POLYMORPHIC POPULATIONS OF THE GARTER SNAKE *THAMNOPHIS SIRTALIS* NEAR LAKE ERIE

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ABSTRACT: Populations of the garter snake *Thamnophis sirtalis* in the Lake Erie area are polymorphic, consisting of striped and melanistic morphs. The frequency of melanistic morphs is similar between sexes but varies greatly among seven island and 15 mainland sites: from 0.00–0.59. Thermoregulatory differences thought to exist between morphs have not resulted in differences between morphs in frequency of reproduction by adult females or in snout–vent length of adults of either sex. Non-selective factors (genetic drift, founder effect) may influence morph frequencies but have not produced significantly greater variance in morph frequency among island sites than among mainland sites.

Key words: *Thamnophis sirtalis*; Polymorphism; Melanism; Island populations; Natural selection; Genetic drift

ISLAND and mainland populations of the garter snake *Thamnophis sirtalis* near Lake Erie exhibit a striking color pattern polymorphism. In addition to the typical striped morph, these populations include a melanistic morph which is uniformly black except for a white patch on the chin and throat (Blanchard and Blanchard, 1940; Conant, 1951). Melanism is inherited in a simple Mendelian fashion with the melanistic allele recessive to the striped allele (Blanchard and Blanchard, 1940). In most species of snakes, melanistic individuals occur only at low frequencies. However, some Lake Erie populations of garter snakes are as much as 59% melanistic.

Melanistic morphs apparently have a thermoregulatory advantage over striped morphs but may suffer a cost resulting from increased predation (Gibson, 1978; Gibson and Falls, 1979). The high frequency of melanistic morphs in the Lake Erie area may reflect a shift in the balance between selection for thermoregulatory ability and selection for crypsis, a shift due to low temperatures brought about by the thermal inertia of Lake Erie (Gibson and Falls, 1979). The thermoregulatory advantage of melanistic morphs may enable them to forage for longer periods or assimilate food

more rapidly, resulting in higher growth rates and larger body sizes. This may provide melanistic morphs with a reproductive advantage by allowing them to reproduce at a younger age, to reproduce more often, or to produce larger numbers of offspring. However, ecological differences among morphs have not been observed in the field (Gibson, 1978).

Non-selective forces such as genetic drift, founder effects, and inbreeding also may influence morph frequencies in Lake Erie populations of garter snakes. Because island populations typically are smaller and presumably more insulated from gene flow than are mainland populations, non-selective forces are expected to result in greater variance in morph frequency among island populations than among mainland populations (Hartl, 1981). In the extreme, island populations may be fixed for alternate morphs.

In this paper, I evaluate the significance of selective and non-selective influences on this garter snake color pattern polymorphism based on a population study at seven island and two mainland sites and on published data from 13 additional mainland sites in the Lake Erie area. I test for selective differences that may result from differential thermoregulatory ability by comparing morphs with respect to snout–vent length (both sexes) and frequency of reproduction (females). I test for non-se-

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lective factors by comparing variance in morph frequency among island sites with that observed among mainland sites.

MATERIALS AND METHODS

Data on garter snakes were collected in conjunction with an investigation of color pattern polymorphism in the Lake Erie water snake, *Nerodia sipedon insularum* (King, 1985, 1986, 1987). Fieldwork was conducted on seven islands (Kellys, Middle, Pelee, North Bass, Middle Bass, East Sister, and West Sister) and at two mainland sites (Little Portage Wildlife Area and East Harbor State Park) from 1980–1985 (Fig. 1). Garter snakes were captured by hand without regard to morph and were individually marked by clipping combinations of ventral scales (Brown and Parker, 1976). Snout–vent length (SVL) and total length (TL) were measured to the nearest 1 cm. Sex was determined by probing the cloacal opening with a blunt probe approximately 1 mm in diameter (Laszlo, 1973). Reproductive condition of females was noted by palpating the abdomen for developing embryos. Snakes were scored by morph (striped or melanistic) and were released at the point of capture, usually within 15 min. Data on the frequency of melanistic morphs at additional sites were compiled from Gibson (1978), Kraus and Schuett (1982), Oldham and Sutherland (1986), and Sattler and Guttman (1976).

Snakes were classified as juveniles or adults using size frequency histograms constructed separately for each sex (Fig. 2). Females <46 cm SVL and males <36 cm were scored as juveniles. Longer snakes were scored as adults. These size cut-offs were corroborated by reproductive data on females (Fig. 2) and by data from other studies. Minimum sizes (SVL) reported for reproductive female *T. sirtalis* are 42.6 cm (Carpenter, 1952), 47 cm (Gregory, 1977), and 50.4 cm (Fitch, 1965). For reproductive male *T. sirtalis,* minimum sizes are 38.7 cm (Fitch, 1965) and 39.7 cm (Carpenter, 1952).

The method of log-linear analysis (Bishop et al., 1974) was used to test for independence among sex, morph, and site, and in females among morph, site, and repro-

ductive status. Tests of independence were based on comparisons of the fit obtained between a model containing and a model lacking a particular interaction, using the log-likelihood ratio, G [see King (1987) for description of a similar analysis]. Models were fit using a screening process provided by BMDP-77 program P3F (Dixon and Brown, 1977). Calculation of G involves logarithms and so all cell frequencies must be >0. As a consequence, 0.5 was added to all cells (Bishop et al., 1974).

Adult SVL was compared between morphs and sexes by analysis of variance (ANOVA) after testing for normality and equality of variances using the SPSS statistical package (Nie et al., 1975). The hypothesis that variance in morph frequency is greater among island sites than among mainland sites was tested using a one-sided F test (Sokal and Rohlf, 1981). A significance level of 0.05 was used in all analyses.

Because of time constraints, some snakes were not sexed or measured. These snakes were excluded from all analyses except the comparison of variance in morph frequency between island and mainland sites. In all analyses, only data from first captures were used.

RESULTS

A total of 818 captures of 759 garter snakes (109 adult males, 345 adult females, 305 juveniles and unsexed adults) were made at the nine sites included in this study. Log-linear analysis of the three-way table of morph, sex, and site revealed significant differences in the morph frequency of adult snakes among the seven sites containing both melanistic and striped morphs (independence of morph and site: $G = 29.41$, df = 6, $P = 0.0001$), but not between males and females (independence of morph and sex: $G < 0.01$, df = 1, $P = 0.95$).

Additional data on morph frequency for five of the sites included in this study (Pelee, Little Portage Wildlife Area, Middle Bass, West Sister, and Kellys), and for 13 other sites in the Lake Erie area were obtained from the literature. Morph frequencies did not differ between published values and values that I obtained for the five sites for which both were available (G
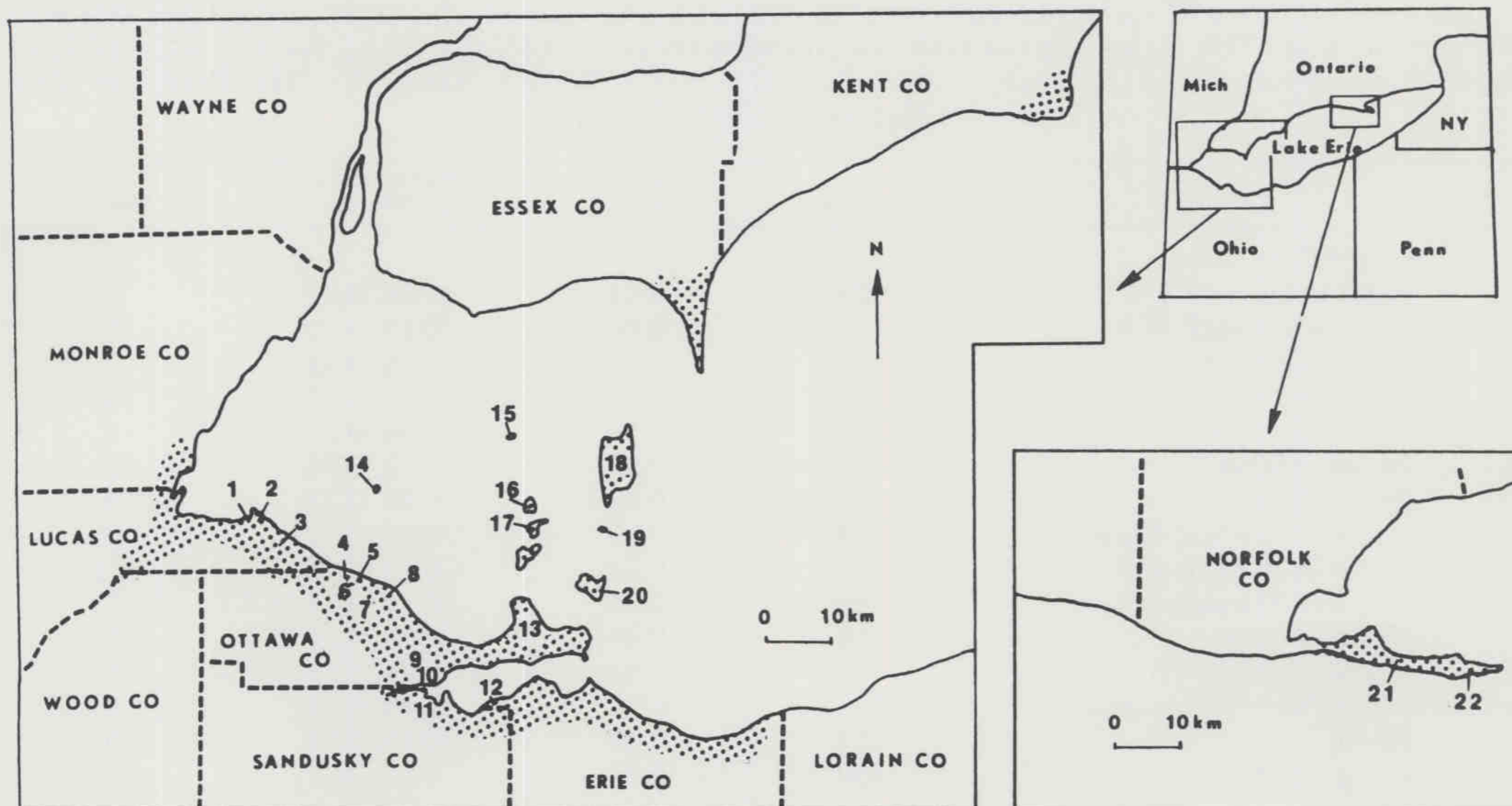
Fig. 1.—Distribution of melanistic garter snakes, *Thamnophis sirtalis*, in the Lake Erie area (stippled areas) based on Conant (1951), Gibson (1978), Kraus and Schuett (1982), Sattler and Guttman (1976), specimen #127196 in the University of Michigan Museum of Zoology, and this study. Sites for which morph frequency data are available (Table 1) are: 1 = Nile's Woods, 2 = Cedar Point NWR, 3 = Bono, 4 = Crane Creek SP, 5 = Magee Marsh, 6 = Ottawa NWR, 7 = Toussaint Creek WA, 8 = Navarre Marsh, 9 = Little Portage WA, 10 = Winous Point, 11 = Ottawa Shooting Club, 12 = Willow Point WA, 13 = East Harbor SP, 14 = West Sister Island, 15 = East Sister Island, 16 = North Bass Island, 17 = Middle Bass Island, 18 = Pelee Island, 19 = Middle Island, 20 = Kellys Island, 21 = Long Point Breakwater, 22 = Long Point Tip (abbreviations as in Table 1). Melanistic garter snakes are apparently absent from North Bass Island (site 16) but are known from the other islands shown.

tests, $P > 0.05$ in all cases), so data were pooled across studies. Across all 22 sites, frequency of the melanistic morph averaged 0.23 and ranged from 0.00–0.59 (Table 1). Sites quite close to each other sometimes differed greatly in morph frequency. For example, North Bass Island and Middle Bass Island, <2 km apart, differed in morph frequency by 17% (test of difference between two proportions, $P < 0.001$; Neter et al., 1978). Long Point Tip and Long Point Breakwater, about 15 km apart, differed by 21% ($P < 0.001$; Gibson, 1978).

Gravid females could be detected by palpation as early as 14 May and increased in frequency over the active season (proportion gravid = 0.05, 0.10, 0.60, and 0.75 among adult females captured in May, June, July, and August, respectively). Proportion of detectably gravid females increased with increasing SVL (proportion gravid = 0.26, 0.42, 0.68, and 0.68 among adult females <61 cm, 61–70 cm, 71–80
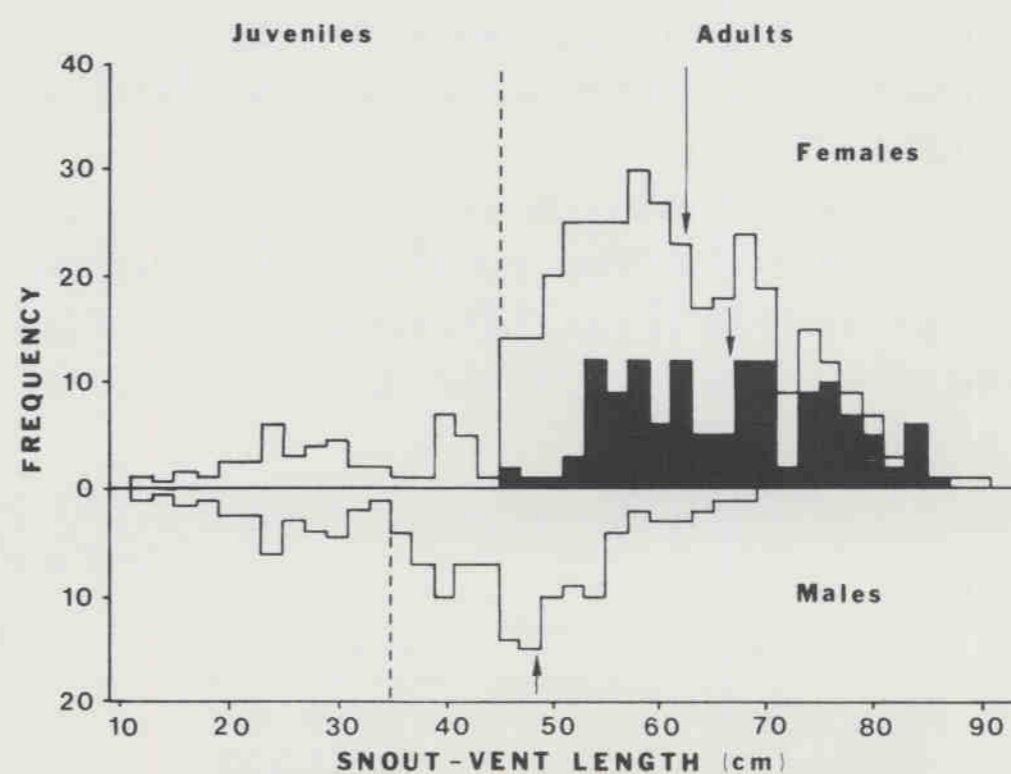

Fig. 2.—Size-frequency histograms for Lake Erie area garter snakes for all sites combined (females above, males below). Gravid females are indicated by the shaded area, nongravid females by the unshaded area. Unsexed snakes <36 cm SVL are divided evenly between males and females. Dashed lines indicate size cut-offs for juvenile and adult snakes (see text). Size intervals are 2 cm. Mean SVL's for adult males (48.7 cm, $n = 109$), adult females (62.3 cm, $n = 345$), and gravid females (66.7 cm, $n = 134$) are indicated by arrows.

TABLE 1.—Frequency of melanistic garter snakes (ages and sexes combined) at sites in the Lake Erie area. For $n < 50$, exact 95% confidence intervals are presented (Beyer, 1968:Table III.5). For $n > 50$, confidence intervals are approximated (Hollander and Wolfe, 1973). WA = Wildlife Area, SP = State Park, and NWR = National Wildlife Refuge.

Site	Sample size	Proportion melanistic	95% confidence interval	Source*
Mainland sites				
Willow Point WA	24	0.04	0.00, 0.21	3
Toussaint Creek WA	33	0.06	0.01, 0.20	3
Crane Creek SP	15	0.07	0.00, 0.32	3
Ottawa NWR	39	0.08	0.02, 0.21	3
East Harbor SP	104	0.10	0.04, 0.15	1
Magee Marsh	30	0.10	0.02, 0.27	3
Nile's Woods	18	0.22	0.06, 0.48	3
Ottawa Shooting Club	24	0.25	0.10, 0.47	3
Little Portage WA	41	0.29	0.16, 0.46	1, 3
Navarre Marsh	20	0.30	0.12, 0.54	3
Winous Point	13	0.31	0.09, 0.61	3
Cedar Point NWR	16	0.31	0.11, 0.59	3
Long Point Breakwater	140	0.36	0.28, 0.44	4
Bono	52	0.40	0.27, 0.53	5
Long Point Tip	460	0.57	0.53, 0.62	4
Island sites				
North Bass Island	78	0.00	0.00, 0.05	1
Kellys Island	17	0.06	0.00, 0.27	1, 3
Middle Island	257	0.13	0.09, 0.17	1
Middle Bass Island	95	0.18	0.10, 0.26	1, 3
West Sister Island	81	0.30	0.20, 0.40	1, 3
Pelee Island	237	0.30	0.24, 0.36	1, 2
East Sister Island	41	0.59	0.42, 0.74	1

* Sources: 1 = this study; 2 = Oldham and Sutherland, 1986; 3 = Kraus and Schuett, 1982; 4 = Gibson, 1978; 5 = Sattler and Guttman, 1976.

cm, and >80 cm, respectively) (Fig. 2). These are minimum estimates of the actual rate of reproduction, because some gravid females may have been misclassified as nongravid.

Log-linear analysis of the three-way table of reproductive condition by morph by site revealed no differences in morph frequency among gravid and non-gravid adult females (independence of morph and reproductive condition, $G = 0.80$, df = 1, $P = 0.37$). This analysis was restricted to adult females captured during the period in which gravid females were detected (14 May–15 August). In addition, Kellys Island and North Bass Island were excluded from this analysis because no melanistic morphs were captured there. Their inclusion would

TABLE 2.—Three-way analysis of variance of SVL by morph, sex, and site for garter snakes at five sites in the Lake Erie area.

Source	Sum of squares	df	Mean square	F	P
Main effects	12,100.123	6	2016.687	49.146	0.001
Sex	4211.570	1	4211.570	102.635	0.001
Morph	50.802	1	50.802	1.238	0.267
Site	5273.723	4	1318.431	32.130	0.001
2-Way interactions	371.749	9	41.305	1.007	0.435
Sex by morph	52.127	1	52.127	1.270	0.261
Sex by site	217.338	4	54.335	1.324	0.261
Morph by site	63.809	4	15.952	0.389	0.817
3-Way interaction	253.284	4	63.321	1.543	0.190
Explained	12,725.156	19	669.745	16.322	0.001
Residual	10,463.804	255	41.035		
Total	23,188.960	274	84.631		

reduce the ability to detect differences in reproductive condition among morphs.

Adult SVL was compared between morphs, sexes, and among sites using a three-way ANOVA with data from the five sites for which at least two adults of each sex and morph were captured (West Sister, Pelee, Little Portage Wildlife Area, Middle Bass, and East Harbor). In this analysis, site and sex each explained a significant amount of the variation in adult SVL; morph and the two-way and three-way interactions were non-significant (Table 2).

Variance in morph frequency for the seven island sites was similar to that for the 15 mainland sites (ratio of island to mainland variance, $F = 1.63$, $0.25 > P > 0.10$). The sites at Long Point Tip and Long Point Breakwater differ from other mainland sites in two ways: (1) they are located on a peninsula and hence are relatively isolated from the mainland, and (2) they are geographically removed from all other sites (Fig. 1). For these reasons, analysis was repeated with these sites excluded. In this case, the ratio of variances approaches statistical significance ($F = 2.58$, $0.10 > P > 0.05$).

DISCUSSION

Thermoregulatory differences thought to exist between melanistic and striped garter snakes have not resulted in differences in frequency of reproduction by females or in SVL of adults of either sex. These results are similar to those of Gibson (1978) for garter snakes at Long Point, Ontario. Gibson found no consistent difference in SVL between morphs, nor did morphs differ in weight-length relationship, or in growth rate. Morphs were also similar in the production of females reproducing and in number of offspring produced.

The lack of an apparent selective difference between striped and melanistic morphs of Lake Erie area garter snakes contrasts with findings for a similar polymorphism in the adder, *Vipera berus*. In that species, melanistic males are larger than normally colored males [Andren and Nilsen (1981); Madsen (1987); but see Forsman and Ås (1987) for contrasting re-

sults]. Because body size contributes to success in male-male combat (Andren and Nilsen, 1981) and mating success (Madsen, 1987) in *V. berus*, melanistic males apparently have a reproductive advantage over normally colored males. The difference in body size between melanistic and normally colored adders apparently is the result of a difference in growth rate (Madsen, 1987) presumably brought about by thermoregulatory differences (Andren and Nilsen, 1981; Madsen, 1987). The reproductive advantage of melanistic adders is thought to be countered in at least two ways. (1) In experiments with model snakes, Andren and Nilsen (1981) found that melanistic morphs were more easily detected by visual predators. (2) Larger males had higher mortality in a year following low food abundance (Madsen, 1987). Madsen (1987) suggested that because larger (mostly melanistic) snakes have higher total energy requirements, they may have lower survivorship during prolonged shortages of food. A similar mechanism may limit body size in Galapagos land iguanas (Snell and Snell, 1987).

A thermoregulatory advantage is thought to be countered by an increased risk of predation in melanistic garter snakes as well (Gibson, 1978; Gibson and Falls, 1979). This conclusion is based on (1) differences in scar frequency and morph frequency between sites thought to differ in predator density and (2) differences in scar frequency between morphs for females at one site [Gibson (1978), but see Schoener (1979) and Jaksic and Greene (1984) on problems with using scar data to assess predation intensity].

A balance between selection for thermoregulatory ability and selection for crypsis does not appear to be sufficient to explain the distribution of melanism in garter snakes. In the Lake Erie area, melanism is restricted to islands, a band along the southwest shore of the lake, and three peninsulas on the north shore of the lake (Fig. 1). Melanistic morphs are absent from much of the Lake Erie area [e.g., lake shore habitats in Pennsylvania: McKinstry (1975), McKinstry and Cunningham (1980), McKinstry and Felege (1974)] and are un-

known from similar mainland and island habitats near the other Great Lakes. Differences in climate or predator faunas are not immediately obvious between those lake shore habitats inhabited by melanistic morphs and those lacking melanistic morphs. Other examples of melanism in snakes are associated with large bodies of water or high elevation (reviewed in Gibson, 1978), but melanism is not restricted to such areas (e.g., *Thamnophis butleri*: Catling and Freedman, 1977; *T. elegans*: Peterson and Fabian, 1984; *T. ordinoides*: Cook, 1984; S. J. Arnold, personal communication). Detailed data on microclimate are needed to test this association further.

The influence of non-selective factors on morph frequencies of garter snakes is not immediately evident. The lack of a statistically significant difference in variance in morph frequency among island compared to mainland sites has a number of interpretations. (1) Variance is similar between island and mainland sites, and non-selective factors are not important. (2) Non-selective factors are important; but the assumption that island sites are more isolated from gene flow than mainland sites, and hence more subject to non-selective factors, does not hold. (3) Non-selective factors are important, but the difference in variance between island and mainland sites is not statistically significant because of small sample sizes. Given seven island and 15 mainland sites, island sites would have to be 2.85 times more variable than mainland sites for the difference to be significant at $\alpha = 0.05$. Interestingly, the striped morph does appear to be fixed on North Bass Island. No melanistic individuals were found among 78 garter snakes captured and many additional garter snakes sighted there. There is no reason to think that North Bass Island differs greatly in predator density or in climate from other nearby islands. Thus, it seems likely that either this population was founded by homozygous striped individuals or that the allele for melanism has been subsequently lost, possibly through random genetic drift.

The effect of random genetic drift is greatest when effective population size is small (e.g., fewer than 100 individuals: Hartl, 1981). Some Lake Erie area populations of garter snake may approach this size. Rough estimates of population size based on recaptures of marked snakes are 117.0 adult females on West Sister Island in 1980 [Lincoln-Peterson method (Caughley, 1977), SE = 36.1] and 161.3 adult females (SE = 38.2) on Middle Island in 1981. (To meet the assumptions of equal probability of capture and of no mortality or recruitment between samples, these estimates were restricted to adult females marked during one survey and recaptured during a second survey 4–5 wk later.) Effective population size may be less than census size because of unequal sex ratio, variation in reproductive output among individuals, and temporal variation in population size (Hartl, 1981). Capture rate did vary among years at some sites and may reflect corresponding changes in population size.

Collecting of garter snakes by humans may also influence population size and morph frequency. Melanistic morphs may be especially susceptible to collection because of their unusual appearance and greater commercial value. It is difficult to assess what impact such collecting might have. Some of the larger islands (e.g., S. Bass, M. Bass, Kellys, and Pelee) receive large numbers of summer visitors and may be particularly subject to removal of snakes. Collecting may be less frequent on smaller islands. However, because of their smaller population sizes, morph frequencies on these islands may be affected more greatly by human collecting.

Demonstrating selective or non-selective processes in nature requires large sample sizes, particularly if these processes are weak (Endler, 1986). Though the sample sizes obtained here exceed those of some other studies (e.g., Andren and Nilsen, 1981; Forsman and Ås, 1987; Madsen, 1987), weak selective or non-selective processes may have gone undetected. The data presented here do provide a baseline for future work. For example, if genetic drift is significant, morph frequencies should change through time and should vary randomly among sites; if morph frequencies

are determined by a balance between selection for thermoregulatory ability and selection for crypsis, morph frequencies should remain relatively constant and differences among sites should be correlated with differences in predation intensity.

LITERATURE CITED

ANDREN, C., AND G. NILSEN. 1981. Reproductive success and risk of predation in normal and melanistic color morphs of the adder, *Vipera berus*. Biol. J. Linn. Soc. 15:235–246.

BEYER, W. H. (Ed.). 1968. CRC Handbook of Tables for Probability and Statistics, 2nd ed. Chemical Rubber Company, Cleveland, Ohio.

BISHOP, Y. M. M., S. E. FIENBERG, AND P. W. HOLLAND. 1974. Discrete Multivariate Analysis: Theory and Practice. M.I.T. Press, Cambridge, Massachusetts.

BLANCHARD, F., AND F. BLANCHARD. 1940. The inheritance of melanism in the garter snake *Thamnophis sirtalis sirtalis* (Linnaeus) and some further evidence of effective autumn mating. Michigan Acad. Sci., Arts Letters 26:177–193.

BROWN, W. S., AND W. S. PARKER. 1976. A ventral scale clipping system for permanently marking snakes (Reptilia, Serpentes). J. Herpetol. 10:247–249.

CARPENTER, C. C. 1952. Growth and maturity of the three species of *Thamnophis* in Michigan. Copeia 1952:237–243.

CATLING, P. M., AND W. FREEDMAN. 1977. Melanistic Butler's garter snakes (*Thamnophis butleri* Cope) at Amherstburg, Ontario. Can. Field-Nat. 91:397–399.

CAUGHLEY, G. 1977. Analysis of Vertebrate Populations. John Wiley and Sons, New York.

CONANT, R. 1951. The Reptiles of Ohio, 2nd ed. University of Notre Dame Press, South Bend, Indiana.

COOK, F. R. 1984. Introduction to Canadian Amphibians and Reptiles. National Museums Canada, Ottawa, Ontario.

DIXON, W. J., AND M. B. BROWN. (Eds.). 1977. BMDP-77 Biomedical Computer Programs, P-Series. University of California Press, Berkeley, California.

ENDLER, J. A. 1986. Natural Selection in the Wild. Princeton University Press, Princeton, New Jersey.

FITCH, H. S. 1965. An ecological study of the garter snake *Thamnophis sirtalis*. Univ. Kansas Mus. Nat. Hist. Publ. 15:493–564.

FORSMAN, A., AND S. Ås. 1987. Maintenance of colour polymorphism in adder, *Vipera berus*, populations: A test of a popular hypothesis. Oikos 50:13–16.

GIBSON, A. R. 1978. The Ecological Significance of a Colour Polymorphism in the Common Garter Snake, *Thamnophis sirtalis* (L.). Ph.D. Dissertation, University of Toronto, Toronto, Ontario.

GIBSON, A. R., AND J. B. FALLS. 1979. Thermal biology of the common garter snake *Thamnophis sirtalis* (L.) II. The effects of melanism. Oecologia 43:99–109.

GREGORY, P. T. 1977. Life-history parameters of the red-sided garter snake (*Thamnophis sirtalis parietalis*) in an extreme environment, the Interlake region of Manitoba. Nat. Mus. Canada Publ. Zool. 13:1–44.

HARTL, D. L. 1981. A Primer of Population Genetics. Sinauer, Sunderland, Massachusetts.

HOLLANDER, M., AND D. A. WOLFE. 1973. Nonparametric Statistical Methods. John Wiley and Sons, New York.

JAKSIC, F. M., AND H. W. GREENE. 1984. Empirical evidence of the non-correlation between tail loss frequency and predation intensity on lizards. Oikos 42:407–411.

KING, R. B. 1985. The Maintenance of Color Pattern Polymorphism in Lake Erie Water Snakes, *Nerodia sipedon insularum*. Ph.D. Dissertation, Purdue University, West Lafayette, Indiana.

———. 1986. Population ecology of the Lake Erie water snake, *Nerodia sipedon insularum*. Copeia 1986:757–772.

———. 1987. Color pattern polymorphism in the Lake Erie water snake, *Nerodia sipedon insularum*. Evolution 41:241–255.

KRAUS, F., AND G. SCHUETT. 1982. A herpetofaunal survey of the coastal zone of northwest Ohio. Kirtlandia 36:21–54.

LASZLO, J. 1973. Probing as a practical method of sex recognition in snakes. Internat. Zoo. Yrbk. 15:178–179.

MADSEN, T. 1987. Natural and Sexual Selection in Grass Snakes, *Natrix natrix*, and Adders, *Vipera berus*. Ph.D. Dissertation, University of Lund, Lund, Sweden.

MCKINSTRY, D. 1975. Notes on the herpetology of Presque Isle State Park, Erie, Pennsylvania. Bull. Maryland Herpetol. Soc. 11:21–26.

MCKINSTRY, D., AND H. CUNNINGHAM, JR. 1980. Reptiles and amphibians of selected Lake Erie streams in northwestern Pennsylvania. Bull. Maryland Herpetol. Soc. 16:88–93.

MCKINSTRY, D., AND S. FELEGE. 1974. Snakes of northwestern Pennsylvania. Bull. Maryland Herpetol. Soc. 10:29–31.

NETER, J., W. WASSERMAN, AND G. WHITMORE. 1978. Applied Statistics. Allyn and Bacon, Boston, Massachusetts.

NIE, N. H., C. H. HALL, J. G. JENKINS, K. STEINBRENNER, AND D. H. BENT. 1975. SPSS Statistical

Package for the Social Sciences, 2nd ed. McGraw-Hill, New York.

OLDHAM, M. J., AND D. A. SUTHERLAND. 1986. 1984 Ontario Herpetological Summary. Essex Region Conservation Authority, Essex, Ontario.

PETERSON, C. R., AND H. J. FABIAN. 1984. *Thamnophis elegans vagrans* (wandering garter snake). Coloration. Herpetol. Rev. 15:113.

SATTLER, P., AND S. GUTTMAN. 1976. An electrophoretic analysis of *Thamnophis sirtalis* from western Ohio. Copeia 1976:352–356.

SCHOENER, T. W. 1979. Inferring the properties of predation and other injury-producing agents from injury frequencies. Ecology 60:1110–1115.

SNELL, H. L., AND H. M. SNELL. 1987. Size of Galapagos land iguanas: Episodic selection resolves a paradox. Am. Zool. 27:123A.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry, 2nd ed. Freeman and Co., San Francisco.