite of other, usually smaller and more temporary, wetlands such as vernal pools that are used by adults and hatchlings as temporary refugia and seasonal food sources. Blanding's turtle habitat also has a large terrestrial component that consists of nesting areas and movement corridors. The terrestrial component of the core habitat is larger than that of many other aquatic turtle species, and both sexes use terrestrial corridors for movements among wetlands and for nesting migrations.

A host of things can affect Blanding's turtles through their impact on either (or both) the wetland or terrestrial portions of their required habitat. Given the wide range of possible threats to populations of Blanding's turtles, three categories of threat appear most important. In rough order of decreasing priority, they are as follows:

- loss and degradation of wetland and terrestrial habitats
- road mortality
- collection

Loss and degradation of wetland and terrestrial habitats: Destruction of resident aquatic habitat is of primary conservation concern because it impacts all stages of the life cycle. Reduction in the numbers of such wetlands can increase risks of mortality for adults and reduce hatchling recruitment into populations. Cultivation to the edge of wetlands and the use of fertilizers, pesticides, and herbicides that wash into wetlands can degrade aquatic habitats. Water management activities related to fish management and agriculture can be detrimental to overwintering Blanding's turtle populations if they are conducted during winter.

Loss or degradation of terrestrial movement corridors can increase the risks of injury and mortality, and in addition may lead to isolation of populations and a subsequent reduction in genetic variation through drift and inbreeding. Reduction in the amount or number of nesting areas through agriculture, forestry, forest succession, introduction of exotics, or development can result in increased risks to females during nesting migrations of longer length or duration. Despite their importance to Blanding's turtles and the amphibian larvae that they feed on, small and temporary wetlands have minimal or no legal protection in many areas. However, conservation easements, local zoning, and education of private and public landowners can help reduce the loss of Blanding's turtle habitat. Such protection must focus on both wetlands (including small wetlands such as vernal pools) and key terrestrial areas near those wetlands.

Road mortality: The propensity for terrestrial movement by Blanding's turtles results in added risk of adult mortality associated with roads and other human activities, problems that tend to impact females more than males because of their extensive nesting migrations. In Michigan we have found females killed by farm equipment such as tractors, hay mowers, and road graders, and some stuck in stock fences. Communicating conservation issues to transportation planners may reduce construction of new roads in movement corridors and between nesting areas and aquatic habitats. Designs for new roads with high traffic volumes should include both barriers and culverts to control turtle movements. Barriers should block access to risky areas and encourage use of culverts that allow turtles safe passage under roads. Road signs can be placed along roadways with high volumes of traffic of both Blanding's turtles and vehicles. In areas with high levels of mortality associated with existing roads, fencing and ecopassages (e.g., culverts, tunnels, bridges) should be installed.

Collecting: In conjunction with their extended longevity and long reproductive lives, collection of adults, juveniles, and hatchlings from small and isolated populations for the pet trade can result in severe reductions and extirpation of populations. Gravid females were collected on roads by motorists during nesting migrations; one was subsequently returned to the University of Michigan's Edwin S. George Reserve (ESGR) when it was found to be marked.

The presence of these threats is exacerbated by a number of factors that make Blanding's turtles particularly susceptible to disturbance. First, Blanding's turtles and many other turtle species have temperature-dependent sex determination and some populations have biased adult sex ratios (e.g., the ESGR population in southeastern Michigan has an adult sex ratio close to 1 male to 4 females). Biased sex ratios are one of the factors that reduce effective population size and can contribute to population instability and reduce the probability of population persistence, particularly for small populations. Further, head-starting programs that include protecting or moving nests to artificial nesting areas run the risk of producing highly biased hatchling sex ratios. Second, reproductive output of Blanding's turtles is low. Females do not begin to reproduce until they are between 14 and 20 years old, do not reproduce every year, and have small clutch sizes, thus resulting in low fecundity. This means that annual survivorship between ages 1 and maturity must average at least 60 percent to maintain population stability. Third, Blanding's turtles are long-lived (even compared to other turtles), and older females appear to have higher survivorship and reproductive output than do younger females. This places primary reproductive importance on a small segment of the population, and because potential reproductive life spans are longer than generation times, it increases the likelihood of inbreeding in isolated populations.

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Introduction

Goal

The current assessment of the Blanding's turtle (*Emydoidea blandingii*) is part of the Species Conservation Project for the Rocky Mountain Region (Region 2) of the USDA Forest Service (USFS). The assessment examines the biology, ecology, and life history of the species with the goal of enhancing conservation and management practices throughout its range and within the geographic area of USFS Region 2. The literature reviewed and summarized for this assessment includes reports, peer-reviewed publications, and descriptions of conservation efforts and techniques applied to Blanding's and other turtles.

Scope, Uncertainty, and Limitations

Fortunately a few long-term studies of the ecology, demography, and life history of the Blanding's turtle make it relatively well known for a species of conservation concern. For 40 of the past 50 years, the life history, demography, and nesting ecology have been intensively studied for one population on the University of Michigan's Edwin S. George Reserve (ESGR) in southeastern Michigan; this provides encouraging news with respect to population stability and conservation and management programs. The population remained essentially stable between 1975 and 1994 without direct intervention (Congdon and Gibbons 1996) beyond maintaining permanent wetlands, temporary wetlands, vernal ponds, and terrestrial habitats required for nesting and movement among wetlands (Congdon et al. 1983, Congdon and Gibbons 1996, Kinney 1999, Congdon et al. 2001). The ESGR study provides empirically robust data on a stable population that makes reasonable demographic projections to other populations possible. A six-year study of a large population of Blanding's turtles in the Weaver Dunes area of southeastern Minnesota provides some excellent data on body size distributions, nesting ecology, the phenology of activity, and movements of adults and hatchlings (Pappas et al. 2001). Over the past decade, aspects of the ecology and status of Blanding's turtles in Kejimkujik National Park, Nova Scotia, Canada have provided information on an isolated northern population (Herman et al 1999, Mockford et al. 1999, Standing et al.1999, McMaster and Herman 2000, McNeil et al. 2000, Standing et al. 2000).

Interpreting and integrating literature from a variety of sources and from studies of different intensities and durations is always difficult, and it requires conservative interpretations based on judgment of the authors. Studies that are particularly site-specific and of short duration were included when they represent the best information available on topics that can be useful for management and conservation planning. Therefore, we try to indicate the relative strength of data supporting statements throughout the assessment.

Peer Review and Publication

This assessment will be published on the Region 2 World Wide website to make the information more readily and rapidly available to biologists, land managers, and the public. The quality, content, and presentation of the Blanding's turtle conservation assessment was improved under the guidance of Peter McDonald (USDA Forest Service, Region 2) and through external peer review prior to release on the Web. Peer review was managed by the Society for Conservation Biology, which employed two experts on this or related taxa.

Management Status and Natural History

Management Status

Federal designations

The Blanding's turtle is currently not listed as threatened or endangered under the federal Endangered Species Act anywhere within its range in the United States. The Bureau of Land Management does not rank this species in any states where it occurs. The range of the Blanding's turtle falls within USFS Regions 2 and 9 (mainly in Nebraska and Iowa). According to the master list of regionally designated sensitive species, only Region 2 lists it as a species of concern.

State designations

Many states list the Blanding's turtle as threatened or endangered (**Table 1**). Further, although the Global Heritage Rank for this species is G4 (apparently secure), its state-level ranks are uniformly higher (S1 = critically imperiled, S2 = imperiled, S3 = rare). This suggests that, despite having a wide range, local populations of Blanding's turtles throughout that range are vulnerable.

Table 1. Status of the Blanding's turtle in Canada and in the United States by region, based on distributions in Froom (1976), Iverson (1992), and Ernst et al. (1994). Global Heritage Rank is G4.

Region	State/Province	Natural Heritage Rank[1]	Special Status
Canada	New Brunswick[2]	—	Not indigenous
	Nova Scotia	S1	Threatened / Endangered
	Ontario	S3?	Endangered
	Quebec	S1	Special Concern / Collection prohibited
New England	Connecticut[2]	—	Not indigenous
	Maine	S2	Endangered
	Massachusetts	S2	Threatened
	New Hampshire	S3	Controlled
	Rhode Island[4]	—	Not indigenous
	Vermont	—	Not indigenous
Middle Atlantic	New York	S2S3	Threatened
	Pennsylvania	S1	Collection prohibited
Great Lakes Region	Illinois	S3	Threatened
	Indiana	S2	Endangered
	Iowa	S3	Protected
	Michigan[5]	S3	Special concern
	Minnesota[5]	S2	Threatened
	Ohio[6]	S2	Threatened
	Wisconsin[5]	S3	Threatened
Southern	Missouri	S1	Endangered
Western (USFS - Region 2)	Nebraska[5]	S4	Commercial
	South Dakota[7]	S1	Endangered

[1]Natural Heritage Program State Ranks (S-Ranks) are used to indicate the probability of extinction of species within state boundaries. Roughly speaking, S1 = critically imperiled, S2 = imperiled, S3 = rare or restricted, S4 = apparently secure, and S5 = demonstrably secure. More detailed descriptions can be found in Keinath et al. (2003), Keinath and Beauvias (2003), and on the NatureServe website (http://www.natureserve.org)
[2]Blanding's turtles may have been introduced
[3]Included in the distribution map (Iverson1992), but considered not indigenous by the Connecticut Department of Environmental Protection
[4]Included in the distribution map (Iverson 1992), but considered not indigenous by the Rhode Island Department of Environmental Management
[5]States with large or studied and apparently stable populations
[6]Collection from state owned or controlled waters prohibited
[7]Distribution based on two specimens (Backlund 1994)

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

Because the largest conservation concern for most aquatic or semi-aquatic reptiles is loss of habitat, the core of any such plan must be preservation of wetland complexes that include the surrounding terrestrial areas required for nesting and movements among wetlands. Although general wetland protection measures could indirectly benefit Blanding's turtles, such measures do not take into account the biology of the species and are therefore likely to be insufficient for long-term conservation.

Similarly, Blanding's turtles fall under the "non-game" classification in those states where they occur, but such designations simply prohibit direct take of animals, are often poorly enforced, and do not address the main threats, which we discuss later in this assessment. Thus, in themselves, non-game regulations are not likely to substantially benefit conservation of Blanding's turtles. State-level threatened and endangered status (**Table 1**) can supplement non-game designations and contribute to conservation efforts, as it has done in Nova Scotia (see below), but the effectiveness of such depends on a variety of factors, including funding of state-level enforcement activities, provisions for habitat conservation, cooperation with other states and federal

agencies, and the ability of state law to impact private landowners. A complete evaluation of the effectiveness of state-level programs is beyond the scope of this assessment, but it is the opinion of the authors that state protections are currently insufficient to insure the range-wide conservation of Blanding's turtles.

The most extensive ongoing management plan for Blanding's turtles is that for Kejimkujik National Park, Nova Scotia, Canada (Herman et al. 1998, 1999). In general, concerns and management proposals appear to apply to most Blanding's turtle populations. In 1999, there were an estimated 130 adult turtles in Kejimkujik Park and 60 adults outside the park. Because the population is near the northern limit of the species' range, low soil temperatures and short summers found in Nova Scotia limit developmental rates of embryos (Standing et al. 2000). Because some females nest on lake beaches, nest flooding associated with storms may be a serious problem. Also, extensive predation of eggs and juveniles from beach nests results in low recruitment, and some development of park facilities in or near nesting areas may be reducing limited nesting habitat.

Blanding's turtles are protected under the Nova Scotia Wildlife Act and the Nova Scotia Endangered Species Act, and they may not be disturbed or collected in any National Park. In 1999, the National Recovery Plan's goals were to realize a self-sustaining population within the species' historical range in Nova Scotia by restoring habitats and ecological processes and by reducing or removing threats to the turtles. Programs supported by this plan include:

- head-starting and releasing juveniles raised in captivity
- determining the genetic structure and variation in Kejimkujik Park and other populations throughout the species' range
- identifying critical habitats for overwintering, foraging, nesting, and juvenile recruitment
- removing a dam at Grafton Lake to restore water depths to historical levels
- involving and educating the public through outreach programs
- creating a Blanding's turtle website
- examining land use in private lands adjacent to Kejimkujik Park.

In the Weaver Dunes area of southeastern Minnesota, turtle crossing signs were installed on a paved road that runs between Blanding's turtle nesting areas and wetlands. Recently the Valentine National Wildlife Refuge (NWR) in Nebraska also installed turtle crossing signs and chain link drift fences to guide Blanding's turtles through culverts under U.S. Highway 83. The refuge has funded a study to evaluate the effectiveness of culverts as road crossings (Lang 2004).

Biology and Ecology

Description and systematics

The full classification of the Blanding's turtle is as follows: Kingdom - Animalia, Phylum - Cordata, Class - Reptilia, Order - Testudines, Family - Emididae, Genus - *Emydoidea*, Species – *blandingii* (Holbrook 1838). The genus name is derived from the Greek *emydos* meaning freshwater turtle and the suffix *oides* denoting likeness with reference to the genus *Emys*. The species name is after Dr. William Blanding, a Philadelphia naturalist that first observed the species.

The taxonomy and phylogeny of Blanding's turtle is currently being revised based on molecular studies (Bickham et al. 1996, Burke et al. 1996, Lenk et al. 1999, Feldman and Parham 2001, Feldman and Parham 2002) and recent discovery of fossils (Hutchison 1981, Holman 1987, Holman 1995). As a result, the Blanding's turtle and the western pond turtle (*Clemmys marmorata*) may be placed in the same genus (*Emys*) as the European pond turtle (*E. orbicularis*). However, it was recently suggested that the recommendation to lump *Emydoidea* and *Actinemys* under the genus *Emys* was incorrect because the authors were not aware of the arguments provided by Holman and Fritz (2001). Crother et al. (2003) recommend the retention of separate genera for *Emys* and *Emydoidea*.

Blanding's turtles are medium-sized (carapace length [CL] of adults 150 to 270 mm in length). Their major feature is a bright yellow chin, throat, and ventral portion of a very long neck (**Figure 1**). The carapace is highly domed and has yellow flecks on a dark background. Plastrons range from a yellow center with dark patterns on the outer edges of each scute, to almost all dark. Although flexibility of the plastron

Figure 1. Photographs of Blanding's turtles showing (**A**) yellow throat and neck (Photograph by Janett Hostetter), (**B**) 70 year old female on the University of Michigan's Edwin S. George Reserve (Photograph by Justin Congdon), and (**C**) a young adult female (Photograph by Owen Kinney).

hinge between the pectoral and humeral scutes varies substantially among populations, most Blanding's turtles can close their anterior plastron, and to a lesser extent their posterior plastron (primarily due to flexibility between the abdominal and femoral scutes).

Hatchlings are essentially miniature adults except for the following characteristics:

- the carapace has a vertebral keel and lacks or has reduced markings
- they are almost circular in shape
- they have very long tails relative to their body length.

Hatchlings range from 29 to 35 mm in length and weigh approximately 10 g (Congdon et al. 1983, Congdon et al. 2000, Pappas et al. 2000). It has been reported that the yellow undersurface of the neck does not appear until 3 years of age (Vogt 1981). However, in Minnesota and Michigan the chin and throat of hatchlings have the same yellow markings (albeit less bright) as those of adults (Congdon unpublished data).

There is only slight sexual size dimorphism, and adults of both sexes are similar in body size and weight (Graham and Doyle 1977, Congdon and van Loben Sels 1991, Rowe 1992b, Germano et al. 2000, Pappas et al. 2000), but males may be slightly larger and heavier. However, there are distinct shape differences between sexes. For a given length, shell height is taller and more domed in females. Males have longer tails, heavier tail bases, and concave posterior plastrons (Gibbons 1968) that result in the posterior section (and the entire plastron) being shorter (Congdon and van Loben Sels 1991, Rowe 1992b, Germano et al. 2000, Pappas et al. 2000). In addition, there are sexual shape differences associated with the width of the plastron and bridge scute morphology (connecting area between the carapace and plastron; Pappas et al. 2000).

Across their range, Blanding's turtles are similar in body size, with the exception of individuals in central-Minnesota where adult males and females averaged about 50 mm larger in body size (>250 mm CL; Sajwaj et al. 1998) than are adults in all other known populations (**Table 2**). Mean and maximum body sizes of adults from Grant and Arthur counties in Nebraska (Rowe 1992b) and from Valentine NWR in Cherry County, Nebraska (Germano et al. 2000) were similar (**Table 3**). Adults from both studies were larger than those from all other populations (Massachusetts, DePari et al 1987; Ontario, MacCulloch and Weller 1988; Michigan, Congdon and van Loben Sels 1991; and southeastern Minnesota, Pappas et al. 2000) with the exception of Camp Ripley in Minnesota (Piepgras and Lang 2000, Sajwaj and Lang 2000) where adults were substantially larger than those in Nebraska.

Distribution and abundance

The major portion of the Blanding's turtle's range is centered in the Great Lakes region of Canada and the United States (**Figure 2**). Relatively large populations appear to occur in Michigan (Gibbons 1968, Congdon and Gibbons 1996), Wisconsin (Ross 1989, Ross and Anderson 1990), Minnesota (Pappas et al. 2000), and Nebraska (Rowe 1992b, Germano et al. 2000). Recently, a population of greater than 5,000 adults was identified in southeastern Minnesota (Pappas

Table 2. Body size and mass of Blanding's turtles from well-studied populations.

		Carapace length (mm)				Body mass (g)				
Location	**Sex**	**Mean**	**SE**	**Range**	**N**	**Mean**	**SE**	**Range**	**N**	**Source**
Nova Scotia	M and F	216	not given	not given	15	1295	not given	not given	15	Power 1989, Standing et al. 1999
Edwin S. George Reserve, Michigan	F	187	0.98	161–217	208	1032	13.32	752–1510	137	Congdon et al. 1993, 2000
	M	194	1.77	171–231	68	1097	2.55	854–1488	38	
Weaver Dunes, Minnesota	F	197	0.4	164–229	670	1079	8.6	690–1790	408	Pappas et al. 2000
	M	213	1.8	177–238	59	1291	45.4	750–1810	43	
Ft. Ripley, Minnesota	F	245	2.0	221–279	42	2200	52.0	1610–3000	42	Sajwaj et al. 1998
	M	260	2.3	228–277	23	2440	57.0	1650–3100	23	
Western Nebraska	F	209	2.4	177–235	35	1336	53.2	740–1820	29	Rowe 1992b
	M	201	4.5	177-238	17	1111	75.3	690–1780	17	

Table 3. Body sizes of Blanding's turtles from Nebraska. (Data from Grant and Arthur counties, Rowe 1992b; from Cherry County, Germano et al. 2000).

			Carapace length (mm)			Body mass (g)		
County	**Site**	**Sex**	**Mean**	**Range**	**N**	**Mean**	**Range**	**N**
Grant	Beem and Doc Lake	F	209.2	177–235	35	1336.0	740–1820	29
Arthur	Swan Lake	M	200.8	177–238	17	1111.0	690–1780	17
Cherry	Valentine National Wildlife Refuge	F	186.1	162–213	19	910.0	630–1380	13
		M	203.7	174–232	21	1174.0	750–1680	19

et al. 2000), and other large populations may exist in Nebraska. Based on a recent survey, over 135,000 occur in the Valentine NWR area in Nebraska (Lang 1994). The Samuel R. McKelvie National Forest and Nebraska National Forest at Halsey are two Region 2 units also situated in the Sandhills and within a relatively small distance from the Valentine NWR. Studies comparing large and small populations across the range of the species would provide useful information on factors limiting population distribution and size.

Populations in Nova Scotia, New England, New York, Pennsylvania, northern Ohio (restricted to areas along Lake Erie), northern Illinois, Indiana, Missouri, and Iowa are small and disjunct. The species is considered disjunct in South Dakota with only two individuals captured in the Big Sioux River area near Sioux Falls (Backlund 1994).

Population trends

Some archeological studies indicate that historical extirpation of peripheral populations of Blanding's turtle have occurred (Preston and McCoy 1971, Jackson and Kaye 1974, Van Devender and King 1975). Early reports indicate that Blanding's turtles were abundant in prairie areas of Illinois, Indiana, Iowa, and Kansas, but their populations had been substantially reduced by the early to mid-1900s (Cahn 1937, Broadman et al. 2002). Observed declines in prairie areas were probably due to the drainage of small and shallow wetlands for agriculture. In many urbanized areas throughout their range, populations of Blanding's turtles have been extirpated or severely reduced and isolated.

Activity and movement patterns

Four major categories of movement occur in Blanding's turtles:

- those associated with winter hibernation that are made primarily by adults and older juveniles in spring and fall (Pappas et al. 2000)
- nesting movements of females (Linck et al. 1989, Congdon et al. 1993, Butler and Graham 1995, Linck and Moriarty 1997, Standing et al. 1997, Kinney 1999)
- hatchlings dispersing from nests (Butler and Graham 1995, Standing et al. 1997, Pappas et al. 2000)
- movements among wetlands primarily in spring and summer (Ross and Anderson 1990, Rowe and Moll 1991, Kinney 1999).

In years with high rainfall that maintain high water levels in wetlands, movements of Blanding's turtles in relation to overwintering are reduced or do not occur (Rowe and Moll 1991). For example, on the ESGR in southeastern Michigan, fewer painted turtles and Blanding's turtles made movements associated with overwintering in wet compared to dry years (Sexton 1957, Scribner et al. 1993, Sexton 1995). Also, there is evidence that the increased risk of death associated with movements may lead to a reduced propensity for movements in the turtles remaining in populations (Dorff 1995, Rubin et al 2001a).

The following summarizes activity patterns of Blanding's turtles in southeastern Minnesota (Pappas et al. 2000) and Michigan. In Minnesota, emergence of adults from overwintering occurred between 13 March and 8 April, and the beginning of nesting began an average of 80 days later (**Table 4**). Over 4 years in Minnesota, nesting seasons began between 26 May and 12 June and averaged 17 (min = 16 - max = 20) days in duration. Over 23 years in Michigan, nesting began between 15 May and 9 July, and nesting seasons averaged 28 (min. = 18 - max. = 42) days (Congdon et al. 2000). Warmer temperatures in the spring resulted in earlier nesting seasons for Blanding's turtles (Congdon et al. 1983).

The predominant pattern is for Blanding's turtle hatchlings to emerge from nests (**Figure 3b**) in the fall (Congdon et al. 1983, Butler and Graham 1995,

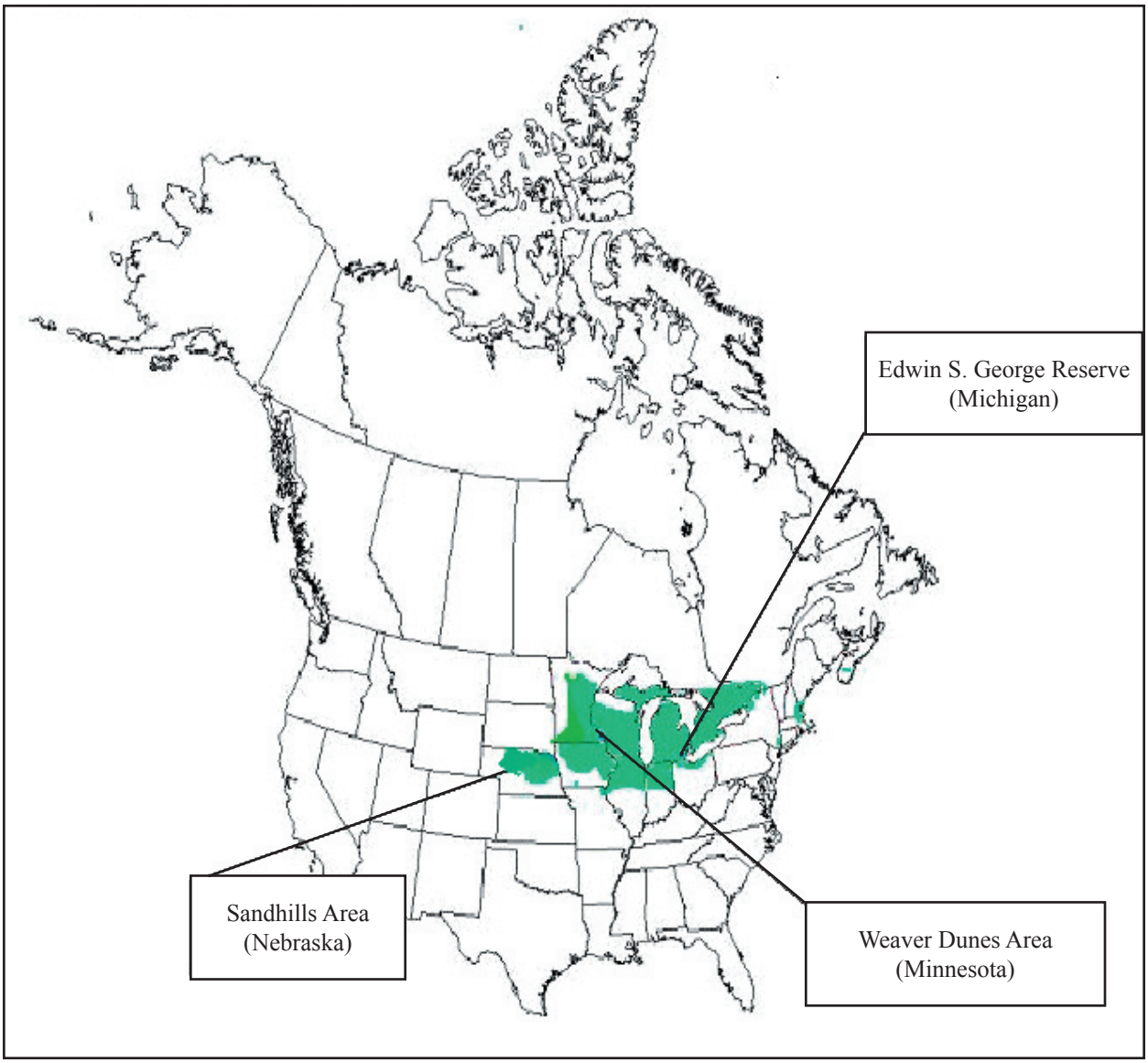

Figure 2. Range map of Blanding's turtles for North America, with locations of areas of major study of the species. The largest known population of the species occurs on the Valentine National Wildlife Refuge in the Nebraska Sandhills, a region in north-central Nebraska that also includes the Samuel R. McKelvie and Halsey units of the Nebraska National Forest in Region 2.

Standing et al.1997, Pappas et al. 2000). In Minnesota, hatchling emergence took place between mid-August and the end of September (approximately 27 days), and the interval between nesting and hatchling emergence activity averaged approximately 82 days (**Table 4**). Capture of hatchlings at drift fences occurred an average of 75 days after nest construction at Weaver Dunes, Minnesota. Time from nest construction to hatchling emergence from nests averaged 84 days in southeastern Michigan (Congdon et al. 1983) and 94 days in Nova Scotia (Standing et al. 1999) (**Table 4**). A few hatchlings captured at drift fences in the early spring in southeastern Minnesota and Michigan indicated that successful overwintering in terrestrial environments can occasionally occur in nests or at other sites (Congdon et al. 1983, Butler and Graham 1995, Standing et al. 1997, Pappas et al. 2000). Two observations support the possibility of terrestrial overwintering of Blanding's turtle hatchlings. First, hatchlings can tolerate temperatures of -2 °C for at least 48 hours (Packard et al. 1999). Second, snow cover provides enough insulation to prevent soil temperatures in southeastern Michigan from dropping below -2 °C during some winters, but in years without adequate snow cover winter mortality occurs (Nagle et al. 2000). In Nova Scotia, Blanding's turtle hatchlings have been

Table 4. Reproductive characteristics of Blanding's turtles from populations covering much of their distribution.

	Clutch Size			Hatchling size (mm)				Nest to hatchling emergence (days)			
Location	**Mean**	**Range**	**N**	**Mean**	**Range**	**N**	**Nesting season**	**Mean**	**Range**	**N**	**Source**
Nova Scotia	10.0	2–15	60	33.3	29.7–36.0	135	15–24 June	97.0	85–110	35	Power 1989, Standing et al. 1999
Long Point, Ontario	7.7	5–12	39	not given	not given	not given	Mid-June–Early July	not given	not given	not given	Petokas 1987, MacCulloch and Weller 1988
Grenadier Island, Ontario	12.6	8–18	74	33.9	31.5–36.0	27	3 June–1 July	not given	not given	not given	Petokas 1987
Maine	9.8	5–13	9	32.7	29.7–35.9	6	10–20 June	94.0	68–118	23	Joyal et al. 2000
Massachusetts	13.0	8–17	95	34.6	not given	235	not given	not given	not given	not given	Graham and Doyle 1979, Butler and Graham 1995
Southeast Michigan	10.0	2–19	759	35.0	26.0–39.0	872	15 May–9 July	84.0	73–104	16	Congdon et al. 1983, Congdon et al. 2000
Southeast Minnesota	9.8	6–15	114	34.5	not given	60	26 May–25 June	82.0	74–92	not given	Pappas et al. 2000
Central Minnesota	17.7	11–24	31	not given	not given	not given	10 June–11 July	83.0	77–89	not given	Sajwaj et al. 1998
Nebraska	14.9	8–22	17	not given	not given	not given	not given	not given	not given	not given	Rowe 1992b

Figure 3. Photographs of Blanding's turtle (**A**) throwing sand with front legs prior to picking a nest site (photograph by Roy Nagle), (**B**) hatchling emerging from a nest in early September (photograph by Justin Congdon), and (**C**) nest being destroyed by a raccoon (photograph by Justin Congdon).

observed to avoid open water following nest emergence and move inland toward shallower wetlands (Standing et al. 1997).

As data from more studies accumulate, it has become apparent that Blanding's turtles are more active at low temperatures than previously suspected. On the ESGR, Blanding's turtles were active within wetlands until early December and emerged as early as 1 March, when body temperatures of captured turtles were less than 3 °C (Sexton 1995). However, movements between wetlands appeared to be restricted until water temperatures reached 8 °C. In Minnesota, courtship activity was observed in March, with individual body temperatures below 3 °C (M. Pappas personal communication 2002).

Habitat

Wetland habitat

Blanding's turtles require a combination of the following habitat elements:

- relatively permanent aquatic areas for long-term residence
- vernal pools and temporary wetlands for foraging and as refuges during terrestrial activities
- terrestrial areas with well-drained soils with minimal vegetation cover for nesting and migration corridors.

Further, to be effective in buffering populations, terrestrial areas surrounding wetlands occupied by Blanding's turtles need to be larger than required by more aquatic species (see below; Burke and Gibbons 1995, Kinney 1999, Semlitsch and Bodie 2003).

Based on the Cowardin wetland classification system, a description of which can be found at http://www.water.ncsu.edu/watershedss/info/wetlands/class.html, Blanding's turtles do not occupy *Marine* or *Estuarine* wetlands, nor are they found in strictly defined *Riverine* habitats. They do occupy both *Lacustrine* and *Palustrine* wetlands. They occur in a variety of wetland types including river oxbows, marshes (**Figure 4a**), swamps, sloughs, permanent bogs, edges of deep and large lakes, shallow lakes, glacial potholes, and ponds. Blanding's turtles also make use of temporary wetlands such as vernal pools (**Figure 4b**, **Figure 4c**), sink holes, ditches, and bogs, and they appear to utilize these habitats as seasonal sources of food. The relative duration and frequency of occupation of the various types of wetlands appear to be influenced by the season of the year; the size, type, and quality of the wetland; and its proximity to other wetlands. On the ESGR, Blanding's turtles are most frequently found to be associated with sedge clumps and fallen trees and in areas of wood swamps and vernal pools that have some exposure to sunlight compared to areas with closed canopies.

Blanding's turtles are not frequently found in open, deep-water areas of lakes, but they do use vegetated areas in the edges of deep lakes and throughout shallow lakes. Wetlands covered with cattail stands were not used in Wisconsin, but cattail stands with open water spaces were used (Ross and Anderson 1990). In southeastern Minnesota, Blanding's turtles selected areas with emergent vegetation and avoided or used less frequently woody terrestrial areas, agricultural areas, some aquatic areas such as open water, and dense floating mats of vegetation (Hamernick 2001). In Nebraska, wetland habitats with Blanding's turtles (Rowe 1992b) were described as shallow, soft-bottomed lakes with primary submergent vegetation (e.g., *Potamageton pectinatus* and *Myriophyllum spicatum*) surrounded by emergent vegetation (e.g., *Scirpus acutus*, *Sagittaria cuneata*, and *Carex* spp.). Ponds located in Logan County, Nebraska were soft-bottomed, primarily with submergent vegetation (e.g., *M. spicatum*, *Ceratophyllum demersum*, and *Ranunculus trichophyllus*) and shoreline stands of emergent vegetation (e.g., *Typha latifolia*, *Scirpus acutus*, and *Carex* spp.).

Young juveniles are found in a narrower range of habitats than are adults (Pappas and Brecke 1992, Barlow 1999). This has important conservation significance, because it is necessary to maintain separate juvenile habitats for adequate recruitment into the adult population. At Weaver Dunes, Minnesota, young Blanding's turtles preferred shallow water areas (<50 mm depth) in sedge tussocks and alder sedge thickets. Alder thicket canopies of <4 m height were preferred by smaller juveniles (mean CL = 77.7 mm), whereas larger juveniles (mean CL = 98.5 mm) were found in areas with no canopy (Pappas and Brecke 1992). Juvenile Blanding's turtles in northeastern Indiana preferred sedge and mixed cattail-sedge areas compared to other areas with less cover, and both juveniles and adults used open water areas infrequently (Barlow 1999).

In Michigan, the deepest areas of the shallow wetlands are used for overwintering by painted

Figure 4. Photographs of Blanding's turtle habitats. (**A**) open marsh habitat (East Marsh) on the Edwin S. George Reserve in southeastern Michigan (photograph by Justin Congdon), (**B**) pothole swamp (photograph by Roy Nagle), and (**C**) wood pond (photograph by Owen Kinney) used for harvesting seasonal food resources and as temporary refuge during terrestrial migrations.

and Blanding's turtles (Sexton 1957, Sexton 1995). Substrates below shallow areas have the potential to freeze and kill Blanding's turtles that are not as resistant to ice crystal formation in cells as are painted turtles, and overwintering in deeper water may pose a problem related to anoxia (Packard et al. 1999, Dinkelacker 2004). The number of individuals that overwinter in wetlands on the ESGR is highest in years with high rainfall amounts and high water levels. When water levels are low, turtles move to the deepest area of a dredged pond to overwinter. Another overwintering site used by Blanding's turtles (and painted and snapping turtles) is in the backwater area of a local creek. Turtles congregate in the muddy substrate of backwater areas out of the main current and presumably where they will not be washed out of the substrate during winter or early spring floods. Some individuals overwinter on land in Illinois (Rowe and Moll 1991) and Ohio (Conant 1938); however, overwintering on land increases the risk of freezing. Dead Blanding's turtles with no injuries or indication of predation were found in early spring on land adjacent to an overwintering site in Minnesota (M. Pappas personal communication 2002). The turtles were frozen after moving onto land, or they emerged, moved onto land, and subsequently died from problems that arose while overwintering.

Terrestrial habitat

One area of uncertainty is the difference between the perception of Blanding's turtles as terrestrial or semi-terrestrial in the early literature (Surface 1908, Cahn 1937, Carr 1952), versus more contemporary reports indicating that they are primarily aquatic with seasonal terrestrial movements (Gibbons 1968, Graham and Doyle 1977, Congdon et al. 1983, Kofron and Schreiber 1985, Rowe 1987, Ross and Anderson 1990, Rowe and Moll 1991, Pappas et al 2000). Early literature almost always mentions that among populations, Blanding's turtles make substantial but variable use of terrestrial habitats. For example, Garman (1892) states that the Blanding's turtle is more often found in water than on land but then describes it as an essentially terrestrial species. The Blanding's turtle was described by Surface (1908) as ". . . a land animal, living in damp fields near water." And Cahn (1937) states that the Blanding's turtle "is a semi-aquatic turtle; in certain regions it is largely a terrestrial species, while in others it is almost entirely aquatic in its habits."

Recent studies indicate that Blanding's turtles are more aquatic than older studies describe. Based on available data, the authors hypothesize that in the past there may have been more inter-population variation in the degree of terrestrial habitat use, and over time the loss of populations making extensive use of terrestrial habitats has been reduced. It may be that early observations of extensive terrestrial movements seasonally by nesting females were mistakenly interpreted as indicative of the species being primarily terrestrial (Pope 1939, Lagler 1943, Gibbons 1968, Kofron and Schreiber 1985). Another possibility is that individuals with a strong propensity to move have recently been strongly selected against (see Extrinsic Threats section), and now populations are made up of individuals that tend to restrict terrestrial movements.

After emerging from terrestrial nests, hatchling Blanding's turtles must solve problems related to dispersing from the nest site, orientation, and finding water. How hatchlings find water under a variety of conditions remains poorly understood at best; visual and olfactory cues and geotaxis have all been suggested as mechanisms (Noble and Breslau 1938, Ehrenfeld 1979). The majority of evidence from marine and freshwater turtles indicates that visual cues are the most important for hatchling orientation and dispersal from nest Ehrenfeld (1979). We do know that under a variety of conditions with respect to distance to water and exposure to dark or light horizons, the orientation and dispersal of Blanding's turtle hatchlings are not random, and hatchlings orient toward dark horizons (Pappas, Congdon, and Brecke unpublished data).

Regardless of perception, Blanding's turtles apparently do make more use of terrestrial environments than many other aquatic species. In general, a good terrestrial habitat would be one with open, well-drained soils for nesting and a mosaic of vernal pools, small wetlands, bogs, and marshes. Nesting generally occurs in terrestrial environments proximate to wetlands (see Nesting in the Reproductive biology section), but often not adjacent to the wetland where the female resides (Congdon et al. 2000). One common attribute of large populations of Blanding's turtles is that they are contiguous areas of well-drained soils that provide suitable nesting areas (Pappas et al. 2000, Lang 2004). Other than nesting females, much of the use of terrestrial habitat appears to be associated with movements among wetlands; however, other factors may also contribute to terrestrial habitat use.

Area requirements and landscape context

The size of activity areas and home ranges varies from less than 1 to 57 ha (**Table 5**), showing that Blanding's turtle area requirements are quite flexible. The lower limit of this range likely represents a

Table 5. Home range size of Blanding's turtles.

	Male home range size (ha)		Female home range size (ha)		
Location	**Mean**	**N**	**Mean**	**N**	**Source**
Wisconsin	0.8	2	0.6	5	Ross and Anderson 1990
Illinois	1.4	4	1.2	3	Rowe and Moll 1991
Southeast Minnesota	56.9	8	18.9	16	Hamernick 2001
Central Minnesota	7.8	6	7.9	13	Piepgras and Lang 2000
Overall mean	16.7	20	7.2	37	

minimum area required for basic survival of individual turtles. Factors such as high population densities and widely distributed resources (i.e., food, cover, mates) can require larger home ranges. At this point, we cannot determine the area required for optimal survival or population viability, because the number and size of activity centers and home ranges appear to be primarily influenced by the composition of the habitats where Blanding's turtles were studied, and none of the cited studies provide data on relationships between home range sizes and specific factors. For example, a study by Hamernick (2001) in southeastern Minnesota, where the total area of contiguous aquatic habitat was far greater than in all of the other studies, found home ranges of males and females that were 17 and 6 times, respectively, the mean values for all other home ranges reported in **Table 5**. Since many isolated wetlands and their surrounding terrestrial habitats are not that large, it is physically impossible for Blanding's turtles living in such areas to have home ranges of that size. Further study is necessary to clarify the relationship between habitat components (and their geographic relationship) with home range size and, moreover, reproductive success.

As noted above, core habitat requirements of Blanding's turtles include a resident aquatic area, peripheral aquatic areas, terrestrial nesting areas, and aquatic and terrestrial corridors for movement among wetlands and nesting areas. All of these components must occur in proximity to support localized populations of Blanding's turtles. Thus, in the absence of developments, roads with high traffic volumes, and heavy contamination, regions with an abundance of permanent wetlands interspersed with smaller temporary wetlands, and nearby upland areas with well-drained soils appear to be the places that can support stable (but not necessarily large) populations of Blanding's turtles. The spatial distribution of the core required habitats units may influence home range size, resource availability, movement patterns, and levels of mortality. Roughly speaking, areas with few and widely-spaced permanent wetlands and few temporary wetlands are not suitable, but we cannot currently define with more precision at what level habitat dispersion becomes sufficient to limit the viability of Blanding's turtle populations.

Seasonal changes in activity or habitat use

Certain features of Blanding's turtle activities change with the season of the year (**Table 6**), and this can therefore alter outcomes of management and conservation programs. Blanding's turtles often make extensive movements associated with 1) overwintering (Spring and Fall), 2) taking advantage of resources in ephemeral wetlands in early Spring, 3) nesting (mid-May to mid-July, and 4) dispersal of hatchlings

Table 6. General categories and phenology of Blanding's turtle activities in USDA Forest Service Region 2, as estimated by the lead author.

Activity	Timing and duration
Overwintering	November - March
Spring emergence	March
Peak mating	March - April
Spring dispersal	April – early May
Nesting	late May – early July
Hatchling emergence and dispersal from nests	late August - September
Movement to overwintering site	late September - October
Enter winter dormancy	November

from nests (late August - September). Movements of Blanding's turtles are greater during wet periods than dry periods. Individuals in the youngest age-class of juvenile Blanding's turtle are found in a narrower range of habitats that are associated with shallow water (Pappas and Brecke 1992), making them more vulnerable to changes in water levels (e.g., seasonal changes, drought, anthropogenic impacts).

Food habits

Blanding's turtles have been reported as omnivorous (Cahn 1937, Conant 1938, Carr 1952, Graham and Doyle 1977) and primarily carnivorous (Lagler 1943, Penn 1950, Kofron and Schreiber 1985, Rowe 1992a). In New England, Penn (1950) examined 92 Emydoidea and found that they had consumed 58 percent crayfish by volume. DeGraaf and Rudis (1983) report that crayfish and other crustaceans comprised about 50 percent of the diet of Blanding's turtles, insects 25 percent, and other invertebrates and vegetable matter 25 percent. Blanding's turtles are also known to eat fish, fish eggs, and frogs (Kofron and Schreiber 1985). In Nova Scotia where crayfish are absent, diets include aquatic insects, such as dragonfly nymphs, aquatic beetles, snails, and fish (Bleakney 1963). In Illinois, Rowe (1992a) found that diets were made up primarily of snails (35.0 percent by volume) followed by crayfish (19.3 percent), earthworms (12.7 percent), and insects (10.3 percent). Some vertebrate food (e.g., fish, tadpoles, frogs, birds) was found in most studies.

Diets are sometimes comprised of food items found in aquatic and terrestrial habitats (Rowe 1992a). While on land, Blanding's turtles have been reported to eat berries, grasses, succulent vegetation, leaves, earthworms, insects, insect larvae, and slugs. In all studies, some plant material was found in Blanding's turtle diets.

Blanding's turtles apparently utilize vernal pools and small temporary wetlands as seasonal sources of food and as mating sites (Pappas and Brecke 1992, Dorff 1995, Linck and Moriarty 1997, Kinney 1999, Pappas et al. 2000). It appears that older Blanding's turtles with higher reproductive output more efficiently exploit such temporary and seasonal food resources (Congdon et al. 2003).

Reproductive biology

Breeding behavior

The following descriptions of the breeding activity of Blanding's turtles are primarily based on the extensive unpublished observations made by Michael Pappas over the past five years in southeastern Minnesota. Breeding behavior begins in March and April as the ice cover on ponds starts to open and water temperatures reach 4 to 6 °C. While breeding behavior was observed in every month of the year except December, January, and February, most breeding activity occurs in the early spring and in the fall when turtles are concentrated at hibernacula. Male turtles appear to become active earlier as they emerge from the mud and begin "searching activity," which includes moving slowly along the bottom of the pond with their necks extended and heads swinging in a left?right arc of approximately 45 degrees. Males may be seeking visual or olfactory stimuli to help locate females, but the initiation of most chase phases (see following) appeared to be initiated by visual detection of moving females within 1 to 6 m.

After a male locates a female, the "chase phase" of breeding begins. Males pursue unreceptive females until they are overtaken, or until visual contact is lost. Some females appeared especially wary and rapidly moved away from approaching males.

Once a female is overtaken, she is mounted from the rear without any apparent courtship. In the mounted position, the male is on top with forelimbs and hind limbs extended to allow his claws to grasp the underside of the female's carapace. Once mounted, the male begins a series of behaviors that appear to persuade the female to present her cloaca for intromission. Males also extend their necks down at a 90-degree angle in front of the female to keep her head withdrawn into her shell (head chinning; Baker and Gillingham 1983). In addition, the male waves his head in front of the female's head and butts or bites to keep her head withdrawn (head waving; Baker and Gillingham 1983). In some cases, the mounted male rises above the carapace of the female and thrusts downward forcibly with his plastron (shell thumping; Baker and Gillingham 1983).

Female turtles can store sperm for more than 2 years (Gist et al. 2001), and clutches of eggs of Blanding's turtles are sometimes fertilized by more than one male (Osentoski 2001).

Nesting

Factors such as exposure to sunlight, low vegetation cover, well-drained soils, and proximity to wetlands, combine to determine the quality of a nesting area. Nests are constructed in open areas exposed to sunlight and with sparse vegetation (Congdon et al. 1983, Linck et al. 1989, Butler 1997, Kiviat 1997, Sajwaj et al. 1998, Kinney 1999, Standing et al. 1999, Congdon et al. 2000). In Maine, nests are sometimes excavated in soil-filled cracks in bedrock (Joyal et al. 2000). Nests constructed in some grassy areas or adjacent to some plants (e.g., wild grape) become "root bound," and hatchlings are unable to dig out of these nests and die. Many Blanding's turtles nest in areas with disturbed soils, such as gardens, driveways, roadways of dirt roads, roadsides, railroad embankments, and fire lanes. Some nests in disturbed areas are at risk of being destroyed by garden tools, farm machinery, road graders, and other motor vehicles. Four percent of observed nests on the ESGR were washed out or deeply buried during thunder storms; others that were constructed in low-lying areas were covered with standing water, and developing embryos apparently drowned.

A common attribute of large populations of Blanding's turtles in the Weaver Dunes area of Minnesota and the Valentine NWR in the Sandhills of Nebraska is the large contiguous area of well-drained soils that provide extensive, high-quality nesting areas (Pappas et al. 2000, J. Lang personal communication 2002).

Reproductive phenology

Blanding's turtles emerge from overwintering sites and become active and mate as the ice melts in early spring (**Table 6**; Pappas et al. 2000). Males and females frequently make long-distance aquatic and terrestrial movements in association with foraging, mating, nesting, and selecting overwintering sites (Congdon et al. 1983, Ross and Anderson 1990, Rowe and Moll 1991, Sexton 1995, Kinney 1999, Piepgras and Lang 2000, Pappas et al. 2000, Hamernick 2001). Movements made just prior to the nesting season of up to 15 km have been recorded in Minnesota (J. Lang and M. Pappas, unpublished data).

Nesting seasons range from early-May through mid-July (Congdon et al. 1983, Congdon et al. 2000; also see **Table 4** for southeastern Minnesota [Pappas et al. 2000]), and higher average temperatures during spring result in early initiation of nesting activity (Congdon et al. 1983). Some females make extensive terrestrial migrations directly associated with nesting. Movements made before nesting can be longer than 7 days and consist of visits to wood pools, temporary marshes, previous nest sites, and finally to the area where the nest is constructed (Congdon et al. 1983, Ross and Anderson 1990, Piepgras 1998, Kinney 1999, Congdon et al. 2000, Pappas et al. 2000, Piepgras and Lang 2000). Females may nest over a kilometer from their residence wetland (>4 kilometers for a female from the ESGR in Michigan (Kinney 1999). Total nesting migrations of females from East Marsh on the ESGR averaged 6.75 days on land between 1982 and 1998 and greater than 10 days on land in 1999 (Kinney 1999). Ruben et al. (2001a) suggest that nesting migrations are less extensive in areas impacted by development and restricted by human disturbance.

Nesting migrations, pre-nesting activity (**Figure 3a**), and nest construction usually begin before dark, and most nests are finished after dark; however, on warm, rainy days nesting may occur at any hour of the day (Congdon et al. 1983, Congdon et al. 2000, Pappas et al. 2000). After nesting, some females return to wetlands during the night of nest construction if 1) the nest is relatively close to a wetland, 2) the nest was completed early in the evening, or 3) ambient temperatures remain high. When nests are relatively far from wetlands, when nest completion was late, or when ambient temperatures stay low, females seek refuge under leaf litter or in dense vegetation and then return to wetlands during daylight hours in subsequent days (Kinney 1999).

In southeastern Michigan and Minnesota, hatchlings emerged from nests from mid-morning to early afternoon in mid-August to early October (**Table 4**; 75 to 110 days after egg laying; Congdon et al. 1983, Congdon et al. 2000, Pappas et al. 2000). In about 50 of the nests, all hatchlings emerged in one day (synchronous emergence); in the other half of the nests, hatchlings emerged over 2 to 4 days (asynchronous emergence). Most hatchlings disperse from nest sites and move directly to water (Congdon et al. 1983, Butler and Graham 1995). However, some hatchlings may spend their first winter on land, but not necessarily in nests (Congdon et al. 1983, Congdon et al. 2000 Pappas et al. 2000). In Nova Scotia, where females

nest on beach areas adjacent to relatively large and cold water lakes, hatchlings avoid moving to open water and instead move inland to more protected and warmer wetlands (Standing et al. 1997, McMaster and Herman 2000, McNeil et al. 2000).

Fecundity and survivorship

Blanding's turtles have a suite of co-evolved life history traits that are associated with high adult survivorship and extended longevity and reproductive-lives that can exceed 50 years. In combination, Blanding's turtle life history/demographic traits (i.e., age at maturity, clutch size and frequency, age specific survivorships) result in cohort generation times that exceed 35 years, and the relative value of adult survival to population stability of approximately two times that of juvenile survival (Congdon et al. 1993); both of these are traits of very long-lived organisms. Comparative life history and demography studies of smaller (more typical) populations and large populations of Blanding's turtles such as those in southeastern Minnesota and Nebraska may reveal some of the mechanisms that regulate population size. Available information for reproductively significant metrics is noted below:

Fecundity: Adult females produce a maximum of one clutch per year, with 10 to 20 percent not reproducing every year, as found in a Michigan population where reproductive frequency of females was 0.8 clutches per year (Congdon et al. 1983, Congdon et al. 1993). Suggestions of production of second clutches (Gibbons 1968, Pritchard 1979, Ernst et al 1994) have not been substantiated in any population studied. Among populations of turtles with similar body sizes, mean clutch size is between eight and 12 eggs with a range of three to 20 eggs (Gibbons 1968, Graham and Doyle 1979, Congdon et al. 1983, Depari et al. 1987, MacCulloch and Weller 1988, Congdon and van Loben Sels 1991, Sajwaj 1998, Pappas et al. 2000, Lang 2004). These studies suggest that the average clutch size of Blanding's turtles from Nebraska (**Table 7**) is larger than that reported for most other populations (i.e., 17 eggs versus 10.6 in Nova Scotia, 7.7 in Ontario, 12.9 in Massachusetts, and 10.0 in Michigan); the exception is the central Minnesota populations, which averaged 17.7 eggs per clutch. In southeastern Michigan, the average clutch size of Blanding's turtles (10 eggs), combined with less than annual reproduction (no females produce more than one clutch of egg per year and approximately 20 percent of adult females skip reproduction in a given year), results in an annual fecundity of 4.0 female eggs per female based on the assumption of an equal hatchling sex ratio (Congdon et al. 1993, Congdon et al. 2000). In cases where hatchling sex ratios are biased, a female or male bias will increase or decrease, respectively, the actual annual fecundity. In southeastern Michigan, the frequency of reproduction increased with the age of females (Congdon et al. 2001). All things being equal, clutch sizes of large-bodied Blanding's turtles in central Minnesota (Sajwaj 1998) would result in an annual fecundity of 7 female eggs per female, almost double that found in other populations. Where adequate samples are available, clutch size increases significantly with body size of females within a population, but egg size is much less variable (MacCulloch and Weller 1988, Congdon and van Loben Sels 1991, Sajwaj 1998, Pappas et al. 2000). Since Blanding's turtles do not generally exhibit indeterminate growth, most of the within population variation in body size is due to variation in both juvenile growth rates and age at maturity (Congdon and van Loben Sels 1993). In a Michigan population, the oldest females (>70 years of age) reproduce more frequently and produce a slightly larger clutch than do younger females (Congdon et al. 2001). Preliminary data suggest that the same is true for older males (Osentoski 2001).

Age at maturity: Even among turtles, Blanding's turtles are long-lived, and in one population females delay maturity for 14 to 20 years (average for females17.5 years; Congdon et al. 1993). Males probably do not reach sexual maturity until 14 years of age in southeastern Michigan and Minnesota (Congdon

Table 7. Reproductive characteristics of female Blanding's turtles in Nebraska (Data from Rowe 1992b; hatchling wet mass from Rowe et al. 1995.

Trait	N	Mean	Range
Clutch size	17	14.9	8 - 22
Clutch mass (g)	9	168.4	92.4 - 235.9
Egg length (mm)	9	35.3	32.1 - 38.4
Egg width (mm)	9	23.9	21.8 - 25.1
Egg wet mass (g)	9	11.8	8.9 - 14.1
Hatchling wet mass (g)	2	7.7	—

and van Loben Sels 1991, Pappas et al. 2000). The slowest growing females reach maturity at later ages and at smaller adult body sizes (Congdon and van Loben Sels 1991, Congdon and van Loben Sels 1993). In populations occupying the northern limits of their range, no females reach maturity until they are at least 18 years of age (R. Brooks personal communication 2003). Body growth in adult Blanding's turtles continues only a few years after they reach sexual maturity (**Figure 5a**, **Figure 5b**); as a result, within population variation in adult body size is a primarily a function of variation in juvenile growth rates and time to attainment of sexual maturity (Congdon and van Loben Sels 1991, Congdon and van Loben Sels 1993).

Adult survivorship: Adult survivorship is high, and some adults reach ages in excess of 70 years (Brecke and Moriarty 1989, Congdon and van Loben Sels 1991, Congdon and van Loben Sels 1993, Congdon et al. 2001). Annual survivorship of adult Blanding's turtles in Michigan is over 96 percent, and compared to young adult females, the oldest females had higher survivorship (Congdon et al. 2001).

Juvenile survivorship: Due to the low number of individuals recaptured, survivorship of juveniles has been difficult to document for ESGR and most other populations studied. A stable cohort model indicated that annual survivorship of juveniles between 1 and 14 years of age has to be high (over 65 percent) to maintain a stable population (Congdon et al. 1993). However, because of high adult survivorship, the number of juveniles recruited into the adult population can be lower than that found in shorter-lived species and still be sufficient to maintain a stable population (Congdon and Gibbons 1990, Congdon et al. 1993, Congdon and Gibbons 1996).

Embryo survivorship: Over 23 years on the ESGR, predation of observed nests ranged from 40 to 100 percent (average 78.2 percent); it was less than 51 percent in 5 years and 100 percent in 9 years (Congdon et al. 2000). Predation rates on turtle nests are generally high, variable, and unpredictable, but because almost all turtles are long-lived, stable populations do not require high nest survivorships to maintain population stability (Congdon and Gibbons 1996). Far more critical is relatively high survivorship of juveniles through sexual maturity (Congdon et al. 1993, Dunham 1993, Congdon et al. 1994, Congdon et al. 2001, Congdon et al. 2003).

Genetic concerns

If exchange of individuals (and genes) among populations becomes less frequent, or impossible, then small, isolated populations of Blanding's turtles are certainly at risk of loss of genetic diversity through drift and inbreeding. Since females have potential reproductive lives of over 50 years, they could come into contact with their sons and daughters, and even grandsons and granddaughters as adults. If there are no mechanisms to prevent mating with offspring, then inbreeding would accelerate the loss of genetic variability and could result in expression of lethal recessive genes.

Using variation in randomly amplified polymorphic DNA, genetic variability among populations of Blanding's turtles was compared from 25 individuals in Illinois, 14 in Nova Scotia, eight in Michigan, and 12 in Wisconsin (Rubin et al. 2001b). Results indicated that levels of genetic variability (i.e., percent polymorphism, mean percent band sharing) were similar among populations in northern Illinois (small, isolated urban populations), Nova Scotia, and Wisconsin, but genetic variability was significantly higher in a larger and less isolated population in southeastern Michigan (ESGR). No unique bands were detected in northern Illinois populations, 16 were found in Michigan, five in Nova Scotia, and one in Wisconsin. Blanding's turtles in Nova Scotia, which have been geographically isolated from the species' main range for 4,000 to 8,000 years, were genetically differentiated from all other populations in the study (Mockford et al. 1999). A plan to artificially exchange individuals among the small, isolated populations may be needed to restore or to prevent further loss of genetic diversity.

Community ecology

Predators and competitors

In the absence of most large carnivores, an adult Blanding's turtle's risk of being seriously injured or killed by predators is low. However, adult females have been found injured (legs missing) or dead (legs and head missing) in nesting areas in about 5 of the 28 years of the ESGR study. At present, the major predator of adult Blanding's turtles on the ESGR appears to be raccoons; however, with inadvertent reintroduction, coyotes may also become a threat.

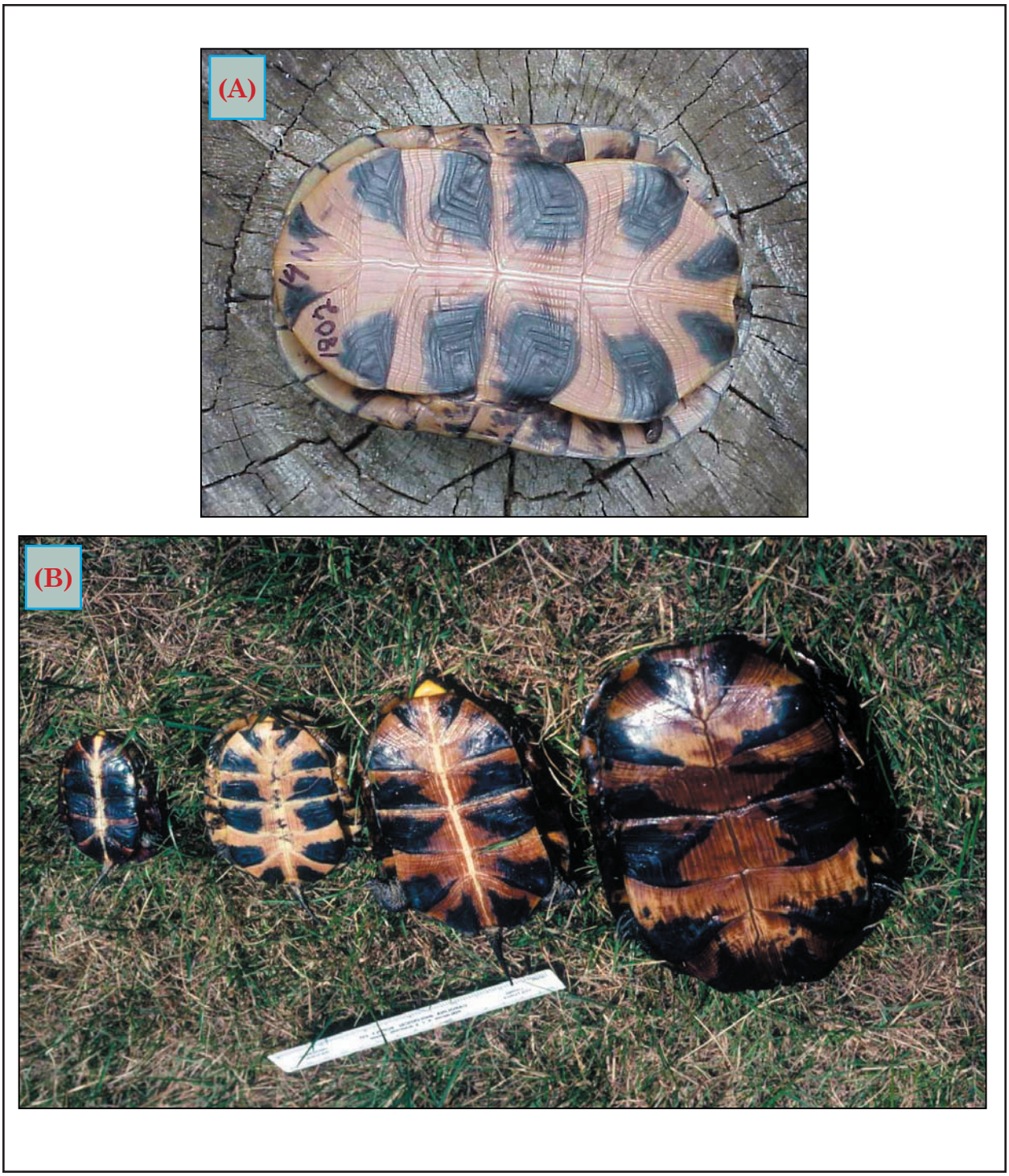

Figure 5. Blanding's turtle plastrons (**A**) juvenile Blanding's turtle approximately 10 years of age showing distinct growth lines that are laid down during the growing season each year, (**B**) Blanding's turtles of different sizes; the light-colored growth areas along the middle seam of the plastron on the three smaller-bodied juveniles indicate recent body growth, whereas the largest-bodied adult has not grown and does not have the light colored area. Photography by Justin Congdon.

Destruction of Blanding's turtle nests by predators is the primary cause of embryo mortality. The absolute amount of nesting habitat and the distance between nesting areas can be important since few and small nesting areas tend to concentrate nests and that often leads to high nest predation rates (Congdon et al. 1983, Congdon et al. 1987, Congdon et al. 2000). Over 23 years on the ESGR, predation of observed nests ranged from 40 to 100 percent (average 78.2 percent), and it was less than 51 percent in 5 years and 100 percent in 9 years (Congdon et al. 2000). Because most predators apparently locate nests by olfaction, eggs within nests are at highest risk of predation in the first 24 to 48 hours after nest construction (Congdon et al. 1983, Congdon et al. 2000). Predators of nests include raccoons, foxes, skunks, and burrowing mammals such as shrews and chipmunks (Standing and Herman 2000). In addition to mammals, crows, ants, and maggots destroy some nests; there has been one anecdotal report of predation by ground beetles (G. Casper personal communication 2005).

Hatchlings remaining in the nest after siblings have emerged are also at risk of being killed by predators. Predators of emerging and dispersing hatchlings include raccoons, foxes, skunks, opossums, burrowing mammals such as shrews and chipmunks, snakes, bullfrogs, and birds such as jays, crows, ravens, grackles, shrikes, kestrels, and other birds of prey (**Figure 3c**).

In developed areas, populations of turtle predators can exist at unnaturally high levels because of human subsidies (e.g., agriculture, garbage, elimination of top predators, inadvertent shelter, deliberate food supplements; Mitchell and Klemens 2000). For example, some people that have moved "out into the country" have established raccoon feeders with lights to observe them at night. A major reduction in fur trade in the late 1980s coupled with subsidized predator populations was associated with a substantial reduction in nest survival (Congdon et al 1993). At present, the primary regulators of raccoon populations in southeastern Michigan appear to be road mortality and cyclic diseases such as Parvo and Distemper. In urban areas, dogs, cats, and rats may destroy additional nests.

Almost nothing is known about the effects of competition in turtles. Since many wetlands are highly productive habitats, demonstrating negative effects attributable to competition may require densities of individuals greater than those found in natural settings. Potential competitors of Blanding's turtles include other species of turtles, and almost all other carnivores and omnivores that occupy wetlands.

Parasites and disease

Although some information on parasites exists for turtles (e.g., Barger 2004), little is known about whether negative effects on populations occur. Helminth parasite diversity in turtles was discussed by Esch and Gibbons (1967) and Ernst and Ernst (1977, 1980). Coccidian parasites, especially hemogregarines such as *Hepatozoon* spp., *Haemogregarina* spp. and *Babesiosoma* spp., are intracellular blood parasites of aquatic herps, including turtles (Siddall and Desser 1991). Other coccidians, such as *Eimeria* spp., are common intestinal parasites of turtles (McAllister et al. 1991). In addition, hemoflagellates, such as *Trypanosoma* spp., infect a wide range of aquatic turtles (Woo 1969). All three parasitic classes of the Phylum Platyhelminthes are represented in herps. Some common genera of monogenean parasites (*Pseudodiplorchis* and *Iagotrema*) are endoparasites of the urinary bladder of freshwater turtles, and *Neopolystoma* spp. infect the conjunctival sac of turtles (Platt 2000). Reptile trematodes are primarily associated with hosts from aquatic habitats, and freshwater turtles may be host to the lung flukes *Heronimus* spp. (Cox et al. 1988), as well as *Spirorchis* spp. that live in the circulatory system (Ernst and Ernst 1977, Esch et al. 1990, Platt 1992, Platt 2000). Roundworms (Phylum Nematoda) live in intestines of turtles, and common reptilian nematode genera are *Spironoura* and *Camallanus* (Esch and Gibbons 1967, Ernst and Ernst 1977, Ernst and Ernst 1980, Esch et al. 1990).

Three families of leeches, the Piscicolidae, the Hirudinidae, and the Glossiphoniidae, contain representatives that are blood-feeding, usually temporary ectoparasites of aquatic turtles, such as *Placobdella* spp. (Siddal and Desser 1991). Turtle leeches may be a significant component of macroinvertebrate diversity in some freshwater habitats.

Symbiotic and mutualistic interactions

There are no published mutualistic or symbiotic interactions between Blanding's turtle and other native species of plant or animal.

Envirogram

Andrewartha and Birch (1984) outline a "Theory of Environment" that seeks to organize the ecology

of a species into a coherent and logically connected web of factors that influence its ability to survive and reproduce. The heart of this endeavor is the envirogram, which orders these factors in a hierarchical dendrogram. The main stem of this dendrogram is comprised of a "centrum" of components that act directly on the species under consideration. From this centrum are branches that "trace pathways from distal causes in the web to proximate causes in the centrum." Region 2 has requested an envirogram for each species that it is being assessed. The envirogram we have developed for Blanding's turtle is presented in **Figure 6**. It is a useful heuristic tool to conceptualize how various factors might affect this turtle, but it must be duly noted that this is not the last word in what is important to this species' survival and reproduction. Our rationale for the included items is noted below.

Geological factors and successional history combine with topography and rainfall to determine the conditions that allow the formation of relatively permanent and temporary wetlands that are the major habitats of Blanding's turtles. The same geological and successional history can combine to provide the sandy, well-drained soils that are a major feature of terrestrial nesting areas for Blanding's and other turtles. Wetlands in turn provide the habitats where Blanding's turtles harvest their food resources. Forest succession can also result in reductions in habitat quality for Blanding's turtles. Shading of marshes by forest succession reduces heat input, productivity, and opportunities for turtles to bask aerially. In northern populations seasonal activity periods are limited and may be less than 6 months, and the period that food resources can be harvested and processed is substantially shorter. Aquatic or aerial basking that raises body temperatures above ambient air and water temperatures allows turtles to increase the rate that food is processed (Congdon 1989).

Forest succession also causes increased shading and reduction of soil temperatures in nesting areas. Lower incubation temperatures result in reduced rates of embryo development, and if low enough, they may result in late-term embryos or hatchlings that are not able to emerge from nests. Over the 31 years of study on the ESGR, such shading resulted in female Blanding's turtles, painted turtles, and snapping turtles abandoning several nesting areas (Congdon unpublished data).

Human land use activities such as creation of wetlands can be beneficial to Blanding's turtles just as wetlands destruction is detrimental. As a general case, both suburban and urban development and attendant alteration and contamination of wetlands appear to always be detrimental.

Predators of nests may initially benefit from forest succession because nest densities increase as suitable nesting areas are reduced in area. If the reduction continues, eventually the number of Blanding's turtles and their nests will decline. If unregulated, human predators (i.e., those exploiting turtles for meat or for the pet trade) can have a serious impact on turtle populations. In contrast, in areas where humans have developed and enforce regulations on the taking of turtles, populations should be sustainable.

Conservation of the Blanding's Turtle in Region 2

Extrinsic Threats

Because Blanding's turtles are long-lived, even compared to many other turtles (Brecke and Moriarty 1989, Pappas et al. 2000, Congdon et al 2001), potential direct and indirect extrinsic threats are magnified by co-evolved life history traits associated with longevity and delayed sexual maturity. High or chronic increases in mortality rates of adults, regardless of the cause, will negatively impact all populations, but they can severely impact smaller, isolated populations (**Table 8**, Appendix; Congdon et al. 1993, Congdon et al. 2001).

Resident and peripheral wetlands

Collectively, degradation or destruction of wetland habitats is responsible for the largest loss of Blanding's turtle populations throughout their recent range (Dahl 1990, Ross and Anderson 1990, Rowe and Moll 1991, Kinney 1999, Pappas et al. 2000). Destruction of core resident habitats impacts all stages of the life cycle and often has obvious consequences for resident turtles (i.e., death or emigration). Subsequent displacement of any species of turtle will often increase mortality rates during emigration and increase densities and potential impacts from competition among turtles at remaining resident wetlands if they are close enough to be reached.

Vernal pools and temporary wetlands are an important component of the Blanding's turtle's core habitat if they occur in conjunction with suitable terrestrial habitat discussed below. The impact of removing one or more temporary wetlands will depend on their number and distribution in an area. While the destruction of small, apparently unoccupied wetlands

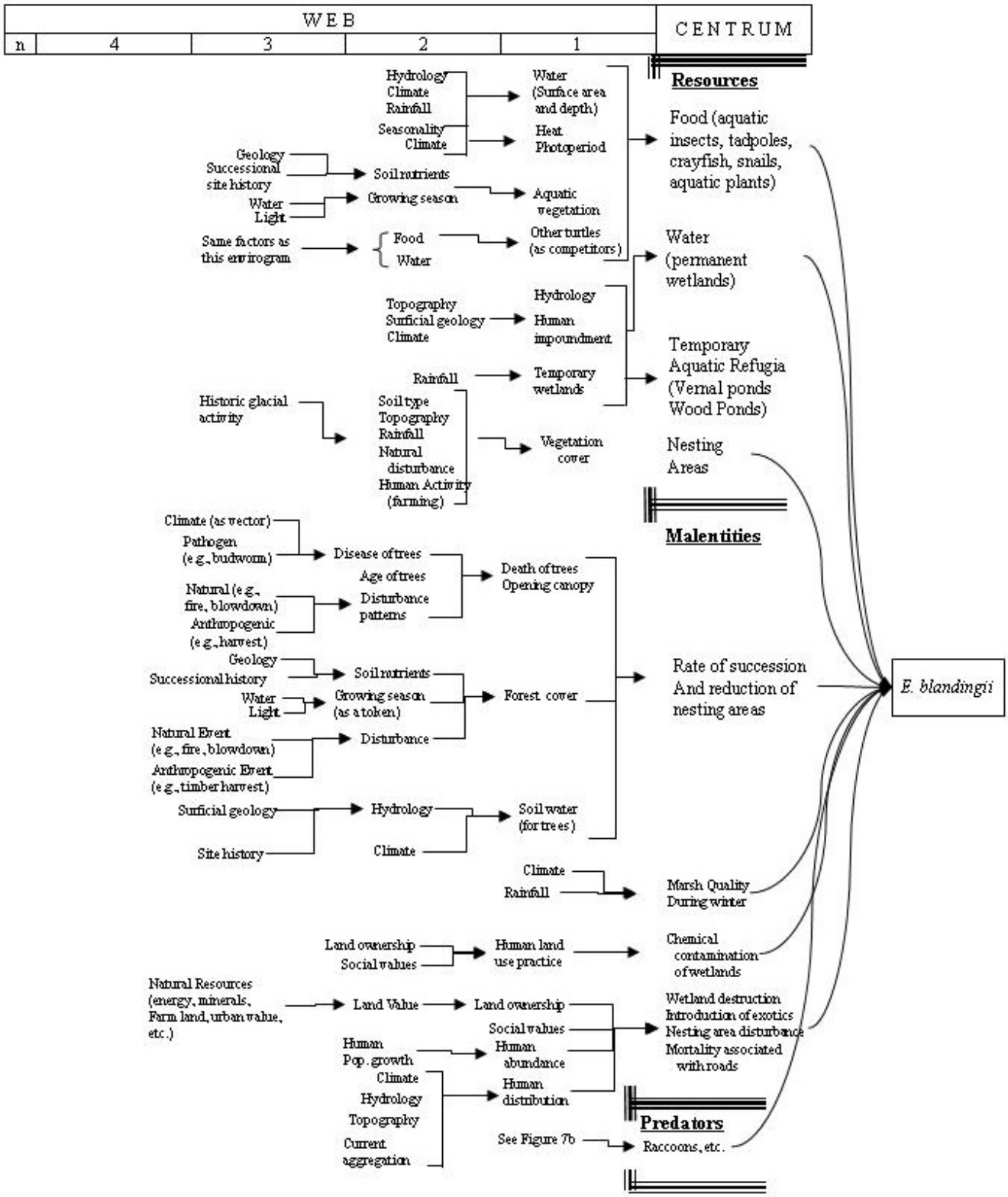

Figure 6. Envirogram of a) habitat, climate, and malentities of Blanding's turtles and b) predators of Blanding's turtles.

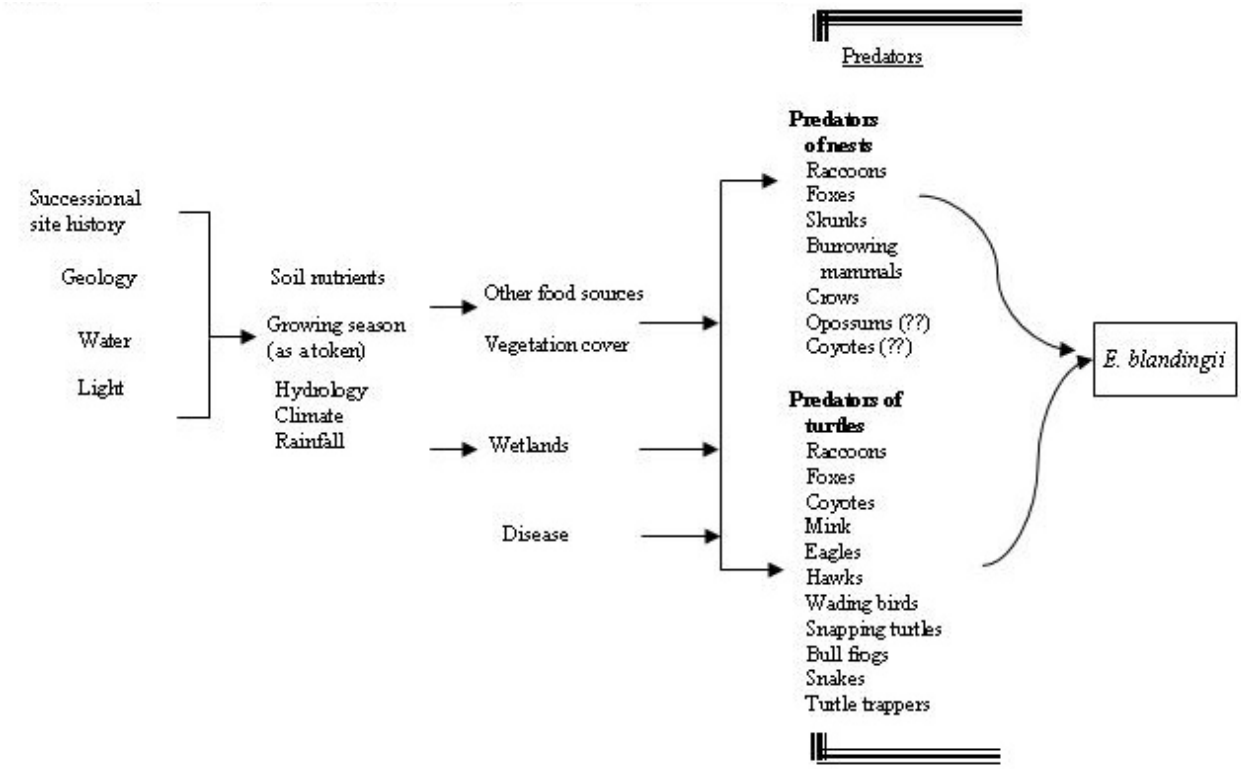

Table 8. Traits of Blanding's turtles on the University of Michigan's Edwin S. George Reserve (based on data from 1975 to 2001).

Trait	Minimum	Maximum	Mean	N
Egg width (mm)	18.4	25.4	23.3	33
Egg mass (g)	5.4	14.9	12.0	27
Hatchling carapace length (mm)	26.0	39.0	35.0	872
Hatchling mass (g)	5	13.0	9.1	846
Age at maturity (yr)	14	21	17.7	27
Clutch size (#)	2	19	10.0	759
Reproductive rate (clutches/yr)	0	1	0.8	not given
Adult sex ratio (M:F)	—	—	1/3.8	not given

may have less acute direct impact on populations than destruction of wetlands in which Blanding's turtles regularly reside, the impact may be severe enough to cause population failure. The loss of seasonal resources found in small wetlands has the potential to reduce reproductive output through production of fewer and smaller clutches of eggs. In addition, fewer temporary refugia will almost certainly result in increased mortality of nesting females, hatchlings dispersing from nests, and individuals moving among permanent wetlands.

An ongoing problem in many areas is the invasion of wetlands occupied by Blanding's turtles by non-native plants such as purple loosestrife (*Lythrum salicaria*) and phragmites (non-native varieties of common reed, *Phragmites australis*). Other invasives, such as *Phalaris arundinacea* (reed canary grass) and *Typha* spp. (cattails) could also pose problems. Purple loosestrife was first noticed on the ESGR in the late 1980's and phragmites in the late 1990's. We do not know of any study of the impacts of invasion by exotics, and at present there are no measurable changes in the population of Blanding's turtles in the aquatic habitats on the ESGR that have been invaded.

Contamination of wetlands

There are no studies of the effects of contamination on Blanding's turtles. However, Blanding's turtles are similar to snapping turtles in that they are both primarily

carnivorous, near the top of the aquatic food chain, and long-lived (Congdon et al. 1993, Congdon et al. 1997). Studies of snapping turtles (Overmann and Krajicek 1995, deSolla et al. 1998) suggest that when Blanding's turtles ingest contaminated food, the contaminant will bioaccumulate over a long period of time. Contamination risks are greater in developed areas, and other risks to turtles in general will be exacerbated by toxicological problems (Guillette 2000, Mayne et al. 2004).

In Nebraska some contaminants of concern are polychlorinated biphenyl compounds (PCBs), dieldrin, and organic mercury. PCBs are a class of aromatic compounds used as plastisizers, heat transfer fluids, lubricants, and wax extenders. They are very persistent in the environment. Production of PCBs was discontinued in the United States in 1977, and their importation was completely stopped in 1982. The pesticide Dieldrin was applied to corn fields for insect control, and wetlands were contaminated by agriculture (and urban) runoff. Legal use of dieldrin in the United States was halted in 1974, but it is also very persistent in the environment. Mercury occurs naturally in the earth's soil and from industrial sources such as the chlorine alkali industry, coal and municipal refuse incinerators, use as a slimacide in the pulp and paper industry, disposal of batteries, vapor discharge lamps, thermometers, and other products. Atmospheric sources of mercury are a major problem in Nebraska and nation-wide. Organic mercury (methyl-mercury) is the most toxic form found in wildlife.

Terrestrial habitat and migration corridors

Terrestrial areas adjacent to, or nearby, wetlands are an important part of the core habitat of Blanding's turtles. Movements among wetlands are often along riparian corridors, but some movements and nesting migrations are directly overland. Threats to adjacent terrestrial environments include both natural succession and invasion by exotic plants, new roads and increased traffic on existing ones, and new developments.

Over the past 30 years succession has resulted in the ESGR being more characterized by mature forests and old fields that are gradually filling in with trees. In addition, the terrestrial shrub autumn olive (*Elaeagnus umbellata*) has become established on the ESGR. It was introduced in the 1830's from China, Japan, and Korea, and it is now found from Maine south to Virginia, and west to Wisconsin. Closed canopy stands of autumn olive have resulted in the complete abandonment of major nesting areas. In addition, fire suppression and forest succession on the ESGR have eliminated three major nesting areas previously used by Blanding's turtles.

Russian olive (*Elaeagnus angustifolia*) may pose future problems for aquatic turtles in Nebraska. This small (15 to 20 ft. tall) tree was introduced from southwestern Europe. It is an ornamental that was until recently planted for windbreaks and wildlife habitat, and its seeds are spread by birds. Russian olive has become established in a wide range of habitats, particularly riparian areas, and where it thrives, it tends to choke out all native vegetation. This species is common along the Platte River, but it can also survive in open rangelands. Invasion of woody species into open areas of well-drained soils will reduce or eliminate their use by nesting Blanding's turtles. As total nesting areas are reduced, nest densities and predation rates will increase in the remaining areas.

Road mortality

In long-lived organisms with low fecundity, like Blanding's turtles, increased mortality of adults associated with roads is a very serious problem and one that impacts more females because of their extensive nesting migrations (Congdon et al. 1983, Rowe and Moll 1991, Kinney 1999, Congdon et al. 2000, Rowe and Moll 1991, Gibbs and Shriver 2003, Lang 2004). Roads located between wetlands and major nesting areas almost always result in increased mortality of females on nesting migrations and hatchlings dispersing from nests. In Michigan, we have found females killed by hay mowers and other farm equipment, stuck in stock fences, and taken by motorists during the nesting season (one was subsequently returned to the ESGR when it was found to be marked). Increased mortality associated with terrestrial movements will impact Blanding's turtles more than many other aquatic turtle species, because adults make frequent, and sometimes extended, movements associated with nesting (May through July) and with overwintering (spring and fall). As traffic volume increases with ongoing development in areas near Blanding's turtle populations, all problems associated with roads increase (i.e., the probability that a turtle can cross safely goes down).

At Valentine NWR, the Blanding's turtle population was estimated to be greater than 135,000 individuals and densities ranged from 20 to 57 individuals per ha, not counting hatchlings and yearlings. Road mortality appeared to be higher in juveniles (60 percent) compared to adults, and mortality rates were higher in the spring and late summer, on weekends, and where roads with high traffic volumes (e.g., Highway

83) are adjacent to or close to aquatic sites (Lang 2004). Although road mortality may not have a great impact on such a large population, smaller isolated populations can be severely impacted or extirpated by chronic road kills of adults. Road signs (**Figure 7**) can be placed along roadways with high volumes of traffic of both Blanding's turtles and vehicles. In areas with high levels of mortality associated with existing roads, fencing and ecopassages (e.g., culverts, tunnels, bridges) should be installed (for an example, see http://www.fhwa.dot.gov/environment/wildlifecrossings/).

Predator populations

Mortality of nests, hatchlings, and a few adults has been caused by a substantial increase in raccoon and other predator populations that resulted from the collapse of the fur trade in the 1980s (see Predators and competitors section above). Populations of predators such as raccoons and foxes are often subsidized by feeding stations maintained by local people and by scavenging from human refuse.

Pet trade

Increased removal of adults, juveniles, and hatchlings from a population for the pet trade (Levell 2000) is also a problem that is particularly damaging to the stability and persistence of small and isolated populations. As populations of wood turtles and box turtles become depleted, pet collectors may shift their attention to Blanding's turtles.

Biological Conservation Concerns

Abundance and abundance trends

Only the survey work on Valentine NWR has been sufficient to make reasonable population estimates of Blanding's turtles relative to Region 2. The Refuge lies in the Sandhills region of Nebraska and in relatively close proximity to the Samuel R. McKelvie National Forest and Nebraska National Forest at Halsey, both administrative units of Region 2 also situated in the Sandhills. The population was estimated to exceed

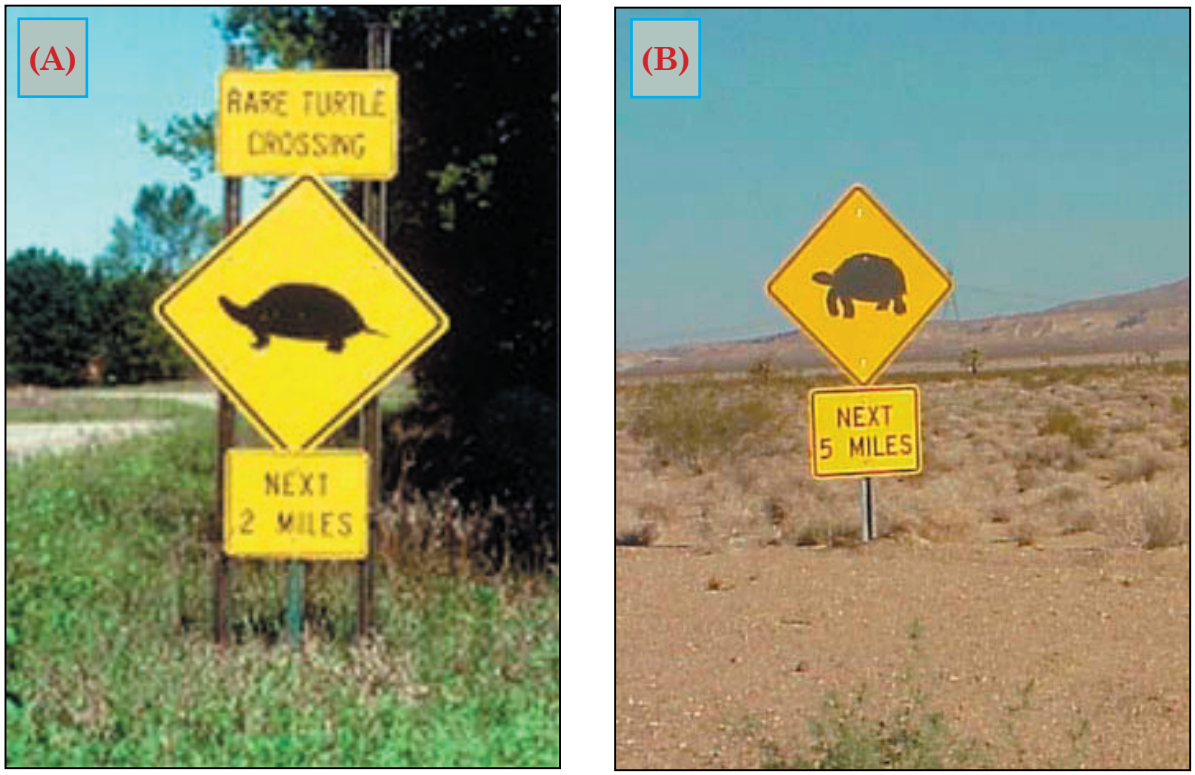

Figure 7. Examples of road crossing signs for (A) Blanding's turtle in southeastern Minnesota, and (B) tortoise in the Mojave Desert in California. Photographs by Justin Congdon.

135,000 Blanding's turtles (Lang 2004), making the Valentine NWR home to the largest known population. However, nearby Sandhill areas with similar densities of wetlands and sand dune habitats should also support Blanding's turtle populations. Data from the studies of Rowe (1992b) and Germano et al. (2000) suggest that populations are relatively large in other parts of Nebraska compared to eastern populations. The populations in Nebraska are apparently large because of abundant aquatic habitats and large areas of suitable nesting habitats, a situation that is similar to that found at Weaver Dunes, Minnesota where the next largest Blanding's turtle population exists. Protections provided at Valentine NWR and at the Weaver Dunes area should promote the stability and persistence of both populations.

Distribution trends

The present range of the Blanding's turtle is restricted to the northern United States and southern Canada; however, during the Pleistocene, this species' range extended at least as far south as South Carolina (J. Knight personal communication 2001). There has been no comprehensive survey of Blanding's turtles throughout its range, and only two long-term studies, one in Michigan (Congdon and Gibbons 1996) and one in Minnesota (Pappas et al. 2000), have documented population trends over two decades. Although the total area of the Blanding's turtle range has only decreased slightly in recent times, there are many areas within the range that have many fewer populations. A combination of habitat destruction and degradation associated with urban and suburban developments has resulted in extirpation or reduction of populations throughout their range, but particularly in heavily populated areas (Dorf 1995, Rubin et al. 2001a, b). Increased mortality of juveniles and adults associated with roads and traffic has also contributed to population declines. Remaining populations are usually small, isolated, and in danger of further declines (Kiviat 1997, Linck and Moriarty 1997, Joyal et al. 2000, Rubin et al 2001a).

An existing (and extreme) case study can be found at Exner Marsh near Lake of the Hills, Illinois (near the greater Chicago area). Blanding's turtles still occur there, but the population has been reduced, and the adult sex ratio is male biased (Hayden 2000). The existing area of the marsh habitat has been reduced and is now surrounded by housing and commercial development and roads with high traffic volumes. The proximity of development has apparently led to contamination of the wetland. Within the few undeveloped areas adjacent to Exner Marsh, there is little suitable nesting habitat, and females that attempt to find nesting sites outside of the area bounded by four major roads are at high risk of being killed. The adult mortality rate and male- biased sex ratio leads to a poor prognosis for the population unless there are interventions such as construction of nesting areas and barriers to keep turtles within the confines of the wetland and adjacent protected land and golf course (Congdon and Pappas 2002).

Habitat trends

Information on habitat trends specific to Blanding's turtles is not readily available. The amount of wetlands in Nebraska has decreased from 2,910,000 acres in 1867 to 1,905,000 acres currently; this is a 35 percent reduction and a proportional reduction from approximately 6 percent to 4 percent of the total area of the state (Dahl 1990). At present, the Nebraska Sandhills region is comprised mainly of extensive rangelands, open water, and wetlands (Rundquist 1983). The majority of wetlands are less than 10 acres but range from less than 1 to 2,300 acres (McCarraher 1977). Most open water lakes and wetlands in the region are supported by a shallow water table associated with the Ogallala Aquifer (Winter 1986). However, despite some wetland loss associated with agriculture, some areas of the Sandhills of Nebraska have suites of wetlands and large expanses of terrestrial areas for nesting. There are no apparent reasons that if such areas exist near Valentine NWR that they should not also support populations of Blanding's turtles.

The above statistics refer largely to major wetland areas, but smaller wetland habitats such as vernal pools and wood ponds are also important to Blanding's turtles. Reduction in the number and quality of small wetlands can contribute to increased mortality of all age classes and increased genetic isolation of populations. We are not aware of data suggesting trends in vernal pool habitat. Unfortunately, in most states only aquatic habitats above some minimum area are protected, so no protection is currently afforded many small wetlands.

Given the low numbers of Blanding's turtles in South Dakota, it can be assumed that any reduction in occupied habitat could result in their extirpation from that state. In contrast, Nebraska populations of Blanding's turtles are more widespread (Rowe 1992b, Germano et al. 2000, Lang 2004) and can be quite large in the Sandhills area and nearby Valentine NWR (Lang 2004). Thus, the effect of habitat trends in Nebraska is likely to be less dramatic and apparent, but they can still result in increased mortality, increased isolation of local populations, and/or localized extirpations.

Intrinsic vulnerability

Potential direct and indirect threats to Blanding's turtles are magnified by life history traits associated with longevity and delayed sexual maturity (Appendix, Congdon et al. 1993, Congdon et al. 2001). Blanding's turtles are long-lived even compared to other turtles (Brecke and Moriarty 1989, Pappas et al. 2000, Congdon et al 2001). Their minimum age at maturity is greater than 14 years and may exceed 20 years in some populations, and annual fecundity is low (i.e., reproductive frequency is less than annual, and they produce less than one clutch of about 10 to 12 eggs per year resulting in annual fecundity of less than five female eggs per female; Congdon and van Loben Sels 1993, Congdon et al. 1993). Delayed sexual maturity, combined with low annual fecundity, requires annual juvenile survivorship to average at least 0.6 between hatching and attaining sexual maturity for recruitment to be adequate for maintaining population stability (Congdon et al. 1993).

In conjunction with the suite of co-evolved traits associated with longevity, one intrinsic trait of Blanding's turtles is their extensive nest migrations that make them, particularly females, vulnerable to being killed on roads and by predators. As areas become developed and either the number of roads or the volume of traffic on existing roads increases, the risks to turtles increase.

Because Blanding's turtles have temperature-dependent sex determination (as do most other species of turtles), global warming may pose potential threats to local populations and change the overall distribution of the species. However, turtles as a group have survived many changes in global climate in their history (over 200 million years).

Conservation Elements, Tools and Practices

Habitat and population management

Conservation of populations of Blanding's turtles is best approached by management of their wetland and terrestrial habitats, but there have been no studies that have investigated the response of Blanding's turtles to changes in environmental factors. The take-home message is that in areas with uncontaminated wetlands, relatively large areas of associated nesting habitat, and minimal road mortality, Blanding's turtle populations are able to remain stable. Specific management approaches as discussed below would represent beneficial management for populations of Blanding's turtles.

Protection of wetlands

Buffer zones should be maintained around wetlands (Burke and Gibbons 1995, Piepgras 1998). Development or surface-altering habitat modification should not occur on, or nearby, wetlands. Cultivation and modification of land should be limited to a minimum of 100 m from wetlands to reduce runoff that may be contaminated with fertilizers, herbicides, and insecticides, or fecal material from cattle.

Buffer zones should also be maintained around small and temporary wetlands. Secondary wetlands near major Blanding's turtles populations should be protected because they serve as temporal sources of food, refugia for adults during seasonal movements and nesting and for hatchlings during dispersal from nests. Loss or reduction of quality of smaller wetland habitats, such as pot holes, vernal pools, and wood ponds, can result in increased mortality of all age classes and potential for increased genetic isolation of some populations.

Water control structures, such as drain-pipes, stand-pipes, and head gates, can pose a threat to Blanding's turtles. Such structures should be screened to prevent turtles from becoming trapped and drowned.

Dikes and causeways often increase risks of injury or mortality associated with vehicles.

Water drawdowns, related to fish and wildfowl management and agriculture, can be detrimental to Blanding's turtle populations if they are conducted during the winter. During the activity season, high road mortality may occur as turtles emigrate from a drained wetland (Dorf 1995, Hall and Cuthbert 2000). If drawdowns are necessary, risks to Blanding's turtles can be reduced by:

- conducting drawdowns during the turtle's active season when they can migrate to other wetlands
- constructing temporary wetlands and then transporting or directing (with fencing) emigrating turtles to them
- capturing and holding turtles in cattle tanks or ponds if drawdown and refilling is done quickly.

Where large Blanding's turtle populations occur in large wetlands, the use of power boats should be limited because heavy powerboat use can lead to Poly-aromatic Hydrocarbons (PAH) contamination, particularly in wetlands with little turnover of fresh water. Power boats also constitute additional risks of injury and death to turtles. Boats also damage the aquatic environment through propeller contact and when water turbulence from motors and wakes or waves uproot vegetation or erode shorelines and increase turbidity. Loss of shoreline "recruitment habitat" may increase mortality rates of hatchlings and juvenile turtles.

Maintenance of terrestrial landscape mosaics

Blanding's turtles are active from as early as March until late October (**Table 6**; Pappas et al. 2000, Lang 2004). Although they spend most of their lives in aquatic habitats, peaks in terrestrial movements occur in the spring and fall as individuals move to and from overwintering sites, and during the nesting season (late May through early July). Gravid females often make relatively long pre- and post-nesting migrations from resident wetlands to smaller temporary wetlands followed by nesting migrations to well-drained terrestrial areas for nesting. Therefore, terrestrial corridors for movements among wetlands and to and from nesting areas are important. Reduction in the quality of terrestrial areas surrounding wetlands can increase risks of injury and mortality of individuals of all age classes and can compromise the integrity and productivity of wetlands.

Burning and mowing: The best way to minimize the impact of mowing and controlled burns is to conduct them when terrestrial activity of Blanding's turtles is least probable. Burns should be scheduled just after early spring dispersal from overwintering sites (April) and in late fall after hatchling dispersal from nests (late August and September). During nesting season (late May through early July) gravid females would be at highest risk of being injured or killed by mowers or fires.

Grazing and terrestrial vegetation control: Because Blanding's turtles nest in areas with limited vegetation and limited shade, grazing and removing trees that invade nesting areas may actually enhance the quality of nesting areas. Overgrazing, however, may increase erosion and the chance of nests being washed out of the ground. Grazing in riparian areas should be discouraged or eliminated. Limiting the tree removal to non-nesting season should minimize any risks to turtles.

Off-road vehicles: Use of off-road vehicles should be discouraged. If it is deemed necessary, their use should be restricted to times when terrestrial activity of turtles is low (**Table 6**).

Roads and traffic

Blanding's turtles are long-lived with annual adult survivorships exceeding 97 percent, and they take over 14 years to reach maturity. They also have low annual fecundity and high nest predation rates (Congdon et al. 1993). Chronic increased mortality of adults will lead to a reduction in stability and the eventual extirpation of a population

Construction of new roads: Prior to construction, assessment of migration zones and nesting areas of Blanding's turtles should be conducted. If possible, new roads should not be built in areas that are corridors of movement and nesting migrations. Design of new roads should include barriers, culverts, or preferably underpasses that allow turtles safe passage (Lang 2004).

Modifying existing roads: Surveys of road mortality should be conducted during spring movements, nesting season, and fall movements of adults and hatchlings dispersing from nests. In areas with high mortality, "turtle crossing" signs (**Figure 7**) should be placed where large numbers of turtles cross roads and highways with high volumes of traffic. If mortality rates remain high, culverts should be installed under roads, and fencing should be placed to encourage turtles to move through the culverts. After construction, monitoring programs should be conducted to determine if mortality rates are reduced in areas with turtle crossing signs and culverts compared to areas without signs or culverts.

Collecting

There are no data on the impacts of collecting on Blanding's turtles. However, researchers of wood turtles have had their study populations wiped out by collectors (R. Brooks personal communication 2003, J. Harding personal communication 2004). Blanding's turtles are sold at prices ranging from $25 to $150 each (Levell 2000).

Other mortality

Some specific techniques targeted at protection of animals, such as protecting nests from surface predators by placing wire cages over them, should be considered

for small, threatened populations. Where warranted, cages should be buried to 10 to 15 cm to deter burrowing mammals. Care should be taken to construct cages so that they do not reduce incubation temperatures by shading the nest (i.e., use as large a wire mesh as possible that will eliminate potential predators). Reduced incubation temperatures will result in hatchling sex ratios biased toward males, and low incubation temperatures can cause problems with embryo development and growth (**Figure 6**). Hobo Loggers (Onset Computer) or I-button (Dallas Semiconductor) temperature loggers can be placed inside and adjacent to cages of different design to determine their impact on ground temperatures before they are used to protect nests.

Inventory and monitoring

Blanding's turtles can be successfully monitored with aquatic trapping (fyke nets and baited traps). Baits such as pig or beef heart, smelt, and sardines have been effective on the ESGR and elsewhere. Searches of terrestrial areas during nesting areas can yield direct information, and counts of destroyed nests can provide supplemental data for estimating numbers of females. Censuses of females can be made in situations where females cross roads or other cleared areas, or where drift fences can be constructed between aquatic areas and major nesting areas. Because Blanding's turtles can be easily identified by their yellow chins and their body size and shape, their presence or absence can be determined by observing aquatic areas in spring and early summer with binoculars or spotting scopes.

During early spring when Blanding's turtles become active, dip netting is very effective. Individuals bask in vegetation mats and when approached go just beneath the surface. If the location has been determined using binoculars, a person in waders can move to the spot where they submerged and dip net or muddle for them. In brief, such issues include identifying inventory and monitoring gaps, standardizing methods, establishing the most representative reference sites, and developing cooperation among programs.

Abundance estimation methods for turtles, such as mark-recapture, are appropriate for small-scale or detailed investigation of population dynamics, but these are expensive and less practical for large-scale or long-term monitoring programs. For larger scale monitoring, detection/non-detection surveys are probably more appropriate. Depending on the goals of the program and the techniques used, data collected should include body size, sex, age class, and physical abnormalities of individuals. Eggs of Blanding's turtles can be collected to determine size, mass, relative composition, contaminant concentrations, and the frequency of hatchling abnormalities at a number of sites. Additional data that should be recorded include date, time of day, location, habitat type, and whether the site is contaminated or not.

Captive propagation and reintroduction

If habitat problems or other factors reduce survival of turtles to the point of extirpation of populations, those factors should be corrected before captive propagation and reintroduction can succeed (Frazer 1992). The value of headstarting programs for hatchling Blanding's turtles depends on the intensity of nest predation rates and mortality rates of young juveniles. If predation rates of hatchlings and juveniles are both high, then headstarting may be effective. However, headstarting programs require intensive efforts to locate females while nesting or in capturing gravid females and obtaining eggs by inducing oviposition with oxytocin. In addition, headstarting of hatchlings has less value than protecting adults because population stability is most dependent on survival of reproductive females (Appendix; Congdon et al 1993).

Information Needs

The following information on Blanding's turtles in Region 2 is needed to properly assess their status and to assist the development and implementation of successful conservation and management plans.

1. The most basic information needed is an extensive assessment of wetlands and associated terrestrial habitats and the distribution and status of Blanding's turtles in USFS Region 2. Particular attention should be paid to the relationship between habitat types and Blanding's turtle densities. At present, only the Valentine NWR population has been examined (Lang 2004). Populations should be categorized from large and stable to small and unstable and in danger of being extirpated in the future. Early identification of incipient problems will enhance the probability of successful management. For example, in Nebraska, there has been one published study of Blanding's turtle reproduction (in Grant and Arthur counties; Rowe 1992b) and one study of body growth and population structure (Valentine NWR, Cherry County; Germano et al. 2000). The proportion of juveniles in the populations was 0.32 in Grant

and Arthur counties and 0.49 at the Valentine NWR; these proportions are high compared to those found in many other studies where juveniles are rare, but see Pappas et al. 2000.

2. Temporary wetlands are important in terms of the success of management and conservation plans for Blanding's turtle. Patterns of use of terrestrial and aquatic habitats should be better documented. Particular focus should be made on the use of temporary wetlands and vernal pools as breeding sites, refugia for adults and hatchlings, and seasonal food sources. Food harvested from small and ephemeral wetlands may be important for growth and survival of juveniles and reproductive output of adult females.

3. The period of winter dormancy in most of the Blanding's turtles range is longer than the period of activity. A complete understanding of the biology of the species requires identification of the locations and characteristics of overwintering sites and determining whether the overwintering sites of adults, juveniles, and hatchlings differ. For example, are the overwintering sites located in close proximity to summer activity areas? If overwintering sites are in different areas than the residence wetlands, it will require more seasonal movements in aquatic or terrestrial corridors that may increase risks of injury or mortality. Also, if movement corridors become degraded or require individuals to cross roads, the risk of mortality associated with overwintering can be substantial.

4. Mortality rates of hatchlings are almost certainly associated with the condition of habitats between nest sites and wetlands. How much increase is there in risks to hatchlings dispersing from nests if temporary wetlands and terrestrial areas used for nesting become degraded?

5. Temporary wetlands often are the first recruitment habitat of hatchling Blanding's turtles. Identifying the type of habitats used by hatchlings and juveniles, their distribution, and their density is important for maintaining recruitment of adults in a population.

6. Particularly for small and isolated populations, patterns of genetic variation within and among populations of Blanding's turtles should be established. Evidence of isolation that is severe enough to reduce genetic diversity in a population may require translocation of individuals among populations.

List of Errata

12/9/09 Corrected spelling of Janet Hostetter's last name on page 2 (Acknowledgments & Cover Photo Credit sections) and page 11 (Figure 1).

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APPENDIX

Life History Model

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The life table demographic analysis of Congdon et al. (1993) provided the basis for a life cycle graph (**Figure A1**) and a matrix population analysis with a post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2000) for Blanding's turtle. The original life table had 110 age classes. Using a self-loop for an "adult" reproductive stage at Stage 20 (arc from Node 20 back to itself in **Figure A1**) greatly simplifies the graph, matrix, and analysis without sacrificing information (McDonald and Caswell 1993). The model has two kinds of input terms: P_i describing survival rates and m_i describing fertilities (**Table A1**). **Table A2** shows the symbolic terms in the projection matrix corresponding to the life cycle graph while **Table A3** gives the corresponding numeric values. The model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female. The population growth rate (λ) is 1.000 based on the estimated vital rates used for the matrix. Although this suggests a stationary population, the value is subject to the many assumptions used to derive the transitions and should not be interpreted as an indication of the general well-being and stability of the population. Other parts of the analysis provide a better guide for assessment.

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. **Sensitivity** is the effect on λ of an **absolute** change in the vital rates (a_{ij}, the arcs in the life cycle graph [**Figure A1**] and the cells in the matrix, **A** [**Table A2**, **Table A3**]). Sensitivity analysis provides several kinds of useful information (see Caswell 1989, pp.118-119). First, sensitivities show "how important" a given vital rate is to λ or fitness. For example, one can use sensitivities to assess the relative importance of survival (P_i) and reproductive (F_i) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimations of vital rates from field studies. Inaccuracy will usually be due to a paucity of data, but it could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing λ of endangered species or the "weak links" in the life cycle of a pest. **Table A4** shows the "possible sensitivities only" matrix for this analysis (one can

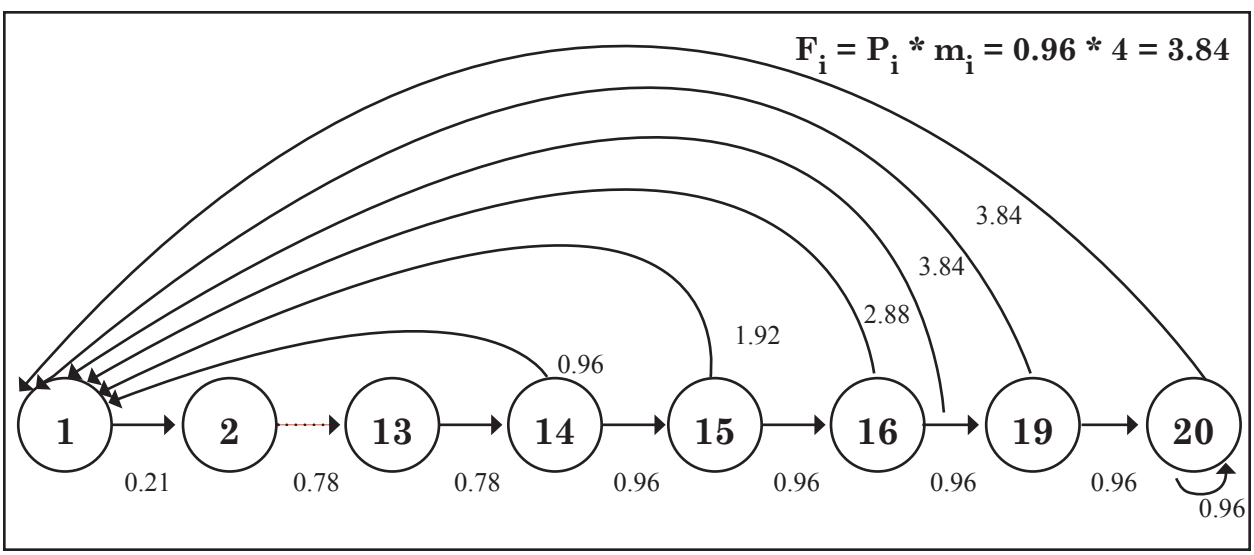

Figure A1. Life cycle graph for Blanding's turtle. Note "adult" self-loop at Stage 20. Note also the ellipsis of Nodes 3-12 (all with $P_i = 0.78$) and of Nodes 17 & 18 (with $P_i = 0.96$ and $F_i = 3.84$). Life cycle has three age-based survival rates: 1st-year, prereproductive (Age-classes 2 through 13) and "adult" reproductive (≥14). Female offspring per female (m_i) increases from 1 at Age-class 14 to 4 at Age-class 17 and above.

Table A1. Parameter values for the component terms (P_i and m_i) that make up the vital rates in the projection matrix for Blanding's turtles.

Parameter	Numeric value	Interpretation
m_{14}	1	Number of female offspring produced by a female in Stage 14
m_{15}	2	Number of female offspring produced by a female in Stage 15
m_{16}	3	Number of female offspring produced by a female in Stage 16
m_a	4	Number of female offspring produced by a fully-developed female
P_{121}	0.21	Annual first-year survival rate of eggs
P_j	0.7826783	Annual survival rate of prereproductives
P_a	0.96	Annual survival rate of reproductive

Table A2. Symbolic values for the input matrix of vital rates, **A** (with cells a_{ij}) corresponding to the Blanding's turtle life cycle graph (**Figure A1**).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1														$P_a m_{14}$	$P_a m_{15}$	$P_a m_{16}$	$P_a m_a$	$P_a m_a$	$P_a m_a$	$P_a m_a$
2	P_1																			
3		P_j																		
4			P_j																	
5				P_j																
6					P_j															
7						P_j														
8							P_j													
9								P_j												
10									P_j											
11										P_j										
12											P_j									
13												P_j								
14													P_j							
15														P_j						
16															P_a					
17																P_a				
18																	P_a			
19																		P_a		
20																			P_a	P_a

Table A3. Numeric values for the input matrix of vital rates, **A** (with cells aij) corresponding to the Blanding's turtle life cycle graph (**Figure A1**, **Table A2**).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1														0.96	1.92	2.88	3.84	3.84	3.84	3.84
2	0.21																			
3		0.783																		
4			0.783																	
5				0.783																
6					0.783															
7						0.783														
8							0.783													
9								0.783												
10									0.783											
11										0.783										
12											0.783									
13												0.783								
14													0.783							
15														0.96						
16															0.96					
17																0.96				
18																	0.96			
19																		0.96		
20																			0.96	0.96

Table A4. Possible sensitivities only matrix, $\mathbf{S_P}$ (remainder of matrix consists of zeros). The transitions to which the λ of Blanding's turtles is most sensitive are highlighted: the survival of eggs (Cell $s_{21} = 0.121$), and the survival of pre-reproductive females ($s_{32} = s_{43} = s_{54} = s_{65} = s_{76} = s_{87} = s_{98} = s_{10\text{-}9} = s_{11\text{-}10} = s_{12\text{-}11} = s_{13\text{-}12} = s_{14\text{-}13} = 0.032$).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1														0.0	0.0	0.0	0.0	0.0	0.0	0.005
2	**0.121**																			
3		**0.032**																		
4			**0.032**																	
5				**0.032**																
6					**0.032**															
7						**0.032**														
8							**0.032**													
9								**0.032**												
10									**0.032**											
11										**0.032**										
12											**0.032**									
13												**0.032**								
14													**0.032**							
15														0.026						
16															0.026					
17																0.025				
18																	0.024			
19																		0.023		
20																			0.022	0.526

calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible – for example, the sensitivity of λ to moving from Age-Class 3 to Age-Class 2).

In general, changes that affect one type of age class or stage will also affect all similar age classes or stages. For example, any factor that changes the annual survival rate of Age-Class 17 females is very likely to cause similar changes in the survival rates of other "adult" reproductive females (i.e., those in Stages 18 through 20). Therefore, it is usually appropriate to assess the summed sensitivities for similar sets of transitions (vital rates). For this model, the result is a summed "reproductive" survival sensitivity of 0.67 (57 percent of total), and a summed "pre-reproductive" sensitivity of 0.384 (32 percent of total), both considerably larger than the sensitivity of λ to the survival rate for eggs (0.12; 10 percent of total). Blanding's turtle populations show little sensitivity to changes in fertility. The major conclusion from the sensitivity analysis is that protection of older reproductive females is the key to population viability.

Elasticity analysis

Elasticities are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance, a change of 0.5 in survival may be a big alteration (e.g., a change from a survival rate of 90 to 40 percent). On the other hand, a change of 0.5 in amphibian fertility may be a very small **proportional** alteration (e.g., a change from a fertility clutch of 3,000 eggs to 2,999.5 eggs). Elasticities are the sensitivities of λ to proportional changes in the vital rates (a_{ij}) and thus largely avoid the problem of differences in units of measurement. The elasticities have the useful property of summing to 1.0. The difference between sensitivity and elasticity conclusions results from the weighting of the elasticities by the value of the original arc coefficients (the a_{ij} cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction (F_i) and survival (P_i) for a given species.

Elasticities for Blanding's turtles are shown in **Table A5**. The λ of Blanding's turtles is most elastic to changes in the survival of the "adult" reproductive females (the multi-age Stage 20 females and those in Age-Classes 17 through 19), survival of "pre-reproductive" females (Age-Classes 2 through 13), and finally first-year survival of eggs. The sensitivities and elasticities for Blanding's turtles correspond exactly in the relative magnitude of the three most important kinds of transitions, a phenomenon that is not always the case in other life histories (*cf.* Townsend's big-eared bat, plains killifish). These survival transitions are therefore the data elements that warrant careful monitoring in order to refine the matrix demographic analysis.

Partial sensitivity and elasticity

Partial sensitivity and elasticity analysis assesses the impact on λ of changes in "lower-level terms" (Caswell 2000, pp. 218 and 232). Some transitions (e.g., F_i) include lower-level component terms (P_i and m_i) related to the different kinds of transitions in the life cycle (e.g., survival and fertility; some models might have growth rates or breeding probability terms). Partial sensitivity results indicate that changes in the P_i (survival rates) will have by far the greatest impact on λ (99.6 percent of the total partial sensitivity). Changes in fertility (m_i) will have far less impact on λ (0.4 percent of the total partial sensitivity). Similarly, P_i terms account for 98.1 percent of the total partial elasticity, with only 1.9 percent accounted for by m_i terms. Again, every aspect of the analysis suggests that Blanding's turtles are most susceptible to environmental change or habitat degradation that affects the survival of older reproductive females.

Other demographic parameters

The **stable (st)age distribution** (SSD; **Table A6**) describes the proportion of each Stage (or Age-class) in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SSD within 20 to 100 census intervals. For Blanding's turtle at the time of the post-breeding annual census (just after the end of the breeding season), eggs should represent 46 percent of the population, 42 percent should consist of juvenile categories stages, and the remaining 12 percent should consist of adult categories stages. **Reproductive values** (**Table A7**) can be thought of as describing the "value" of a stage as a seed for population growth relative to that of the first (newborn or, in this case, egg) stage. The reproductive value of the first stage is always 1.0.

Table A5. Elasticity matrix, **E** (remainder of matrix consists of zeros). The λ of Blanding's turtles is most elastic to changes in the survival of eggs and pre-reproductive females ($e_{21} = e_{32} = e_{43} = e_{54} = e_{65} = e_{76} = e_{87} = e_{98} = e_{10\text{-}9} = e_{11\text{-}10} = e_{12\text{-}11} = e_{13\text{-}12} = e_{14\text{-}13} = .0254$).

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1																				
2	**.0254**																			
3		**.0254**																		
4			**.0254**																	
5				**.0254**																
6					**.0254**															
7						**.0254**														
8							**.0254**													
9								**.0254**												
10									**.0254**											
11										**.0254**										
12											**.0254**									
13												**.0254**								
14													**.0254**							
15														.0251						
16															.0246					
17																.0238				
18																	.0229			
19																		.022		
20																			.0211	.5054

Table A6. Stable stage distribution (right eigenvector) for females. At census, 46 percent of individuals in the population should be newborns (eggs), 42 percent will be pre-reproductives, 12 percent will be reproductive adults. Almost 10 percent of the population will be 20 years of age or older.

Stage	Description	Proportion
1	Eggs	0.456
2	Prereproductive	0.096
3	"	0.075
4	"	0.059
5	"	0.046
6	"	0.036
7	"	0.028
8	"	0.022
9	"	0.017
10	"	0.013
11	"	0.011
12	"	0.008
13	"	0.006
14	First reproduction (mi = 1)	0.005
15	Reproductive (mi = 2)	0.005
16	Reproductive (mi = 3)	0.005
17	Reproductive (mi = 4)	0.004
18	"	0.004
19	"	0.004
20	Reproductive ($m_i = 4$) ≥ Age Class 20	0.099

A female individual in Stage 2 is "worth" 4.8 female eggs, and so on (Caswell 2000). The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). As in many species with high clutch sizes and low first-year survival, the peak reproductive value (95.9 at Stage 17 and older) is considerably higher than that of the eggs (**Table A3**). Unlike in humans (Keyfitz 1985) and many species of mammals and birds, the reproductive value peaks some time after the age of first reproduction, largely because of the increased fertility of older, larger females. Again, we see that "adult" females are the most important stage in the life cycle. The cohort generation time for Blanding's turtles was 39.4 years (SD = 24.5 years). The mean age of females in the final mixed-age stage (Node 20 in the life cycle diagram) was 43.0 years (SD = 24.5 years).

Stochastic model

We conducted a stochastic matrix analysis for Blanding's turtles. We incorporated stochasticity in several ways, by varying different combinations of vital rates or by varying the amount of stochastic fluctuation (**Table A8**). Under Variant 1 we altered the fertilities (F_i). Under Variant 4, we varied only the survival of the "20 and older adult" female self-loop, $P_{20,20}$. Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the SSD under the deterministic model. Beginning at the SSD helps to avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 cycles). We varied the amount of fluctuation by changing the standard deviation of the random normal distribution from which the stochastic vital rates were selected. The default value

Table A7. Reproductive values for females. Reproductive values can be thought of as describing the "value" of an age class as a seed for population growth relative to that of the first (newborn or, in this case, egg) age class. The reproductive value of the first age class is always 1.0. The peak reproductive value is highlighted in bold type.

Stage	Description	Proportion
1	Eggs	1.000
2	Prereproductive	4.762
3	"	6.08509
4	"	7.77678
5	"	9.93794
6	"	12.6987
7	"	16.22623
8	"	20.734
9	"	26.4955
10	"	33.85786
11	"	43.26527
12	"	55.28629
13	"	70.64765
14	First reproduction (mi = 1)	90.27728
15	Reproductive (mi = 2)	93.043
16	Reproductive (mi = 3)	94.924
17	Reproductive (mi = 4)	**95.884**
18	"	**95.884**
19	"	**95.884**
20	Reproductive (m_i = 4) ≥ Age-c Class 20	**95.884**

was a standard deviation of one quarter of the "mean" (with this "mean" set at the value of the original matrix entry [vital rate], a_{ij} under the deterministic analysis). Variant 88 affected the same transition as Variant 2 ($P_{20,20}$) but was subjected to only half as much variation (SD was one eighth of the mean). We calculated the stochastic growth rate, $log\lambda_S$, according to Eqn. 14.61 of Caswell (2000), after discarding the first 1,000 cycles in order to further avoid transient dynamics.

The stochastic model produced two major results. First, altering only the "20 and older adult" survival rate had a much more dramatic effect on λ than did altering all the fertilities. This "20 and older" survival rate is the self-loop on the last node of **Figure A1**. For As an example of the contrasting effects, the median ending size (10,174) under the changed varying fertilities of Variant 1 was essentially the same as the starting size of 10,000. In contrast, varying the survival of the oldest females under Variant 44 resulted in a median ending size of 11.8. This difference in the effects of stochastic variation is predictable from the sensitivities and elasticities. λ was much more sensitive to $P_{20,20}$ than it was to the entire set of fertilities, F_i. Second, large-effect stochasticity on highly sensitive/elastic transitions has a negative effect on population dynamics. This negative effect occurs despite the fact that the average vital rates remain the same as under the deterministic model – the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2000). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. For Blanding's turtles under the adult survival Variant 44, 92 out of 100 trials of stochastic projection went to extinction vs. 0 under the fertilities Variant 1. Variant 88 shows that the degree-magnitude of fluctuation has a potentially large impact on the dampening detrimental effects of stochasticity. Decreasing the degree-magnitude of fluctuation also decreased the severity of the negative impacts – the number of extinctions went from 92 in Variant 44 to 5

Table A8. Summary of eight variants of stochastic projections for Blanding's turtles. Two variants of the models are projected.

	Variant 1	Variant 2	Variant 3	Variant 4	Variant 5	Variant 6	Variant 7	Variant 8
Input factors:								
Affected cells	F_i	P_1	P_i	P_{max}	$P_i + P_{max}$	$F_i + P_1$	P_{max}	P_{max}
S.D. of random normal distribution	1/4	1/4	1/4	1/4	1/4	1/4	1/6	1/8
Output values:								
Deterministic λ	1.0005	1.0005	1.0005	1.0005	1.0005	1.0005	1.0005	1.0005
# Extinctions / 100 trials	0	0	0	92	99	0	41	5
Mean extinction time	—	—	—	1,032.9	961.9	—	1420.0	1,712.2
# Declines / # surviving populations	38/100	35/100	75/100	7/8	1/1	34/1000	53/59	80/95
Mean ending population size	10,817.0	11,087.0	9,513.1	1,438.2	53.3	11,598.5	6,058.4	16,849.9
Standard deviation	2,651.0	2,910.8	14,557.1	3,860.7	0.0	4,191.6	24,673.4	73,940.4
Median ending size	10,174.72	10,627.72	3,634.63	11.83	53.3	11,165.54	100.12	286.62
Log λ_s	0.00001312	0.00002932	-0.00034793	-0.00858412	-0.00976373	0.0000186	-0.00407427	-0.00158334
λ_s	1.0000	1.0000	0.9997	0.9995	0.9903	1.0000	0.9959	0.9984
% reduction in λ	0.00352091	0.00190071	0.0396191	0.8595386	0.976408	0.00297284	0.411412	0.163034

in Variant 88 when the degree-magnitude of fluctuation was halved. These results suggest that populations of Blanding's turtles are relatively tolerant to stochastic fluctuations in production of eggs (due, for example, to annual climatic change or to human disturbance) but extremely vulnerable to variations in the survival of adult stages. Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. A possible concern is that anthropogenic impacts may induce variation in previously invariant vital rates (such as annual adult survival), with consequent detrimental effects on population dynamics.

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