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Growth and Development of Larval *Rana temporaria*: Local Variation and Countergradient Selection

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ABSTRACT.—I raised tadpoles of the Common Frog (*Rana temporaria*) from populations in eight source ponds in southern Sweden, in a common garden experiment at two densities. Tadpoles from different populations differed in development rate; those from source ponds with high tadpole densities developed faster than those from less crowded ponds. Thus, differences among ponds in tadpole performance, which were documented in previous field studies, must have a genetic or maternal component. This result of source pond crowding likely resulted from microevolution and is an example of countergradient selection. In contrast, I found no significant effect of source pond hydroperiod; tadpoles from temporary ponds grew and developed at a rate similar to those from permanent ponds. Tadpoles of *R. temporaria* can respond plastically to pond drying by increasing development rate. I suggest adaptive plasticity in development rate decreased selection by pond drying in natural ponds.

Local character variation is found in many species and arises from direct effects of environment on the phenotype or from underlying genetic variation. Phenotypic variation may be adaptive, which is usually referred to as adaptive plasticity (Via et al., 1995; Pigliucci, 1996), or nonadaptive, having the character of environmental modulation (sensu Smith-Gill, 1983). Similarly, genotypic variation may be adaptive (an effect of microevolution) or the result of nonadaptive processes (i.e., genetic drift or founder effect). In amphibians, two major causes of variation are those related directly to pond quality and those related to differences among eggs from which larvae hatched. The latter includes both genetic and maternal effects, such as egg size (Rossiter, 1996; Bernardo, 1996; Loman, 2002a).

In southern Sweden, growth and development of Common Frog (*Rana temporaria*) tadpoles, differ among ponds (Loman, 2002b). Ponds studied had several environmental gradients that could influence tadpole growth and development rate, including pond hydroperiod. In the study area (and in other parts of its distribution), Common Frogs frequently breed in ponds that regularly dry before or during metamorphosis

(Cooke 1985; Kutenkov and Panarin, 1995; Loman, 1996, 2002b). This may cause catastrophic mortality, but tadpoles of Common Frogs partly counter this (at least under laboratory conditions) by accelerating development when subject to cues suggesting pond drying (Loman, 1999; Merilä et al., 2000a). Another gradient was tadpole density, which varied considerably among ponds (Loman, 1996, 2002c). At high densities, tadpoles tend to develop more slowly and metamorphose later than those growing under low densities (Wilbur, 1977; Loman, 1999; Brady and Griffiths, 2000).

Recently, cogradients and countergradient selection (Fig. 1) have attracted renewed interest from ecologists studying character variation (Berven et al. 1979, Conover and Schultz, 1995). Cogradients selection (Fig. 1A) occurs when selection pushes the reaction norm in the same direction as the trait expression that is plastically induced in that environment. For example, when fish were present, salamander (*Ambystoma barbouri*) larvae reduced activity, thus reducing feeding rate (Sih et al., 1992). Under standard laboratory conditions, reduced activity and feeding were most pronounced for larvae from populations at sites with fish; presumably these

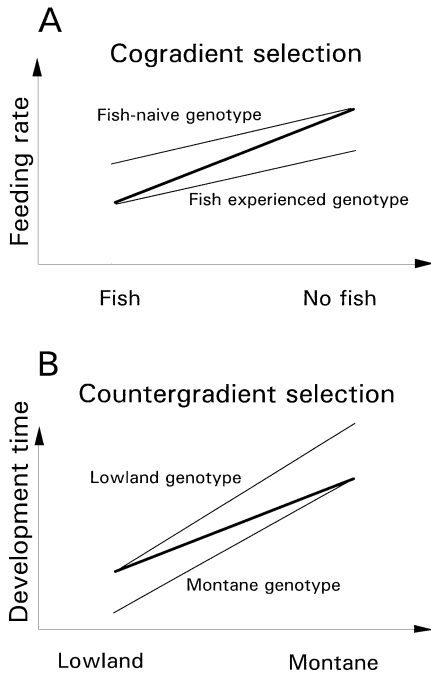


FIG. 1. Graphic representation of two examples of (A) cogradient and (B) countergradient selection. Thick lines depict the phenotypic response by local animals over two gradients (presence of predatory fish and elevation). Thin lines depict expected response of two extreme genotypes if they were translocated to various environments along the clinal gradient. Figure modified from Berven et al. (1979).

behaviors were selected traits (Storfer and Sih, 1998). Countergradient selection (Fig. 1B) is the opposite situation and occurs when the genetic response to an environmental gradient opposes the phenotypic response. Berven et al. (1979) found tadpoles of *Rana clamitans* in a montane environment developed more slowly than conspecifics from a lowland environment. However, when raised under standardized conditions, tadpoles from montane populations developed faster than those from lowland populations (Fig. 1B). A similar result was found in Common Frogs (Merilä et al., 2000b). In general, cogradient selection is expected when phenotypic variation is caused by adaptive plasticity, whereas countergradient selection is expected when phenotypic variation is caused by non-adaptive environmental modulation (Lardner, 2000).

My present study had two goals. First, I determined to distinguish between the two major causes of variation in growth and development: direct environmental effects versus maternal and genetic effects. I did this by means of a "common garden" experiment (Fauth, 1998). Tadpoles of Common Frogs from eggs laid in different source ponds were raised under identical conditions in outdoor tanks and monitored their performance. Second I determined to analyze effects of source pond hydroperiod and tadpole density on tadpole performance under standard conditions and

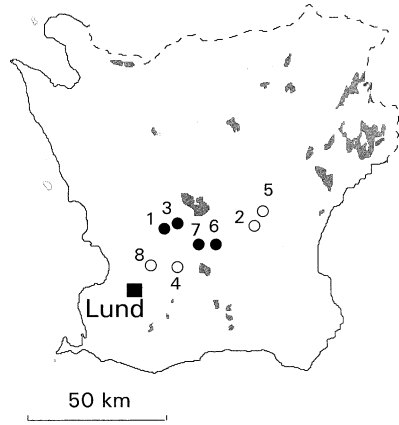


FIG. 2. Map of the province Skåne in southern Sweden. Locations of the eight source ponds are indicated; permanent ponds are open circles and temporary ponds filled. Hatched areas are lakes. Numbers refer to the ponds for cross-reference with Figure 3.

to determine whether cogradient or countergradient selection had occurred.

MATERIALS AND METHODS

Source Ponds.—The eight source ponds were located in central Skåne, the southernmost province of Sweden (Fig. 2). Maximum distance between ponds was 40 km and pond area was 50–750 m². I classified each pond into one of two categories: temporary or permanent. Four study ponds were temporary; that is, from 1990–1997 pond drying caused tadpole mortality (complete or partial) in 5–6 yr. The other four ponds were permanent and never dried during this 8-yr period. I calculated a crowding index for each pond by dividing the total number of ranid egg clumps (mean of 1990–1993) by pond area. Moor Frogs (*Rana arvalis*) and Common Frogs were the only anurans present in the study ponds. I used their combined density because their tadpoles have a similar ecology and are known to compete (Lardner, 1995).

I collected eggs from 10 Common Frog spawn clumps from each study pond in April 1992. Eggs from spawn laid early were placed at about +5°C for up to five days. Other eggs were kept at room temperature, so all hatched 20–22 April. All hatchlings from one pond, regardless of spawn clump, were released into one container from which four random samples were taken, two with 10 and two with 40 tadpoles. On 27 April, these samples were introduced into 32 outdoor tanks each containing 80 liters of water. I added a standard ration of dry leaves added before tadpoles were introduced. Tadpoles fed on algae growing on leaves and on tank walls.

Response Variables.—I measured body length and hind leg length of all tadpoles on 2 June 1992. I monitored tanks at least every other day as tadpoles approached metamorphosis. I removed, measured (body length, tail length, and weight), and released all tadpoles observed with a tail less than about 1.5× body length.

TABLE 1. Results of ANOVA on effects of tadpole tank density (high vs. low), source pond hydroperiod (permanent vs. temporary), and source pond (nested within pond hydroperiod) on tadpole and metamorph performance.

Response	Source	SS	DF	F	P
Tadpole body size	Tadpole density	45.057	1	261.0	<0.001
	Hydroperiod	0.504	1	2.92	0.101
	Pond	1.528	6	1.47	0.230
	Error	3.967	23		
	Total	51.056	31		
Relative leg length	Tadpole density	0.037	1	71.7	<0.001
	Hydroperiod	0.002	1	3.13	0.090
	Pond	0.020	6	6.36	<0.001
	Error	0.012	23		
	Total	0.071	31		
Day of metamorphosis	Tadpole density	61.442	1	38.362	<0.001
	Hydroperiod	4.527	1	2.827	0.106
	Pond	63.091	6	6.565	<0.001
	Error	36.838	23		
	Total	165.898	31		
Metamorph size	Tadpole density (T)	32.884	1	413.308	<0.001
	Hydroperiod (H)	0.246	1	3.094	0.092
	T*H	0.390	1	4.906	0.037
	Pond	0.470	6	0.984	0.460
	Error	1.750	22		
	Total	35.740	31		

Tadpoles hatched synchronously so body length on 2 June was a measure of growth rate. I used two measures of development rate. One was tadpole relative leg length (hind leg length divided by body length) on 2 June, and the other was time to metamorphosis (Gosner stage 45, McDiarmid and Altig, 1999). For metamorphs captured with a tail < 30% of body length, this was defined as the capture day; for those with tails > 31% body length, I added one day, and for those with a tail longer than the body (about 1% of all metamorphs), I added two days to estimate time to metamorphosis.

I also used a composite measure of size at metamorphosis that combined growth and development rates, computed as the first principal component of metamorph body length and mass. This PC explained 98.6% of the variation in length and weight. With equal growth rates, a fast-developing tadpole metamorphoses early and at a smaller size than one that develops more slowly and metamorphoses later. Also, with equal development rate, a fast growing tadpole will metamorphose at a larger size than a slow growing tadpole.

Statistical Tests.—I tested effects of experimental tadpole density (10 or 40 tadpoles/tank), source pond hydroperiod (permanent or temporary), source pond crowding (spawn clumps laid/pond area) and source pond (1-8) on response variables two ways. First, I used a nested ANOVA that included experimental tadpole density, source pond hydroperiod, and source pond (nested under hydroperiod). Next, I used ANCOVA with experimental tadpole density, source hydroperiod, and source pond crowding. Two tests were used because it was not possible to simultaneously test pond and source pond crowding; there was only one crowding value associated with each source pond. Response variables were mean tadpole and metamorph

values for individual tanks. Except when specifically noted in tables, interactions were not statistically significant and removed before final analysis.

RESULTS

Tadpole Growth.—Tadpoles raised at high density were smaller than those raised at low density and, therefore, grew at a comparatively lower rate (Tables 1–2; significantly different y-intercepts in Fig. 3A). Body length was independent of source ponds (Table 1) and hydroperiod. However, source ponds with higher egg densities yielded smaller tadpoles (Table 2, significant slopes in Fig. 3A).

Tadpole and Metamorph Development.—Both measures of development rate yielded similar results. Tadpoles had relatively shorter hind legs and metamorphosed later when raised at high density (Tables 1–2, significantly different y-intercepts in Fig. 3B–C). Tadpoles from different source ponds differed in relative hind leg length and had different dates of metamorphosis (Table 1). Both measures of development rate were independent of hydroperiod. Source ponds with higher egg densities yielded tadpoles that developed faster and metamorphosed earlier (Table 2; significant slopes in Fig. 3B–C).

Metamorph Size.—Metamorphs from high density treatments were smaller than those from low density treatments (Tables 1–2; significantly different y-intercepts in Fig. 3D). Metamorph size was independent of source ponds (Table 1), hydroperiod, and source pond egg density (Tables 1–2, Fig. 3D). However, there was an interaction between experimental tadpole density and source pond hydroperiod on time for metamorphosis (Tables 1–2, Fig. 3D). Metamorphs from permanent ponds in low- (but not high-) density tanks were larger than those from temporary ponds.

TABLE 2. Results of ANCOVA on effect of experimental tadpole density (high vs. low), source pond hydroperiod (permanent/temporary), and source pond egg density (egg clumps/m²) on tadpole and metamorph performance. The general linear model in these tests differs from those in Table 1; egg density (a continuous variable) replaced source pond.

Response	Source	SS	DF	F	P
Tadpole body size	Tadpole density	45.057	1	263.0	<0.001
	Hydroperiod	0.254	1	1.49	0.233
	Egg density	0.714	1	4.18	0.050
	Error	4.784	28		
	Total	50.809	31		
Relative leg length	Tadpole density	0.037	1	43.7	<0.001
	Hydroperiod	0.000	1	0.45	0.510
	Egg density	0.008	1	9.26	0.005
	Error	0.024	28		
	Total	0.069	31		
Day of metamorphosis	Tadpole density	61.442	1	26.698	<0.001
	Hydroperiod	0.567	1	0.243	0.626
	Egg density	35.491	1	15.422	0.001
	Error	64.438	28		
	Total	161.938	31		
Metamorph size	Tadpole density (T)	32.884	1	441.333	<0.001
	Hydroperiod (H)	1.246	1	1.960	0.173
	T*H	0.390	1	5.239	0.030
	Egg density	0.208	1	2.793	0.106
	Error	1.750	27		
	Total	36.478	31		

DISCUSSION

Evidence for Microevolution.—In natural ponds, I found variation in time to and size at metamorphosis of about 30 days and 4 mm within years, respectively (Loman, 2002b). The present study demonstrated these differences reflected not only differences in pond quality but also maternal effects, genetic differentiation, or both.

What caused populations to differ? I considered two alternatives: nongenetic (maternal effects) and genetic explanations. If nongenetic egg differences were responsible, egg characteristics must promote slow growth and fast development, the pattern found for tadpoles from crowded ponds. This would be a nongenetic but possibly adaptive maternal trait: trans-generational phenotypic plasticity (Mousseau and Fox, 1998). Although impossible to refute, this combination of egg traits seems unlikely. Large eggs tend to hatch tadpoles that grow and develop quickly, whereas tadpoles from small eggs grow and develop slowly (Berven and Chadra, 1988; Kaplan, 1998; Loman, 2002b). Neither pattern is consistent with that shown by tadpoles from high- or low-density source ponds in this study because growth and development were negatively correlated.

Alternatively, if genetic differences were responsible, there must be an adaptive link from pond characteristics to development strategy. Indeed, under high competition, it would be advantageous to develop quickly, even at the expense of growth rate (Werner, 1986). Growth rate often is under genetic influence (Travis et al., 1987; Blouin, 1992) and genetic differentiation is possible between neighboring populations. Reh and Seitz (1990) and Sinsch (1992) found genetic

differentiation among populations of *R. temporaria* and *B. calamita*, respectively, at a landscape scale similar to that in my study. Other studies also have observed local variation in tadpole growth and development rate (Augert and Joly, 1993; Lardner, 1997, 1998; Fauth, 1998; Miaud et al., 1999; Gómez-Mestre and Tejado, 2002). Genetic differences between closely situated sites have been documented in allozyme studies or otherwise inferred (Berven, 1982a, 1982b; Andrén et al., 1989; Reh and Seitz, 1990; Regnaut, 1997).

If local adaptation is a common phenomenon, this may be bad news for frog restocking programs because introduced individuals may not be genetically optimal in their new environment (Storfer, 1999; Lardner, 2000). The good news from my study is that much genetic variation may be present in neighboring populations, suggesting traits could quickly evolve toward a local optimum. Thus, introductions should include sufficient individuals to preserve the full genetic variation from source populations or include individuals from several source populations to bolster genetic variation available for an adaptive response.

Pond Hydroperiod and Cogradient Selection.—If differences in development rate were caused by local adaptation, pond hydroperiod should be an important selective force. Tadpoles from temporary ponds are expected to evolve faster development rates than those from permanent ones: an example of cogradient selection. Surprisingly, hydroperiod did not affect tadpole growth and development in this common garden experiment, nor in another experiment on *R. temporaria* (Loman and Claesson, 2003). Common Frogs are developmentally plastic, and development rates increase under threat of desiccation (Laurila and

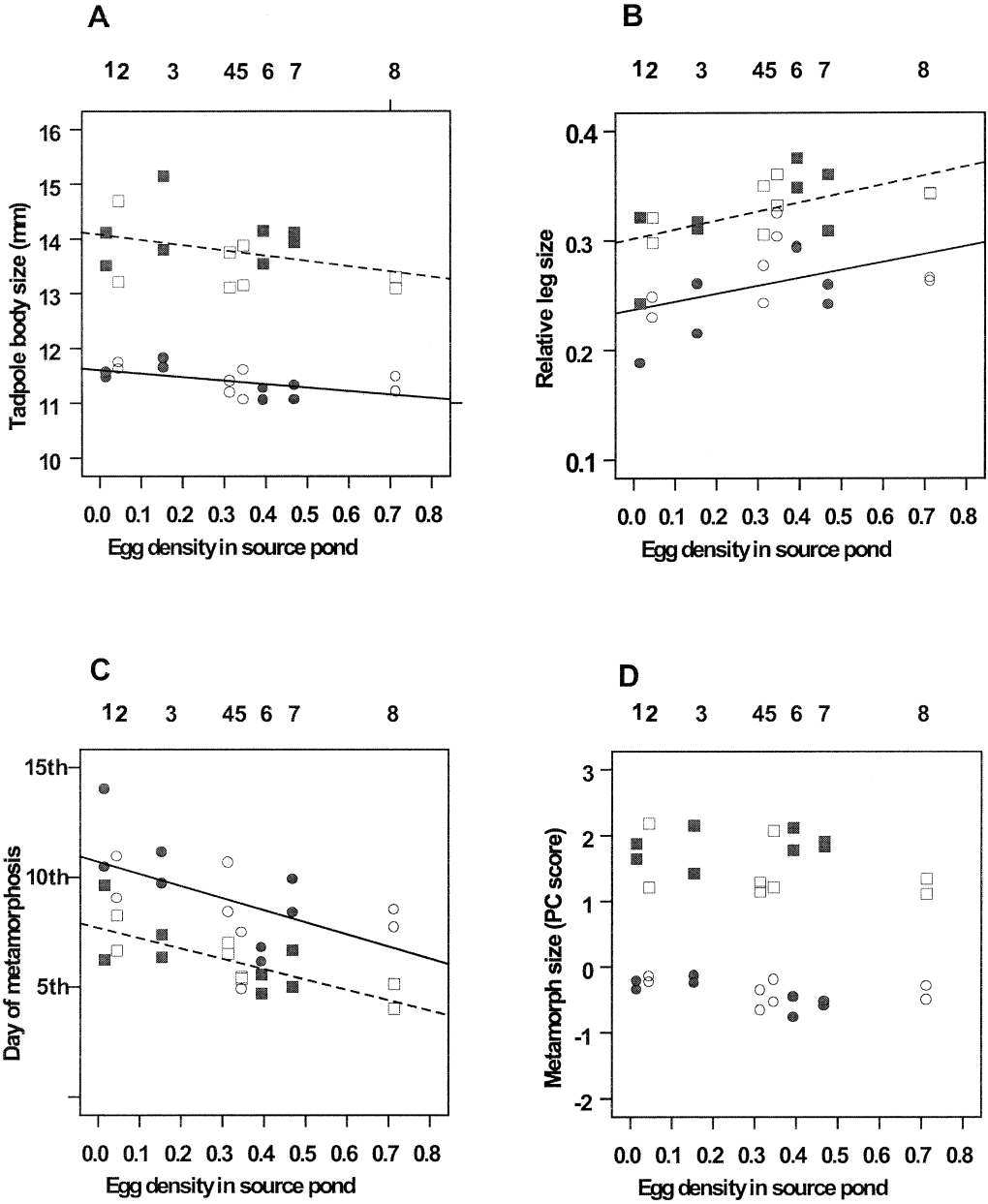


FIG. 3. Tadpole and metamorph responses in experimental tanks. Symbols are means for all tadpoles in a tank. Circles are high-density tanks and squares are low-density tanks. Filled symbols are for tadpoles from permanent source ponds. Open symbols are for tadpoles from temporary source ponds. Egg density was mean spawn clumps in 1990–1993 divided by pond area (m^2). Regression lines were computed separately for high- (continuous lines) and low- (dashed lines) density tanks. Numbers above columns of symbols refer to source ponds as labeled in Figure 2. Relative leg size (B) is tadpole hind leg length divided by body length. Day of metamorphosis (C) is date in June. Metamorph size (D) is the first principal component of metamorph length and mass.

Kujasalo, 1999; Loman, 1999, 2002b; Merilä et al., 2000a). Plasticity may decrease selective pressure (Lardner, 2000) to increase development rate in ponds prone to early summer drying. However, as tadpoles do die from drying in these ponds, selective pressure

remains operable. Thus, although selective pressure may be present, plasticity in development rate may weaken selection enough to make it undetected in this study. Cogradient selection also was not found in studies of tadpole antipredator behavior (Laurila, 2000)

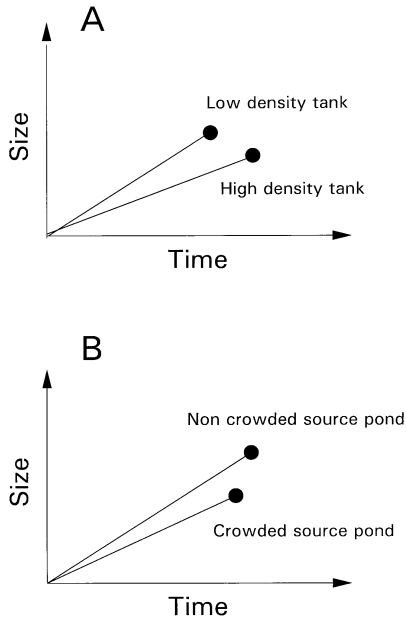


FIG. 4. Contrasting growth and development trajectories for tadpoles raised in (A) low- and high-density tanks and (B) from crowded and noncrowded source ponds (but in a standard laboratory environment), respectively. Filled circles symbolize time and size at metamorphosis.

and fish morphology (Mittelbach et al., 1999), both characters with a plastic component.

Competition and Countergradient Selection.—Tadpoles from eggs laid in ponds with a high density of spawn clumps and presumably high tadpole competition, developed faster and were smaller than those from low competition ponds. Thus, differences did not represent a difference in general “quality,” but rather a trade-off: tadpoles from high-competition ponds increased development at the cost of growth.

Source pond competition and experimental competition gave rise to two different tadpole growth and development patterns. Tadpoles from high-density tanks grew and develop slowly (Fig. 4A) compared to those from low-density tanks. Tadpoles from crowded source ponds grew slowly but develop quickly, compared to those from less crowded source ponds (Fig. 4B). The first pattern represents a direct effect of an adverse condition, an environmental modulation (Smith-Gill, 1983), whereas the second can be interpreted as the outcome of trade-offs between growth and development under different selective regimes. A similar effect (Fig. 4A) of direct resource variation was found for *Hyla gratiosa* and *Hyla squirella*. When resources (food levels) were manipulated sufficiently early, tadpoles on low food rations developed and grew more slowly than those with more food (Travis, 1983; Beck, 1997).

Tadpoles tend to develop more slowly under competition both in laboratory studies (Wilbur, 1977; Loman, 1999) and in natural ponds (Smith, 1983; Berven, 1990; Loman 2001). This is likely to be a non-

adaptive effect. In my study, tadpoles from crowded source ponds developed faster than those from uncrowded ponds: an example of countergradient selection. My study supports Lardner’s (2000) hypothesis that countergradient selection is mainly expected if phenotypic variation is nonadaptive. There are several known cases of countergradient selection, including development rate of *R. temporaria* (Martin and Miaud, 1999; Merilä et al. 2000b), growth, development and maturation in other frogs and tadpoles (*Rana sylvatica*, Berven, 1982a,b), growth in fish (*Menidia menidia*: Conover and Present, 1990; *Lepomis gibbosus*: Arendt and Wilson, 1999), and in other plants and animals (reviewed in Conover and Schultz, 1995). In contrast, cogradient selection is uncommon and does not appear to influence local variation in *R. temporaria*.

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Estimation of Flattened Musk Turtle (*Sternotherus depressus*) Survival, Recapture, and Recovery Rate during and after a Disease Outbreak

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ABSTRACT.—We estimated survivorship, recapture probabilities and recovery rates in a threatened population of Flattened Musk Turtles (*Sternotherus depressus*) through a disease outbreak in Alabama in 1985. We evaluated a set of models for the demographic effects of disease by analyzing recaptures and recoveries simultaneously. Multiple-model inference suggested survival was temporally dynamic, whereas recapture probability was sex- and age-specific. Biweekly survivorship declined from 98–99% before to 82–88% during the outbreak. Live recapture was twice as likely for male turtles relative to juveniles or females, whereas dead recoveries varied only slightly by sex and age. Our results suggest modest reduction in survival over a relatively short time period may severely affect population status.

Techniques available to analyze mark-recapture data have improved significantly over the last two decades. In addition to providing population estimates, these biometric tools allow biologists to carefully examine model assumptions, and to use demographic analysis to identify factors affecting population status (Pollock et al., 1990; Lebreton et al., 1992; Nichols, 1992). Estimates of survivorship, capture biases, capture probabilities, and recovery rates aid understanding resilience of species to environmental change and in determining whether and how population structure responds to perturbations. Analysis of mark-recapture data also

allows researchers to quantify uncertainty associated with population parameters and sampling biases. Models employing information criteria (Akaike, 1973; Pradel, 1996) offer insight into population processes while avoiding the pitfalls of traditional statistical hypothesis testing. Such shortcomings include undue reliance on test statistics with arbitrary significance levels (*P*-values), testing of biologically trivial null hypotheses, and overemphasis on statistical power, all of which can impair inference and lead to spurious conclusions (Howson and Urbach, 1991; Johnson, 1999; Anderson et al., 2000). An information-theoretic approach, facilitated by powerful computer programs (e.g., Program MARK; White and Burnham, 1999), evaluates a set of alternative models with empirical

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