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Elasticity Analysis of an Age-Structured Population Dynamics Model for the Pecos Bluntnose Shiner

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ABSTRACT—Abundance of the Pecos bluntnose shiner *Notropis simus pecosensis* has decreased over the last 40 years and it is now federally protected. Using published life-history information for the Pecos bluntnose shiner and related species, we developed an age-structured population model for the Pecos bluntnose shiner. We then used elasticity analysis to determine which life-history stages had the greatest effect on population growth rate. We found that population dynamics of the Pecos bluntnose shiner are most influenced by age-0 survival (explaining 47% of variation in population growth rate) and reproduction by age-1 individuals (40% of variation in population growth rate). Consequently, management and recovery efforts might most profitably be directed toward increasing early survival and reproduction.

Prairie river systems have been extensively modified during the last 50 years. Construction of reservoirs, agricultural withdrawals, flood control projects, and other anthropogenic activities have altered historic patterns of stream discharge. In particular, these activities have caused a general decrease in both the magnitude and variability of stream discharge in prairie streams (Pfleiger and Grace 1987; Patton and Hubert 1993). Associated with these changes has been a decrease in the distribution and abundance of a number of fish species (Cross and Moss 1987; Sublette et al. 1990; Limbird 1993; Bonner and Wilde 2000).

Historically, the bluntnose shiner *Notropis simus* was widely distributed throughout the Rio Grande and its tributaries. The distribution and abundance of the species has decreased since the 1950s and it has become extirpated from throughout the entire Rio Grande with the last specimen being collected in 1964 (Bestgen and Platania 1990). Extant populations of the bluntnose shiner are represented only by a distinct subspecies, the Pecos bluntnose shiner *N. s. pecosensis*, which is confined to the Pecos River, New Mexico (Chernoff et al. 1982; U. S. Fish and Wildlife Service 1992). The distribution and abundance of the Pecos bluntnose shiner have decreased over the past 40 years (Hatch et al. 1985) and the subspecies was formally listed as Threatened in 1987 (Sublette et al. 1990; U.S. Fish and Wildlife Service 1992).

The Pecos bluntnose shiner is poorly known and little information is available on its biology and life history. The most comprehensive study of the species was conducted by Hatch et al. (1985) who provide information on abundance, distribution, and age structure of the Pecos bluntnose shiner. Hatch et al. (1985) also report preliminary reproductive information for a small number of females collected near the end of the spawning season. Bestgen and Platania (1990) and Platania and Altenbach (1998) provide the only other published information on reproductive ecology of the Pecos bluntnose shiner.

The paucity of life-history information for the Pecos bluntnose shiner makes it difficult to identify and implement appropriate conservation and recovery actions (U.S. Fish and Wildlife Service 1992). In cases such as this, models provide a means for understanding population dynamics and assessing the potential merits of alternative management actions. Models such as the Leslie matrix population model have a long history of use in conservation biology (Caswell 2001). The Leslie matrix model is a deterministic age-structured population dynamics model that requires estimates of age-specific survival and age-specific fecundity as parameters. In this paper, we develop a Leslie matrix population model for the Pecos bluntnose shiner, present the results of elasticity and sensitivity analyses performed on the model, and discuss the implications of our results for the conservation of the Pecos bluntnose shiner.

METHODS—Population age-structure information for Pecos bluntnose shiner was obtained from Hatch et al. (1985). Three age classes (ages 0, 1, and 2) were present in length-frequency distributions reported by Hatch et al. (1985). Age-0 individuals represented about 77% of all individuals collected, age-1 individuals represented 19%, and age-2 individuals comprised 3%. From these data, we estimated annual survival of Pecos bluntnose shiner from age-1 to age-2 as 0.2170.

Reliable estimates of age-specific fecundity and duration of spawning season for the bluntnose shiner are not available. As a surrogate, we used fecundity data for a closely related species, the Arkansas River shiner *Notropis girardi* (Bonner 2000). Hatch et al. (1985) suggested that fecundity of Pecos bluntnose shiner was approximately 46% lower than that of Arkansas River shiner. However, this estimate was based on two mature specimens collected in a single sample near the end of the reproductive season. Both the Arkansas River shiner and the Pecos bluntnose shiner are multiple spawning species (Platania and Altenbach 1998). Therefore, proper determination of fecundity requires that samples be taken throughout the entire duration of the

reproductive season (Rinchart and Kestemont 1996; Lowerre-Barbieri et al. 1998). Bonner (2000) used histology to determine age-specific fecundity of Arkansas River shiner by enumerating ovarian follicles that were undergoing germinal vesicle breakdown (signifying spawning in progress) or that were spent (indicating spawning within the past 12 to 24 h). Average daily counts of ovarian follicles then were multiplied by the number of days in the spawning season (May through August) to estimate total fecundity. Bonner (2000) found that age-2 Arkansas River shiners disappeared from his samples by mid-June. Therefore, although the potential fecundity of age-2 individuals is greater than that of age-1 individuals, they have a shorter spawning season and, hence, lower total fecundity than do age-1 individuals. Based on Bonner's results for Arkansas River shiner, we estimate total fecundity for Pecos bluntnose shiner to be 472 for age-1 individuals and 316 for age-2 individuals.

From the information described above, we obtained estimates for all necessary parameters for the Leslie matrix, except age-0 survival (from ovum to age-1). When all elements of the Leslie matrix are known, the rate of population growth λ can be estimated (Caswell 2001). Alternatively, if the rate of population growth is known, or can be assumed to take some value, any one missing element of the matrix can be estimated (Vaughan and Saila, 1976). Therefore, we assumed that Pecos bluntnose shiner populations were static, with a rate of population growth $\lambda = 1$, and used the method of Vaughan and Saila (1976) to estimate age-0 survival. We recognize that stream-fish populations fluctuate from year to year and population growth is likely not static, however, because estimates of population growth based on data are not available, it was necessary to assume a static population growth rate in order to calculate age-0 survival.

We used elasticity analysis (Benton and Grant, 1999) to identify which life-history stages most influence population growth of Pecos bluntnose shiner. Elasticity analysis estimates the proportional change in population growth rate for a given change in a population rate parameter (i.e., age-specific fecundity, age-specific survival, etc.). This analysis is useful for identifying which life-history stages most influence population dynamics and, therefore, which might be most responsive to management actions (Benton and Grant, 1999).

Due to the general lack of specific life-history information for Pecos bluntnose shiner, we used simulation to perform a sensitivity analysis to determine how robust our results are to changes in life-history parameters used in our Leslie matrix. This approach provides a quantitative assessment of potential effects of uncertainty in parameter estimates (Mills et al., 1999). For each age-class we modeled age-specific

TABLE 1—Age-specific elasticities for Pecos bluntnose shiner, *Notropis simus pecosensis*.

	Age-0	Age-1	Age-2
Survival	0.4698	0.0603	0
Fecundity	0	0.4698	0.0603

fecundity as a normally-distributed variable with mean (\bar{x}) and variance (s^2) equal to the observed fecundity. Our simulations intentionally encompass an extremely wide range of potential fecundities. Age-specific survival (S) was modeled as binomial variable with mean S and variance $S \times (1-S)$. We allowed all life-history parameters to vary during each simulation. One thousand simulations were conducted and the resulting elasticity estimates were recorded.

RESULTS—Age-specific survival estimates used to construct the model were: age-0 survival = 0.0018 and age-1 survival = 0.2167. Age-specific fecundity estimates used to construct the model were: age-0 fecundity = 0, age-1 fecundity = 472, and age-2 fecundity = 316. The life-history parameters with the greatest elasticities (Table 1) were age-0 survival (0.47) and age-1 fecundity (0.40). Incremental changes in these two life-history parameters have, by far, the greatest effect on Pecos bluntnose shiner population growth. Elasticities for age-1 survival and age-2 fecundity were relatively small.

Our simulations showed that although a substantial range in elasticities for each parameter was possible, in most cases the results were comparable to those from our Leslie matrix model (Fig. 1). Simulation elasticities for age-0 survival ranged from 0.34 to 0.49, but most (99%) were greater than 0.40. Similarly, simulation elasticities for age-1 fecundity ranged from 0.03 to 0.49, but most (82%) were greater than 0.3500. Likewise, estimates were variable for age-1 survival and age-2 fecundity with most (87%) simulations resulting in elasticities of less than 0.1000. These simulations provide evidence that the elasticities obtained from our Leslie matrix model are at least qualitatively correct even given the substantial uncertainty in our estimates of individual life-history parameters.

DISCUSSION—Our results suggest that population growth rates of Pecos bluntnose shiner are most sensitive to changes in age-0 survival and age-1 fecundity. Specifically, population growth rate is largely determined by the number of individuals surviving

from ovum through the first reproductive season. This result has important management implications. Although Pecos bluntnose shiner can survive into their second year (Hatch et al. 1985), a single poor year, affecting age-0 survival or reproduction by age-1 fish, can markedly reduce population size. Following a poor year, surviving (age 2) individuals would neither be sufficiently abundant nor have the reproductive capacity to allow the population to recover. Further, given the low survival rate we estimated for age-0 fish, populations of Pecos bluntnose shiner are unlikely to recover from such an event under “average” conditions. Instead, exceptionally favorable years would be required to increase population size. These same considerations suggest that a series of favorable, or unfavorable, years can have a multiplicative effect on population growth. Management efforts that alter age-0 survival could be expected to have rapid and extensive effects on population size.

Altered discharge regimes caused by reservoir construction and water management practices within the Rio Grande basin has resulted in the decline, extirpation, or

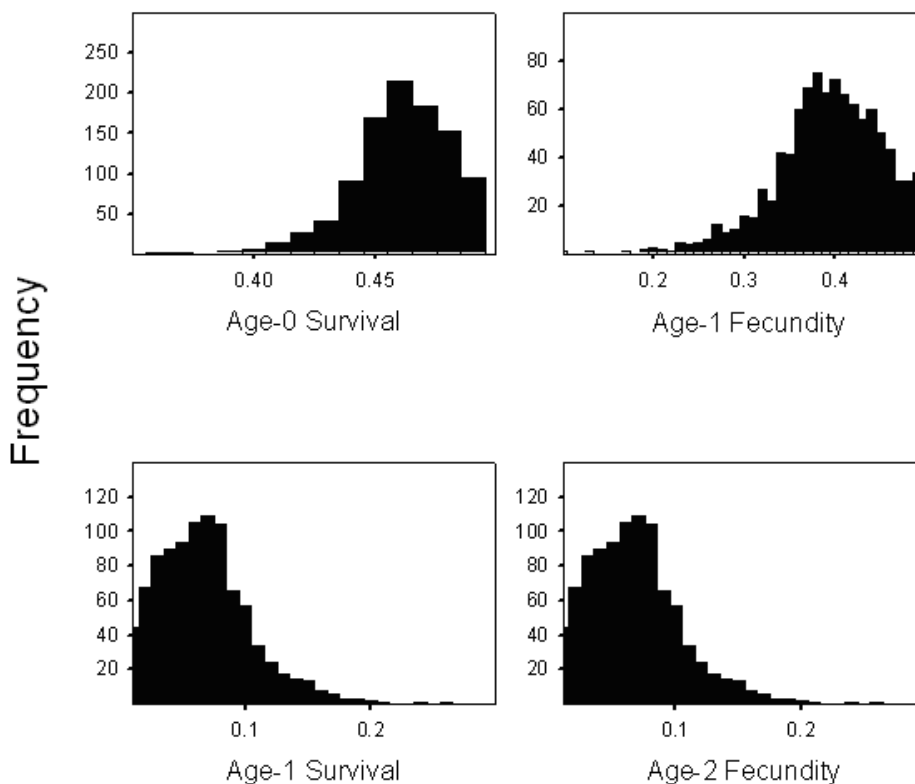


FIG.1—Frequency distributions of simulated elasticities for Pecos bluntnose shiner, *Notropis simus pecosensis*.

extinction of numerous cyprinid species native to the basin (Hatch et al. 1985; Bestgen and Platania 1990; Platania and Altenbach 1998). Two hypotheses potentially explain these declines. First, dewatering of streams may have resulted in a loss of specific habitat features or habitat types important to Rio Grande cyprinids. Second, reduced stream discharge may reduce the number of days during the reproductive season with sufficient discharge to suspend and transport ova. This would, in effect, shorten the spawning season and could result in reproductive failure during particularly dry years.

Fish species that require specific habitat types or features to complete their life history are particularly susceptible to declines due to habitat loss. It is not entirely clear whether prairie-stream cyprinids generally have close associations with specific habitat features. For example, Bonner (2000) found evidence of habitat selection and partitioning among several prairie-stream fishes, including the Arkansas River shiner, in the Canadian River, Texas. In contrast, Polivka (1999) concluded that Arkansas River shiner used all habitat types present in the South Canadian River, Oklahoma. Pecos bluntnose shiner were collected from every major habitat type except stagnant pools but were most common in main channel habitats (Hatch et al. 1985).

Many prairie-stream fishes including Pecos bluntnose shiner broadcast spawn as nonadhesive, semi-buoyant ova (e.g., Platania and Altenbach 1998). Once ova are released, they are transported downstream in the current while they develop. Discharge must be sufficient to keep the ova in suspension until newly hatched larvae can leave the main channel (Platania and Altenbach 1998). If discharge is insufficient to keep the ova afloat, they settle to the bottom where they become covered with sediments and suffocate. Documented declines in numerous members of this broadcast-spawning reproductive guild have coincided with reductions in stream discharge in prairie-stream systems during the past 50 years (e.g., Cross and Moss 1987; Pigg et al. 1999; Bonner and Wilde 2000).

Our results provide no particular insight into which of these two hypotheses is more likely. However, our results do suggest that research might be most profitably directed toward understanding those factors influencing habitat use and availability and survival of age-0 Pecos bluntnose shiners.

The major limitation of our model is in the quality of age-specific survival and fecundity estimates, which are based on limited samples and information obtained from another species. Despite this limitation, sensitivity analysis suggests that our results are at least qualitatively correct: under almost every possible scenario, age-0 survival and age-1 fecundity have the greatest elasticities and, consequently, the greatest effects

on population growth rate. A second limitation of our model is that we assumed a static population in order to estimate age-0 survival, thus, our model cannot be used to predict changes in population size at this time. However, given several years of abundance data, the model can be modified to allow prediction of population size as a function of stream discharge or habitat availability.

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