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Historic and Current Amphibian and Reptile Distributions in the Island Region of Western Lake Erie

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ABSTRACT.—Records of amphibians and reptiles from the island region of western Lake Erie (Essex County, Ontario; Erie and Ottawa counties, Ohio) span more than a century and include 50 species, 35 of which have been recorded from at least one of 19 islands. Local colonization events, transient species, population declines and local extirpations occurring within this century are evident from these records. Furthermore, these records provide a baseline for monitoring future changes in distribution. Unusual components of the Lake Erie amphibian and reptile fauna include unisexual, polyploid and hybrid ambystomatid salamanders; a population of redback salamanders (*Plethodon cinereus*) consisting almost entirely of lead-back morphs; populations of Lake Erie water snakes (*Nerodia sipedon insularum*) that are highly variable in color pattern and provide an exceptionally clear example of the effects of natural selection and gene flow, and populations of common garter snakes (*Thamnophis sirtalis*) consisting of up to 50% jet-black melanistic individuals. Total number of amphibian and reptile species is positively correlated with island area but uncorrelated with distance to the mainland; however, among salamanders, species numbers decrease with increasing distance to the mainland.

INTRODUCTION

The island region of western Lake Erie includes taxa and biological communities not found elsewhere and thus makes a unique contribution to the biota of Ohio and Ontario (Clapp, 1916; Conant and Clay, 1937; Boerner, 1984; Downhower, 1988; Catling and Brownell, 1995). The region is underlain by limestone and dolomite which resisted glaciation (Calkin and Feenstra, 1985), resulting in a series of islands that range from 0.5–4261 ha, <2–21 m above mean lake level, and 0.3–22.4 km from the nearest mainland point. The biota of the island region has a long history of investigation (Downhower, 1988; Bolsenga and Herdendorf, 1993) and as a consequence, the distribution of amphibians and reptiles (and other taxa) is known in considerable detail. The Ohio State University's F. T. Stone Laboratory on Gibraltar and South Bass islands has provided a base for biological research since 1895 and early herpetological work in the region includes that of Roger Conant (Conant, 1982) and Charles Walker (staff member and herpetology instructor at the F. T. Stone Laboratory 1938–1947; Langlois, 1949). Since European settlement in the early 1800s, islands and adjacent mainland areas have been much modified by human activity (wetland

drainage, quarrying, grazing, crop production, recreation; Kaatz, 1955; Hatcher, 1971) and a variety of organisms have undergone changes in distribution and abundance as a consequence (Duncan and Stuckey, 1970; Weseloh *et al.*, 1988). Our purpose was to document historic and current distributions of amphibians and reptiles in the island region of western Lake Erie, to draw attention to population declines and extirpations that have occurred on some islands, and to provide baseline data for monitoring future changes in distribution. In addition, we review four unusual components of the island region's amphibian and reptile fauna. Finally, we consider distribution patterns in a biogeographical context.

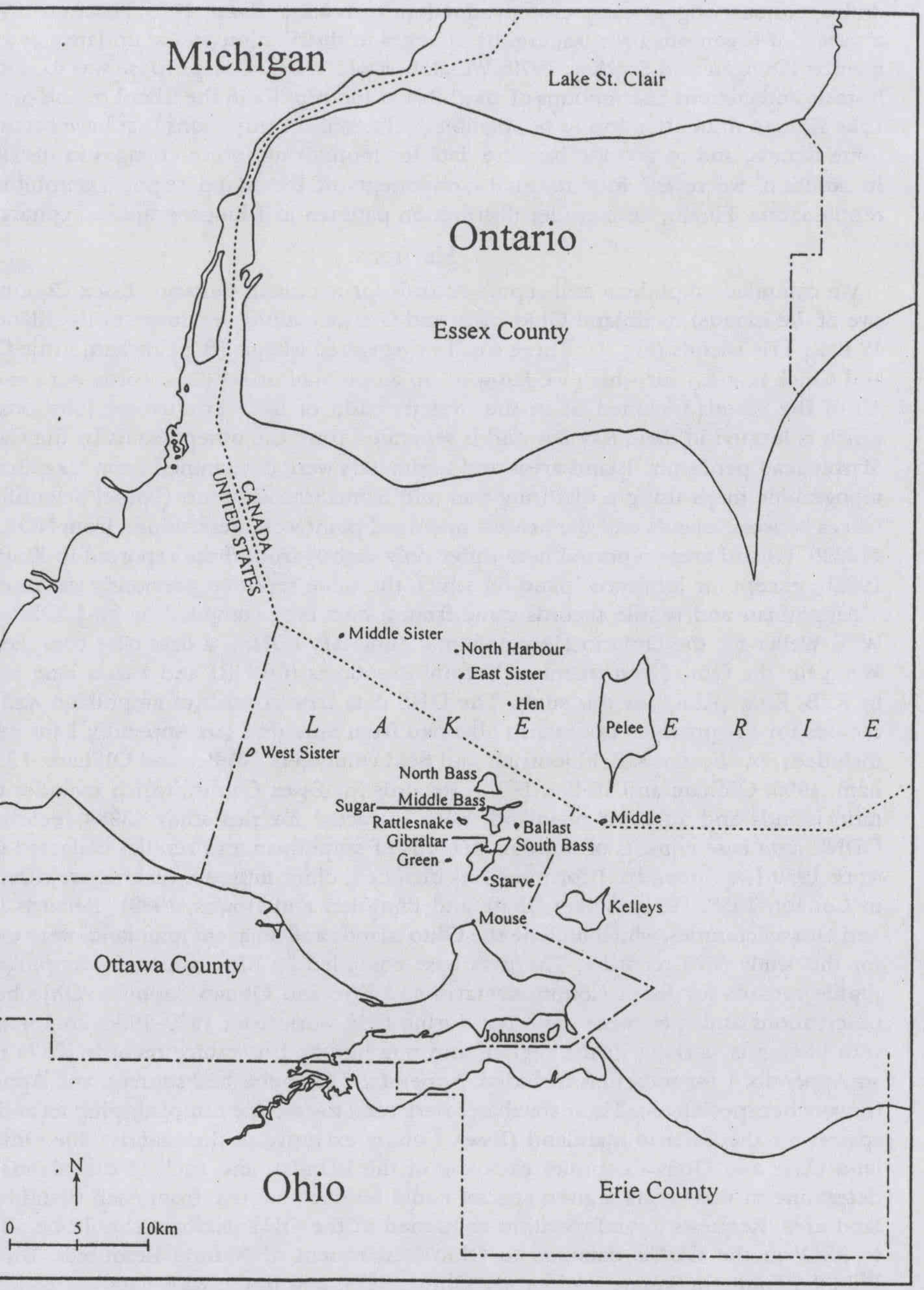
METHODS

We compiled amphibian and reptile records for mainland Ontario (Essex County exclusive of the islands), mainland Ohio (Erie and Ottawa counties exclusive of the islands) and 19 Lake Erie islands (Fig. 1). Three small unvegetated islands (Big Chicken, Little Chicken and Chick islands) for which we know of no amphibian or reptile records were excluded. All of the islands included lie in the western basin of Lake Erie except Johnsons Island which is located in Sandusky Bay and is separated from the other islands by the Catawba/Marblehead peninsula. Island areas and perimeters were determined from lake charts and topographic maps using a digitizing pad and SigmaScan software (Jandel Scientific). Distances between islands and the nearest mainland point were determined from NOAA chart #14830. [Island areas reported here differ only slightly from those reported in King (1987, 1988b) except for Johnsons Island for which the value reported previously was in error.]

Amphibian and reptile records came from a data base compiled by M. J. Oldham and W. F. Weller for the Ontario Herpetofaunal Summary (OHS), a data base compiled by D. Wynn for the Ohio Department of Natural Resources (ODNR) and a data base compiled by R. B. King (RBK) for this study. The OHS data base consists of amphibian and reptile records for the province of Ontario obtained from museums (*see* Appendix 1 for museums included), publications, field journals and field volunteers (Weller and Oldham, 1988; Oldham, 1990; Oldham and Weller, 1992). Records for Essex County, which includes the Ontario islands and adjacent mainland, were extracted for this study (3984 records). The ODNR data base consists of museum records of amphibian and reptiles collected in Ohio since 1950 (*see* Appendix 1 for museums included; older museum records are summarized in Conant, 1938, 1951; Walker, 1946; and Pfingsten and Downs, 1989). Records for Erie and Ottawa counties, which include the Ohio islands and adjacent mainland, were extracted for this study (675 records). The data base compiled by RBK consists of amphibian and reptile records for Essex County, Ontario and Erie and Ottawa counties, Ohio based on observations and specimens collected during field work from 1979–1996, communication with biologists working in the region, and museum and literature records (2874 records; *see* Appendix 1 for museums included, Appendix 2 for published sources, and Appendix 3 for voucher specimens). These databases were used to compile lists of amphibian and reptile species for the Ontario mainland (Essex County exclusive of the islands), the Ohio mainland (Erie and Ottawa counties exclusive of the islands), and each of the islands and to determine in what years a given species could be documented, from each island or mainland area. Requests for information contained in the OHS database should be addressed to MJO; in the ODNR database to Ohio Department of Natural Resources, Division of Wildlife, Fountain Square, Columbus, Ohio, 43224; and in the RBK database to RBK. Our use of common names follows Collins (1990).

RESULTS AND DISCUSSION

Fifty species of amphibians and reptiles (12 salamanders, 11 frogs and toads, one lizard, eight turtles, 18 snakes) were documented from island and mainland areas included in this



G. 1.—The island region of western Lake Erie, showing the 19 islands and adjacent mainland areas ssex County, Ontario and Erie and Ottawa counties, Ohio, included in this study

study (Table 1). Thirty-five species (eight salamanders, eight frogs and toads, seven turtles, 12 snakes) were recorded on at least one island (Table 1). Number of species per island ranged from one to 24 and number of islands on which a given species occurred ranged from one to 19.

Our earliest record was a 1793 report of "rattlesnakes" on Middle Bass Island (McDermott, 1947), although the true identity of these snakes is uncertain (*see* "Questionable Records"). Our earliest records based on specimens were an eastern hognose snake (*Heterodon platirhinos*) collected in Erie County, Ohio, in 1886 (OSUZM833) and a Lake Erie water snake (*Nerodia s. insularum*) collected on South Bass Island in 1893 (USNM40068). All but three species (*Ambystoma laterale, A. texanum, Storeria occipitomaculata*) were recorded from the region by 1950. However, records for individual islands have continued to accumulate (Table 1).

QUESTIONABLE RECORDS

Records of uncertain validity were enclosed in parentheses and denoted with a question mark in Table 1 and are explained more fully below.

Coluber constrictor.—Records of racers on West Sister Island (C. B. Stein, 1974, unpubl. rep. to the U.S. Department of the Interior; D. Alexander, 1975, unpubl. student paper on file at the F. T. Stone Laboratory) are not supported by specimens, photos or additional observations. Racers have been collected or observed on several other islands (Table 1) although none are close to West Sister Island.

Crotalus horridus.—Records of timber rattlesnakes on Pelee, Middle Bass, Rattlesnake and Mouse islands (McDermott, 1947; Langlois, 1964; C. A. Campbell, 1971, unpubl. rep. to the Ontario Department of Lands and Forests; 1976, unpubl. rep. to the Ontario Ministry of Natural Resources Division of Parks) are apparently not based on specimens or direct observation, nor are we aware of other records from these sites. Specimens of timber rattlesnakes are known from South Bass Island and the Catawba/Marblehead peninsula of the Ohio mainland.

Diadophis punctatus.—A record of a ringneck snake on Pelee Island (D. Alexander, 1975, unpubl. student paper on file at the F. T. Stone Laboratory) is not supported by specimens or additional observations. Ringneck snakes have been collected regularly on South Bass Island and a single individual was captured, photographed and released on Middle Bass Island (King, 1987, 1988b).

Elaphe vulpina.—A record of fox snakes on Sugar Island (Mr. Keny, pers. comm. to RBK) is not supported by specimens or additional observations but fox snakes are common on nearby Middle Bass Island and are proficient swimmers (Conant, 1951).

Lampropeltis triangulum.—Records of milksnakes on Pelee and East Sister island (Jones, 1912; D. Alexander, 1975, unpubl. student paper on file at the F. T. Stone Laboratory) are not supported by specimens or additional observations nor have milksnakes been reported from any other islands.

Sistrurus catenatus.—Records of massasaugas on Pelee Island (C. A. Campbell, 1971, unpubl. rep. to the Ontario Department of Lands and Forests; 1976, unpubl. rep. to the Ontario Ministry of Natural Resources Division of Parks) are apparently not based on specimens or direct observations nor have massasaugas been reported from other islands.

Thamnophis sirtalis.—A record of "black snakes" on North Harbor Island (Jones, 1902) may refer to melanistic garter snakes (*see* "Unusual Components of the Island Region's amphibian and reptile fauna"). This record is not supported by specimens or additional observations but garter snakes are common on nearby East Sister Island.

Ambystomatid salamanders.—Because of changes in taxonomy and the occurrence of hy-

ation (Uzzell, 1964; Oldham, 1984a), we have listed records of *Ambystoma jefferson-*
n, A. laterale and *A. texanum* not based on morphometrics, karyology, serology or
ular genetics together with records of known hybrids (including the Kelleys Island
ander, *A. nothagenes*; Kraus, 1985a) as "Hybrid and unidentified *Ambystoma*" in Table
cords of *A. laterale* and *A. texanum* that are based on morphometrics, karyology, se-
or molecular genetics and records of *A. maculatum, A. opacum* and *A. tigrinum* are
separately.

ords known to be based on misidentification were excluded. Records of Kirtland's
(*Clonophis kirtlandii,* Langlois, 1964) and red-bellied water snake (*Nerodia erythro-*
fasciata; Morse, 1904; Jones, 1912) represent misidentified Lake Erie water snakes
pedon insularum; Conant, 1934; Conant and Clay, 1937). A record of a smooth green
(*Opheodrys vernalis*) from South Bass Island appears in the card catalog of the Royal
io Museum (ROM5799). However, this card is marked "Delete and Destroyed - Dis-
d" and along with other cards similarly annotated, apparently refers to a discarded
nen for which reliable identification was not possible (R. MacCulloch, pers. comm.).

INTRODUCTIONS AND COLONIZATIONS

tributions of several amphibian and reptile species may have changed over the period
hich we have records due to natural or human-assisted introductions and colonizations.
na catesbeiana.—Langlois (1964) reports releasing bullfrog tadpoles into a pond on
le Bass Island in 1932, but suggests that this species may have been present before
late. A record of bullfrogs on Pelee Island in 1910 (Jones, 1912) supports this sugges-
Thus, it is unclear whether bullfrog records for some islands represent natural pop-
ns, descendants of introduced individuals or both.

rapene carolina.—Eastern box turtle records for the Ontario mainland and Pelee Is-
are thought to represent escaped or released pets, although the possibility that a native
lation exists at these sites cannot be ruled out (Cook, 1984; Oldham, 1984b).

idophis punctatus.—A single record of a ringneck snake on Middle Bass Island may
sent a recent colonization event (King, 1987, 1988b). Ringneck snakes are present on
y South Bass Island (Langlois, 1953, 1964) and the adjacent Catawba/Marblehead
nsula of the Ohio mainland (Conant, 1938).

gina septemvittata.—Queen snakes are known from Kelleys Island only since 1980 and
have recently colonized the island, presumably from the Ohio mainland (King, 1987,
b). Queen snakes were not recorded from Essex County, Ontario, until 1985 (Oldham,
) but records for Erie and Ottawa counties, Ohio, date from 1908 (Table 1).

o additional lines of evidence attest to the colonization ability of some amphibians
reptiles found on the Lake Erie Islands. First, high rates of gene flow occur among
d and mainland populations of water snakes (*Nerodia sipedon*) and garter snakes
mnophis sirtalis) (King and Lawson, 1995; Lawson and King, 1996). Second, some
es found on the Lake Erie islands (*Ambystoma jeffersonianum, Plethodon cinereus, Bufo*
icanus, Hyla versicolor, Pseudacris crucifer, Chrysemys picta, Elaphe vulpina, Nerodia si-
n, Thamnophis sirtalis) have colonized islands in the upper Great Lakes that were
erly inundated by high water levels (King, 1988b).

WAIFS AND TRANSIENTS

mphibians and reptiles represented by a single observation or specimen from a given
d may represent waif or transient individuals rather than representatives of resident
ding populations. This is especially likely for pond-breeding amphibians and for turtles
lands lacking inland aquatic habitats (*Acris crepitans* on Gibraltar Island, *Bufo ameri-*

TABLE 1.—Distribution of amphibians and reptiles on 19 islands and adjacent mainland areas (Essex County, Ontario; Erie and Ottawa counties, Ohio) of western Lake Erie. Shown is the span of years over which there are records (for species for which there are records in three or more years) or the year of each record (for species for which there are records in one or two years). Records of unknown date are indicated by dashes. Less than (<) and greater than (>) symbols are used to denote records prior to and after the year indicated (these records come from published sources for which year was not specified). Questionable records are enclosed in parentheses and denoted with a question mark (see text for details). Records based on apparent misidentification were omitted (see text for details)

	Mainland		Island						
	Ohio	Ontario	Pelee	Kelleys	South Bass	Middle Bass	North Bass	Johnsons	West Sister
Island area (ha)			4261	1143	619	312	285	117	32
Island perimeter (km)			34.0	18.6	17.5	12.7	8.4	5.3	2.4
Distance to mainland (km)			13.5	5.1	4.5	9.5	13.3	1.1	13.4
Salamanders									
Ambystoma hybrids and unidentified	1941–1994	1984, 1985	1917–1995	1946–1986	1940–>1950	1938–1996	1924–1974		
A. laterale		1984	1980–1984			1937, 1940			
A. maculatum	>1950	1981–1987		1985	>1950	<1950			
A. opacum	<1950>			1985		1978–1994			
A. texanum	1994		1983–1989	1963–1986	1938–1945	1929–1947			
A. tigrinum	<1950–1964	1915							
Desmognathus fuscus	>1950–1972			1928, 1960	1921–1957		1989–1990		
Eurycea bislineata	1907–1972								
Necturus maculosus	1908–>1950	1966–1993			1942–>1950	1943–1961	1929–1979		
Notophthalmus viridescens	1951		1950–1995	1972, 1976	1940–1995	1943			
Plethodon cinereus	1905–1994	1982–1993							
P. glutinosus	1974–1982								
P. richmondi	1971–1982								

TABLE 1.—Extended

	Island											
	Middle	Rattlesnake	East Sister	Sugar	Green	Middle Sister	Ballast	Gibraltar	Mouse	Hen	North Harbour	Starve
Island area (ha)	23	20	17	12	7	5	5	3	3	3	1	0.5
Island perimeter (km)	2.1	2.6	2.3	1.7	1.2	1.2	1.0	0.9	0.9	0.7	0.6	0.3
Distance to mainland (km)	15.6	10.0	19.1	11.3	6.7	15.8	10.6	7.8	0.3	22.4	17.9	4.3
Salamanders												
Ambystoma hybrids and unidentified												
A. laterale												
A. maculatum												
A. opacum												
A. texanum												
A. tigrinum												
Desmognathus fuscus												
Eurycea bislineata												
Necturus maculosus	1982											
Notophthalmus viridescens												
Plethodon cinereus	1989–1996					1996						
P. glutinosus												
P. richmondi												

TABLE 1.—Continued

	Mainland		Island						
	Ohio	Ontario	Pelee	Kelleys	South Bass	Middle Bass	North Bass	Johnsons	West Sister
Island area (ha)			4261	1143	619	312	285	117	32
Island perimeter (km)			34.0	18.6	17.5	12.7	8.4	5.3	2.4
Distance to mainland (km)			13.5	5.1	4.5	9.5	13.3	1.1	13.4
Frogs									
Acris crepitans	1940–1991	1913–1962	1920–1993	1956, 1959		1941–1993	1928–1954		
Bufo americanus	<1904–1994	1920–1995	1910–1995	1951–1989	1942–1996	1928–1995		1991	
B. woodhousii	1941–1992	1913–1949	1936–1960	1961					
Hyla versicolor	1902, 1994	1920, 1941							
Pseudacris crucifer	1940, 1994	1920–1993	1910						
P. triseriata	<1904–1995	1962–1995		1960, 1985					
Rana catesbeiana	<1946–1994	1913–1993	1910–1995		1939–1962	<1946–1983			
R. clamitans	<1904–1994	1920–1995	1987–1993	1980		1952, 1969	1969–1995		
R. palustris	<1946								
R. pipiens	1940–1995	1913–1993	1910–1992	1939–1980	<1946	1939–1952	1941		1938
R. sylvatica	<1904								
Lizards									
Eumeces faciatus	1958–1994	1890–1993							
Turtles									
Apalone spinifera	<1904–1980	<1939–1995	1971						
Chelydra serpentina	<1904–1994	1913–1993	1910–1992	1952–1982	<1938–1979	1952, 1981			
Chrysemys picta	<1904–1994	1913–1995	1910–1995	1979–1983	1939–1981	1939–1996	<1938–1996	1982	
Clemmys guttata	<1938–1941	1913–1992	1987, 1989						
Emydoidea blandingii	1900–1994	1913–1995	1910–1995	1982, 1983	1952, 1960	1928–1980	1939–1984		
Graptemys geographica	<1904–1980	1920–1993	1980–1992		1930–1968			1991	
Sternotherus odoratus	1900–1933	1913–1989							
Terrapene carolina	<1938–1994	1960–1990	1974, 1988						

	Island											
	Middle	Rattlesnake	East Sister	Sugar	Green	Middle Sister	Ballast	Gibraltar	Mouse	Hen	North Harbour	Starve
Island area (ha)	23	20	17	12	7	5	5	3	3	3	1	0.5
Island perimeter (km)	2.1	2.6	2.3	1.7	1.2	1.2	1.0	0.9	0.9	0.7	0.6	0.3
Distance to mainland (km)	15.6	10.0	19.1	11.3	6.7	15.8	10.6	7.8	0.3	22.4	17.9	4.3
Frogs												
Acris crepitans								1947				
Bufo americanus	1979, 1981			1989								
B. woodhousii								1970				
Hyla versicolor												
Pseudacris crucifer	(1979?)											
P. triseriata												
Rana catesbeiana	1979–1988	1989	1988		1989			1942				
R. clamitans	1980											
R. palustris												
R. pipiens												
R. sylvatica												
Lizards												
Eumeces faciatus												
Turtles												
Apalone spinifera								1938, 1981				
Chelydra serpentina	1992		1992									
Chrysemys picta												
Clemmys guttata												
Emydoidea blandingii					1930							
Graptemys geographica								1938				
Sternotherus odoratus												
Terrapene carolina												

TABLE 1.—Continued

	Mainland		Island						
	Ohio	Ontario	Pelee	Kelleys	South Bass	Middle Bass	North Bass	Johnsons	West Sister
Island area (ha)			4261	1143	619	312	285	117	32
Island perimeter (km)			34.0	18.6	17.5	12.7	8.4	5.3	2.4
Distance to mainland (km)			13.5	5.1	4.5	9.5	13.3	1.1	13.4
Snakes									
Carphophis amoneus	1941–1945								
Clonophis kirtlandii	<1938–1956								
Coluber constrictor	<1904–1980	1906	1910–1995	<1938–1996	<1938–1996	1938–1981		1982	(1975?)
Crotalus horridus	<1938–1951	1918	(—?)		1929–1961	(1793?)			
Diadophis punctatus	1918–1970		(1975?)		1930–1995	1984			
Elaphe obsoleta	1904	1910, 1915	1910		<1938, 1950				
E. vulpina	1897–1996	1913–1995	1909–1995	1956–1996	<1938–1995	<1938–1996	1979–1996	1981–1983	1980, 1992
Heterodon platirhinos	1886–1946	1907–1979	1910, 1939	1958–1996	1920s				
Lampropeltis triangulum	1908–1957	1909–1986	(1910?)						
Nerodia sipedon	1895–1996	1900–1994	1910–1995	1894–1996	1893–1996	1934–1996	1937–1996	1981–1983	1938, 1939
Opheodrys vernalis	1897–1994	1984, 1985							
Regina septemvittata	1904–1996	1985, 1992		1980–1982				1981–1991	
Sistrurus catenatus	1907–1968	<1881–1993	(—?)						
Storeria dekayi	1905–1996	1913–1994	1950–1995	1956–1985	<1938–1995	1942–1996	1940–1996		
S. occipitomaculata		1984–1992			1937–1996				
Thamnophis butleri	1904–1995	1976–1994							
T. sauritus	<1938	—							
T. sirtalis	1900–1996	1881–1995	1910–1995	1939–1996		1939–1996	1939–1996		1938–1996

TABLE 1.—Extended—Continued

	Island											
	Green	Middle Sister	Ballast	Gibraltar	Mouse	East Sister	Hen	North Harbour	Starve	Rattlesnake	Middle	Sugar
Island area (ha)	7	5	5	3	3	17	3	1	0.5	20	23	12
Island perimeter (km)	1.2	1.2	1.0	0.9	0.9	2.3	0.7	0.6	0.3	2.6	2.1	1.7
Distance to mainland (km)	6.7	15.8	10.6	7.8	0.3	19.1	22.4	17.9	4.3	10.0	15.6	11.3
Snakes												
Carphophis amoneus					(<1964?)							
Clonophis kirtlandii												
Coluber constrictor												
Crotalus horridus										(<1964?)		
Diadophis punctatus												
Elaphe obsoleta												
E. vulpina			1996	1962–1996						<1938–1989	1981, 1982	1980–1992
Heterodon platirhinos												
Lampropeltis triangulum												(1975?)
Nerodia sipedon	1930, 1948	1941	1927–1996	1931–1996	1934		1986–1990	1939	1939	1907–1996	1939–1992	1939–1992
Opheodrys vernalis												
Regina septemvittata												
Sistrurus catenatus												
Storeria dekayi	1938–1992		1996	1933–1996						1930–1996	1940–1992	1980–1987
S. occipitomaculata												
Thamnophis butleri												
T. sauritus												
T. sirtalis	1981		1996	1960				(1901?)		1989–1996	1949–1992	1992, 1996

canus on Middle and Sugar islands; *B. woodhousii* on Gibraltar Island; *Rana catesbeiana* on Middle, Rattlesnake, East Sister, Green and Gibraltar islands; *R. clamitans* on Middle Island; *R. pipiens* on West Sister Island; *Apalone spinifera* on Gibraltar Island; *Chelydra serpentina* on East Sister and Middle islands; *Emydoidea blandingii* on Green Island; *Graptemys geographica* on Gibraltar Island).

POPULATION DECLINES AND LOCAL EXTIRPATIONS

Population declines and local extirpations have affected a number of amphibian and reptile species in the Lake Erie area (*e.g.,* Ehrlich and Camin, 1960; Conant and Clay, 1963; Conant, 1982; Kraus and Schuett, 1982). Some declines have been the intentional result of human activities (extermination of snakes by pigs and humans, Ehrlich and Camin, 1960; Hatcher, 1971; Conant, 1982). Others may be a secondary result of human activities (*e.g.,* habitat modification) or natural processes.

Pond-breeding amphibians.—Recent records (post-1960) are lacking for some pond-breeding amphibians on islands from which they were previously recorded (*e.g.,* ambystomatid salamanders from South Bass and North Bass islands, *Notophthalmus viridescens* from Kelleys and South Bass islands, *Acris crepitans* from Kelleys and North Bass islands, *Pseudacris crucifer* from Pelee Island, *Rana pipiens* from South Bass, Middle Bass and North Bass islands). Although some species may have been overlooked during recent field work, degradation and loss of breeding habitat (inland ponds) may have resulted in extirpation of pond-breeding amphibians at some sites (Downs, 1978; King, 1993a). Population declines of *A. crepitans* on Pelee Island and the Ontario mainland have led to provincial protection in Ontario (Oldham, 1992).

Necturus maculosus.—Mudpuppies are encountered infrequently in waters of the island region (*e.g.,* by ice anglers or as prey of water snakes, Oldham, 1988; King, 1993a). Apparent decreases in Lake Erie mudpuppy populations are reported by Pfingsten and Downs (1989).

Graptemys geographica.—Common map turtles once were abundant at Terwilliger's Pond adjacent to the F. T. Stone Laboratory on South Bass Island (Langlois, 1964), but none have been recorded on that island since 1968. Common map turtles persist in small numbers on Pelee and Johnsons islands and on the Ohio and Ontario mainland.

Coluber constrictor.—Racers are found on several of the larger islands (Table 1) but because Pelee Island is the only Ontario location where racers persist, this species has been given provincial protection (McKeating and Bowman, 1977).

Crotalus horridus.—Timber rattlesnakes found on South Bass Island and the Catawba/Marblehead peninsula of mainland Ohio were often killed (Langlois, 1951, 1964) and no records more recent than 1961 are known. Timber rattlesnakes appear to have been extirpated from the island region although fox snakes (*Elaphe vulpina*) are sometimes mistakenly identified as rattlesnakes by island residents and visitors. Because the region is well isolated from other timber rattlesnake populations (*e.g.,* in southern Ohio and western Pennsylvania; Conant and Collins, 1991), natural recolonization of the island region by this species is unlikely.

Heterodon platirhinos.—Eastern hognose snakes continue to be recorded on Kelleys Island. However, records from South Bass and Pelee islands date from the 1920s and 1930s (Table 1) and it seems unlikely that hognose snakes persist at these sites.

Nerodia sipedon.—Water snakes are the most widely distributed species included in this study; specimens have been collected from each of the 19 islands (Table 1). However, no water snakes were found during repeated searches on West Sister and Green islands and shorter searches on Middle Sister and North Harbour islands by RBK, MJO and coworkers during the 1980s and 1990s, suggesting that this species has been extirpated on these is-

ds. Declines in water snake numbers have occurred on those islands where populations sist (King, 1986), resulting in provincial protection on Canadian islands and proposed eral protection on U.S. islands (McKeating and Bowman, 1977; Eldridge and Winsor, 3). Water snakes persist on Rattlesnake and Middle islands despite past eradication ef- s (Conant, 1982; Ehrlich and Camin, 1960); either these efforts were not completely cessful or water snakes recolonized these islands. We are unaware of recent field work Mouse or Starve islands and the current status of water snakes (and other amphibians reptiles) on these islands is unknown.

UNUSUAL COMPONENTS OF THE ISLAND REGION'S AMPHIBIAN AND REPTILE FAUNA

mbystomatid salamanders.—Ambystomatid salamanders from the island region exhibit sual patterns of polyploidy, hybridization and unisexual reproduction (Downs, 1978; gart *et al.*, 1985; Kraus, 1985a, 1985b, 1989; Bogart and Licht, 1986; Bogart *et al.*, 1987; gart, 1989; Licht, 1989; Lowcock, 1989; Hedges *et al.*, 1992). On Pelee Island, *A. laterale* *A. texanum* occur together with unisexual diploid, triploid and tetraploid hybrids con- ing genomes from *A. laterale* and *A. texanum*; on Kelleys Island, *A. texanum* and *A. inum* occur together with unisexual diploid, triploid and tetraploid hybrids containing omes from *A. laterale, A. texanum* and *A. tigrinum*; on Middle Bass Island, *A. texanum* urs together with unisexual diploid and triploid hybrids containing genomes from *A. rale* and *A. texanum*; and on North Bass Island, unisexual diploid and triploid hybrids taining genomes from *A. laterale* and *A. texanum* occur. Interestingly, there are no fiable records of one or more parental species from some islands with hybrid popula- s (*A. laterale* apparently is absent from Kelleys, Middle Bass and North Bass islands; *A. inum* apparently is absent from North Bass Island), warranting further work on these nds. Unfortunately, it is uncertain whether ambystomatid populations persist on North s Island; no records since 1972 are known to us. Colonization events and changes in ribution are thought to have been particularly important in promoting interspecific ridization in ambystomatid salamanders (Lowcock, 1989).

Plethodon cinereus.—The redback salamander occurs as a striped redback morph and a peless leadback morph (Conant and Collins, 1991). Morph frequencies vary geograph- ly, perhaps due to an association between color morph and physiology (Lotter and Scott, 7; Moreno, 1989). Although *P. cinereus* is locally abundant on South Bass island, redback rphs are exceedingly rare (0 of 144 salamanders, Pfingsten and Walker, 1978; 1 of 132 manders, Reichenbach, 1981; 0 of 100 salamanders, RBK, pers. observ.). Recently dis- ered populations on Rattlesnake and Middle Sister islands also consist of leadback rphs (Rattlesnake Island: n = 5, RBK, pers. observ.; Middle Sister Island: n = 5, Oldham, 6). Redback morphs are more common in nearby Ohio mainland populations (7–80%, = 22–230, Pfingsten and Walker, 1978) and it is unknown whether differences in morph quency between island and mainland populations are the result of natural selection posed by climatic differences or stochastic processes resulting from isolation.

Nerodia sipedon.—Reduction in color pattern among island water snakes relative to main- d populations has led to designation of island populations as *N. s. insularum,* distinct m mainland *N. s. sipedon* (Conant and Clay, 1937; 1963). Color pattern variation is netically based and island–mainland differences appear to represent a balance between ural selection favoring a reduced pattern along rocky island shorelines and gene flow m populations inhabiting mainland marshes where patterned morphs are favored (King, 3b, 1993c; King and Lawson, 1995).

Thamnophis sirtalis.—Populations of garter snakes in the Lake Erie area include high quencies (up to ca. 50%) of jet-black melanistic individuals (King, 1988a; Lawson and

King, 1996). Melanistic morphs have an apparent thermoregulatory advantage in cool, lakeshore habitats but may suffer higher predation than typical striped morphs (Gibson and Falls, 1979, 1988). Geographic variation in the relative advantage of striped vs. melanistic color pattern together with gene flow among populations may be responsible for variation in morph frequency among sites in the Lake Erie area (Lawson and King, 1996).

BIOGEOGRAPHY

Most of the amphibians and reptiles found in the island region as defined here are found in other lakeshore counties of Ohio, Michigan and Ontario (Conant, 1938, 1951; Walker, 1946; Kraus and Schuett, 1982; Weller and Oldham, 1988; Holman *et al.*, 1989; Pfingsten and Downs, 1989; Harding and Holman, 1990, 1992). However, two species recorded from mainland Essex County, Ontario, were lacking from mainland Erie and Ottawa counties in Ohio. *Ambystoma laterale* has been recorded in nearby Lucas County, Ohio (Kraus, 1985b; Pfingsten and Downs, 1989), but *Storeria occipitomaculata* is absent from all Ohio counties bordering Lake Erie (Conant, 1951). Twelve species recorded from mainland Erie and Ottawa counties, Ohio, were lacking from mainland Essex County, Ontario. Of these, *Desmognathus fuscus, Eurycea bislineata, Plethodon glutinosus, P. richmondi, A. opacum, A. texanum, Clonophis kirtlandii* are distributed mostly S or E of the area included here (Conant and Collins, 1991) and their absence from Essex County is not surprising. *Notophthalmus viridescens, Rana palustris, R. sylvatica* and *Diadophis punctatus* are found in neighboring Kent County, Ontario, and in lakeshore counties in Michigan (Weller and Oldham, 1988; Harding and Holman, 1992; Holman *et al.*, 1989) and their absence from mainland Essex County is unexplained. The worm snake, *Carphophis amoneus,* is unusual in that it has been recorded from a single locality in Erie County (a marl prairie N of Castalia, Ohio) that is isolated by more than 150 km from other known worm snake localities in the southern third of Ohio (Conant, 1951). Six specimens were collected from the Erie County site by C. F. Walker in 1941 and 1942 (F. T. Stone Laboratory herpetological collection #775, 795, 922-924) and by N. B. Green in 1945 (UMMZ 95933) but the current status of this population is unknown.

On a larger scale, species found in the island region exhibit a variety of biogeographic patterns. Some species are distributed nearly continuously across much of eastern North America (*e.g., Chelydra serpentina, Chrysemys picta, Nerodia sipedon, Thamnophis sirtalis*), whereas others have restricted ranges centered near the southern Great Lakes (*e.g., Clonophis kirtlandii, Elaphe vulpina, Thamnophis butleri*) (Conant and Collins, 1991). The extension of prairie habitat (the 'prarie peninsula') into western Ohio may explain the presence in the Lake Erie area of some species with more western distributions (*e.g., Ambystoma texanum, A. tigrinum, Acris crepitans*) as well as gaps SW of Lake Erie in the distribution of other species (*e.g., Notophthalmus viridescens, Storeria occipitomaculata, Diadophis punctatus*).

Except for snakes, most species of amphibians and reptiles were restricted to the five largest islands (Table 1). Exceptions include apparent waifs and transients noted earlier; *Plethodon cinereus,* the single terrestrially breeding salamander found on the islands; and *Necturus maculosus,* which is a lake (rather than island) resident. Among snakes, four species stand out as being widely distributed on islands of all sizes: *Elaphe vulpina, Nerodia sipedon, Storeria dekayi* and *Thamnophis sirtalis.*

On islands, number of species is according to Island Biogeography Theory often positively correlated with island area and negatively correlated with distance to the mainland. Such a pattern is expected when species numbers result from an equilibrium between colonization and extinction: extinction rates should decrease with increasing population size, and

ABLE 2.—Species–area and species–distance relationships for all amphibians and reptiles recorded slands in Lake Erie; for amphibians and reptiles recorded in 1980 or later; and for salamanders, s and toads, turtles and snakes. Questionable records (enclosed in parentheses and denoted with uestion mark in Table 1) were excluded. Island area (ha), distance to the nearest mainland point), and number of species were $\log_{10}$ transformed prior to analysis. Because log(0) is undefined, ds lacking salamanders, frogs or turtles were excluded from analysis of species–area and species–nce relationships for those taxa. For species–area relationships, slopes and intercepts come from ple linear regression of species number on island area, r^2 is the coefficient of determination, and the associated two-tailed probability. For species–distance relationships, r is the product-moment elation coefficient or partial correlation coefficient (controlling for island area) and P is the as-ated two-tailed probability

		Species–area relationship				Species–distance relationship: Simple correlation		Species–distance relationship: Partial correlation	
Taxa	# of Islands	Slope	Intercept	r^2	P	r	P	r	P
	19	0.38	0.18	0.77	<0.001	0.11	0.647	0.21	0.394
since 1980	16	0.31	0.20	0.66	<0.001	−0.34	0.204	−0.15	0.596
manders	8	0.28	−0.25	0.67	0.013	−0.76	0.028	−0.74	0.058
gs and toads	13	0.25	−0.13	0.49	0.008	0.10	0.755	0.30	0.347
tles	10	0.23	−0.13	0.69	0.003	−0.16	0.663	−0.14	0.714
kes	19	0.24	0.15	0.66	<0.001	0.09	0.720	0.14	0.587

nce island area, and colonization rates should decrease with increasing distance from rce populations (MacArthur and Wilson, 1967). However, other factors (habitat diversity, nd age) may also be important determinants of species number. A previous analysis of tiles on nine Lake Erie islands showed a positive relationship between species number l island area but no relationship between species number and distance to the mainland ng, 1987, 1988b). Extending this analysis to include additional islands and taxa corrob-tes this result: species number is significantly positively correlated with island area but correlated with distance to the nearest mainland point regardless of whether all am-bian and reptile records are included or only recent (1980 or later) records are included ble 2). Because different taxa (*e.g.*, salamanders, frogs, turtles, snakes) may exhibit dif-ent species–area and species–distance relationships, we also analyzed each taxon sepa-ely. For all four taxa, species number was significantly positively correlated with island a (Table 2). For frogs, turtles and snakes, species number was not correlated with dis-ce to the mainland, whereas for salamanders there was a significant negative correlation ween species number and distance to mainland (Table 2).

On land-bridge islands, a positive correlation between species number and island area no correlation between species number and distance to the mainland can occur when ufficient time has elapsed for species numbers to decline to a extinction-colonization uilibrium (Wilcox, 1978; Case, 1983). This may be the case for islands in Lake Erie which e been isolated from the mainland for only about 4000 yr (Calkin and Feenstra, 1985). wever, there may be other reasons why the number of amphibian and reptile species on Lake Erie islands is uncorrelated with distance to the mainland. Some islands are close other islands that could serve as sources of colonists, masking any species-distance rela-nship based on island-mainland distances. For example, Gibraltar Island, which has nine cies of amphibians and reptiles compared to just four or fewer species on other similarly ed islands, lies nearly 8 km from the nearest mainland point but is just 0.2 km from

South Bass Island with 22 species, and 1.4 km from Middle Bass Island with 19 species. In addition, species lists for some islands may be incomplete or inflated by inclusion of non-resident (waif or transient) species.

Other components of the Lake Erie island biota also show a positive correlation between species number and island area and provide examples of colonization and local extinction (*e.g.*, vascular plants: Duncan and Stuckey, 1970; Klinkenberg, 1988; isopods: Dexter *et al.*, 1988; spiders: Beatty, 1988; beetles: Will *et al.*, 1995; butterflies: Nault *et al.*, 1989; colonial waterbirds: Weseloh *et al.*, 1988; mammals: Campbell *et al.*, 1988; Jackson, 1988). As with amphibians and reptiles, changes in distribution of these taxa reflect habitat changes resulting from human activities (Duncan and Stuckey, 1970; Weseloh *et al.*, 1988). Although it is unlikely that human impacts can be prevented entirely, data such as we present here are valuable in assessing and potentially mitigating these impacts.

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APPENDIX 1

Museum collections included in the OHS, ODNR, and RBK data bases: American Museum of Natural History, New York, New York (ODNR, RBK); Bowling Green State University, Bowling Green, Ohio (ODNR); California Academy of Sciences, San Francisco, California (RBK); Canadian Museum of Nature, Ottawa, Ontario (OHS, RBK); Carnegie Museum of Natural History, Pittsburgh, Pennsylvania (OHS, ODNR); Chicago Academy of Sciences, Chicago, Illinois (OHS, RBK); Cincinnati Museum of Natural History, Cincinnati, Ohio (ODNR, RBK); Cleveland Museum of Natural History, Cleveland, Ohio (ODNR, RBK); College of Wooster, Wooster, Ohio (ODNR); Cornell University, Ithaca, New York (OHS, RBK); Dayton Museum of Natural History, Dayton, Ohio (ODNR); Defiance College, Defiance, Ohio (ODNR); Ehrhart Museum, Antwerp, Ohio (ODNR); Field Museum of Natural History, Chicago, Illinois (RBK); Florida State Museum, University of Florida, Gainesville, Florida (RBK); F. T. Stone Laboratory, Put-in-Bay, Ohio (RBK); Illinois Natural History Survey, Urbana, Illinois (RBK); Louisiana State University Museum of Zoology, Baton Rouge, Louisiana (RBK); Marshall University, Huntington, West Virginia (ODNR); Miami University, Oxford, Ohio (RBK, ODNR); Milwaukee Public Museum, Milwaukee, Wisconsin (OHS, ODNR); Montgomery County Herpetological Survey, Ohio (ODNR); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (OHS, RBK); Museum of Vertebrate Zoology, University of California, Berkeley, California (RBK); National Museum of Natural History, Washington, District of Columbia (OHS, ODNR); Natural History Museum of Los Angeles County, Los Angeles, California (RBK); Ohio State University Museum of Zoology, Columbus, Ohio (ODNR, RBK); Ohio University, Athens, Ohio (ODNR); Royal Ontario Museum, Toronto, Ontario (OHS, RBK); University of Guelph, Guelph, Ontario (OHS); University of Illinois Museum of Natural History, Urbana-Champaign, Illinois (RBK); University of Kansas Museum of Natural History, Lawrence, Kansas (RBK); University of Michigan Museum of Zoology, Ann Arbor, Michigan (OHS, ODNR, RBK);

University of Ottawa, Ottawa, Ontario (OHS); University of Western Ontario, London, Ontario (OHS); Wilfrid Laurier University, Waterloo, Ontario (OHS).

Appendix 2

Published sources of records included in the RBK data base: Bogart and Licht (1986), Bogart *et al.* (1985); Bogart *et al.* (1987), Camin and Ehrlich (1958), Camin *et al.* (1954), Catling and Freedman (1980a, 1980b), Conant (1938, 1951, 1965, 1982), Conant and Clay (1937), Cook (1964, 1984), Dance and Campbell (1981), Downs (1978), Ehrlich and Camin (1960), Green (1989), Hamilton (1951), Jones (1902, 1912), King (1985), Kraus (1985a; 1985b), Kraus and Schuett (1982), Langlois (1964), Licht and Bogart (1990), Logier (1925), Logier and Toner (1961), Lowcock and Bogart (1992), McDermott (1947), Mineau and Markel (1981), Morse (1904), Oldham (1986), Patch (1919), Pfingsten and Downs (1989), Pfingsten and Walker (1978), Reichenbach (1981), Taverner (1914), Thomas (1949), Uzzell (1962), Walker (1946).

Appendix 3

Voucher specimens included in the RBK data base and deposited in the Field Museum of Natural History (FMNH) and California Academy of Sciences (CAS) (specimens in the FMNH are part of the snake stomach-contents collection and are not individually cataloged): *Ambystoma* sp. (larvae)—FMNH; *Emydoidea blandingi*—CAS (photos); *Coluber constrictor*—CAS198602–198603; *Diadophis punctatus*—CAS (photos); *Elaphe vulpina*—CAS198470, 198605; *Heterodon platirhinos*—CAS198604; *Necturus maculosus*—FMNH; *Nerodia sipedon*—CAS198467–198469, 198484, 198506–198515, 198546–198573, 198578–198580, 198582, 198595–198601; *Plethodon cinereus*—CAS198606–198609; *Rana catesbeiana*—FMNH; *Rana pipiens*—FMNH, *Regina septemvittata*—CAS (photos); *Storeria dekayi*—CAS197642–197879, 1987881–197882; *Storeria occipitomaculata*—CAS197641; *Thamnophis butleri*—CAS197638–197640; *Thamnophis sirtalis*—CAS197638–197640, 198460–198466, 198471–198483, 198485–198505, 198516–198545, 198574–198577, 198581, 198583; 198588–198594.