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ASSESSING POPULATION-SPECIFIC AND ENVIRONMENTAL INFLUENCES ON BLUEGILL LIFE HISTORIES: A COMMON GARDEN APPROACH

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Abstract. Investigations into vertebrate life histories have demonstrated trade-offs between growth and reproduction that can result in individual and population-specific variation in life-history strategies. Mechanisms to explain variation among populations, however, often remain unidentified. We examined the relative strength of genetic (population source) and environmental (population social structure) factors on variation in growth and timing of maturation for juvenile male bluegill in a common garden experiment. We placed juvenile male bluegill collected from two different wild source populations, one with parental males that are large (>190 mm total length) and one with parental males that are stunted (<155 mm total length), in a common environment and varied the social structure by controlling the presence or absence of large, mature, male bluegill collected from a third population. Juvenile male bluegill from both populations allocated significantly more energy to reproduction in the absence of large males than in their presence. Within ponds, differences in growth and maturation rates between juvenile males from the two source populations were small but significant. These results indicate both genetic and environmental components to growth and maturation in bluegill but emphasize the importance of social interactions in shaping individual life-history strategies.

Key words: bluegill; common garden; Lepomis macrochirus*; maturation; ponds; population; social influence; trade-offs.*

Introduction

A fundamental tenant of life-history theory is that organisms must make trade-offs between somatic growth and reproductive activities (Williams 1966, Gadgil and Bossert 1970, Bell 1980, Partridge and Harvey 1988). For organisms with indeterminate growth, such as fish, this trade-off is particularly significant because fecundity is often directly related to body size (Roff 1984, Fox 1994). Life-history theory predicts that size and age at maturation should evolve to maximize the lifetime reproductive success of the individual (Gadgil and Bossert 1970, Fox 1994). As a consequence, variation in timing of maturation within and among populations is common, and individuals do not always mature at the earliest opportunity (Roff 1984, Bertschy and Fox 1999). Although evidence for variable life-history strategies and documentation of the costs and consequences associated with that variation appears in the literature (see Reznick 1985 for review), underlying mechanisms driving population-specific variation often remain unexamined.

Both genetic and environmental factors can control the expression of early life-history traits (Haugen 2000). Genetic differences associated with population-specific variation in growth and maturation rates have been documented for various species of fish, particularly those in the family Salmonidae (e.g., Ricker 1981). Genetic control of timing of maturation is seen in the Montezuma swordtail (*Xiphophorus montezumae*), a species in which the timing of maturation is based on the presence of an ''early'' or ''late'' allele for a gene located on the sex chromosome (Kallman 1983). A number of environmental variables can also influence life-history strategies, and one that has been shown to have considerable influence on growth and maturation rates is the social structure of a population, e.g., large, mature males inhibiting maturation of smaller males (Borowsky 1978, Bushman and Burns 1994, Jennings et al. 1997, Danylchuk and Tonn 2001). For example, the presence of either large, mature males or large juvenile males inhibits maturation of small,

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juvenile male platyfish (*Xiphophorus variatus* Meek; Borowsky 1978, 1987). Similarly, small fathead minnows (*Pimephales promelas* R.) modulate their seasonal reproductive activity based on the social structure of the population, becoming mature and spawning only in the absence of large, socially dominant males (Danylchuk and Tonn 2001). Combined, these studies elucidate the myriad mechanisms that can influence individual life histories. However, the relative importance of these variables has not been assessed, and the variable outcomes of these studies suggest the need to simultaneously consider the relative influence of genetic and environmental factors in a single experiment.

Bluegill (*Lepomis macrochirus*) populations exhibit complex social structures, and the life histories of individuals can be shaped by social interactions within the population (e.g., Gross 1982, Jennings et al. 1997). Jennings et al. (1997) showed that the presence of large, mature males delayed the maturation of immature males. As has been the case with other species, however, the potential for genetic contribution to variation in the observed growth and maturation schedules was not assessed. It is possible that historical selection differences among populations could cause evolutionary divergence among those populations, resulting in genetic differences in life-history strategies. On the other hand, plasticity in the timing of maturation might be universal across bluegill populations; all individuals may be able to respond facultatively to environmental cues and mature at a time that optimizes their fitness. The underlying question is, what is the relative contribution of genetic and environmental factors to population-specific variation in life histories?

In this experiment, we assess the importance of genetics (population source) and environment (social interactions based on varying population size structure) in determining maturation schedules by rearing bluegill in a common environment. Juvenile individuals from two populations with different size structures and maturation schedules were used to establish experimental populations with varying social structures (presence or absence of large, mature male bluegill). We centered our analyses on males because males of many species, including bluegill, often experience strong sexual selection (e.g., Gross 1982, Jennings and Philipp 1992, Morris et al. 1992) that results in large variation in male growth rates and size at maturation within and among populations.

Materials and Methods

Two lakes in southeastern Illinois with established bluegill populations were chosen as sources for the juvenile males, Paris Lake, which contains a historically stunted bluegill population (mean total length of mature parental male bluegill ±1 SE, 151 ± 3.9 mm; $n = 200$) and Lincoln Trail Lake, which contains a historically nonstunted bluegill population (198 ± 4.2 mm, $n = 450$). Parental males in the stunted population, in addition to being smaller, generally mature at a younger age than parental males in the nonstunted population (D. D. Aday, *unpublished data*). Both populations were sampled extensively via seining and electrofishing in 1996–1997 to determine the abundance, size, and age structure of the resident bluegill population. These populations were resampled annually (1997–2000) to ensure temporal stability in population parameters. Large, mature, parental males and mature females used in the experiment were collected from a third population, Forbes Lake (also in southeastern Illinois), to avoid any relatedness with either group of juveniles.

Immature bluegill collected from each of the two source populations were added to six 0.04-ha experimental ponds at a density of 150 fish (75 from each source) per pond. Densities were within the range of natural systems (Wahl and Stein 1988), and allowed us to (1) account for initial mortality and (2) obtain a reasonable sample size of males (because only immature fish were stocked it was not possible to separate males from females). After stocking, ponds were monitored daily to remove dead or moribund fish; mortality was consistent among ponds and no mortality was observed after 6 d. Prior to establishing these experimental populations, all juveniles were measured (total length, TL), given a distinctive fin clip to identify population source, and a subsample ($n = 100$; 50 from each source population) of the juveniles was removed from the initial collection. Each individual removed from the subsample was weighed, dissected to determine maturity status by visual inspection of the gonads, and aged using annual rings on scales (Regier 1962). After addition of juveniles from both source populations and five mature females from the third population to each pond, five mature males (also from the third population) were added to half of the ponds, creating a split-plot design. Mature individuals of both sexes ranged from 175–190 mm in TL.

Experimental populations were established on 15 May. After three months, the experiment was terminated, ponds were drained, and all immature bluegill were collected, euthanized in MS-222, sorted by source population of origin (all fin clips were retained and unequivocally identified), and frozen. For analysis, all juvenile bluegill were thawed, measured (TL), weighed, and dissected to determine sex. For males, two metrics were used to assess maturity status. The primary indication of maturation was the gonadosomatic index (GSI) for individuals, which was calculated as the ratio of wet gonad mass to total wet fish mass. Second, we assigned a gonad score (1–5) to each male

to indicate maturity status based on sperm production capability; a gonad score of 1 indicated total lack of gonad development (gonads invisible or just strings weighing <0.01 g), whereas scores of 2–5 indicated some relative degree of further gonad development (5 representing a fish in spawning condition with white testes that emitted sperm when palpated at the time of collection; Aday et al. 2002).

Also at the conclusion of the experiment, to compare the maturation status of fish in the experimental ponds with their cohorts remaining in the wild source populations, we again sampled the two source populations, collecting individuals (n = 100; 50 per population) of the same size and age cohort of the juvenile bluegill used in the experiment. These individuals were returned to the laboratory and processed identically to that of the experimental fish.

Results

The size and maturity status of immature fish placed into the experimental ponds was similar at the beginning of the experiment; i.e., there was no difference (t test, $F_{1, 898} = 0.94$, $P = 0.33$) in initial total length of fish from the stunted (TL = 82.0 ± 0.75 mm [mean ± 1 SE], n = 450) and nonstunted (TL = 83.1 ± 1.07 mm, n = 450) source populations. There was also no difference (t test, $F_{1,98} = 1.00$, $P = 0.32$) in the mass of individuals removed from the initial subsample (nonstunted, 8.8 ± 0.51 g, n = 50; stunted, 7.9 ± 0.81 g, n = 50). In addition, all subsampled fish were aged 1–2 yr and exhibited no gonad development or secondary sexual characteristics (i.e., all were sexually immature).

Maturation schedules

We found both an effect of source population (split-plot, two factor ANOVA; $F_{1,4} = 13.0$, $P = 0.02$) and social structure ($F_{1,4} = 108.5$, $P = 0.0005$) on maturation schedules of juvenile males. The mean GSI of males was higher in individuals from the nonstunted population (0.10 ± 0.01, n = 165, vs. 0.07 ± 0.01, n = 134 in the stunted population) and when large males were absent (Fig. 1, open bars, separated for stunted and nonstunted individuals). There was no significant interaction ($F_{1,4} = 0.06$, $P = 0.82$) between these factors in the model. Because both main factors had a significant influence on GSI, we examined the relative strengths of each factor by partitioning the variance in the model with type III sums of squares. These results indicated that the environmental effects (presence or absence of large males), which explained 53% of the total variation in the model, were much stronger than effects due to source population differences, which explained only 6% of the variation. The second measure of maturation, gonad score, showed similar results; gonad scores of experimental males were higher ($F_{1,4} = 10.07$, $P = 0.03$) when large males were absent (2.0 ± 0.08) than when they were present (1.1 ± 0.03). There was also no significant interaction ($F_{1,4} = 3.48$, $P = 0.14$) between the main factors (genetics and environment) on the gonad score of juveniles. The influence of mature males on gonad score is, biologically, quite meaningful. In the treatment with large males present, the mean gonad score of 1.1 indicates essentially no gonad development whatsoever. In the treatment with large males absent, however, the mean gonad score of 2.0 indicates that most males experienced at least some degree of maturation of the testes. Combining males with gonad scores of 2–5 from treatments with and without large males revealed that over 60%

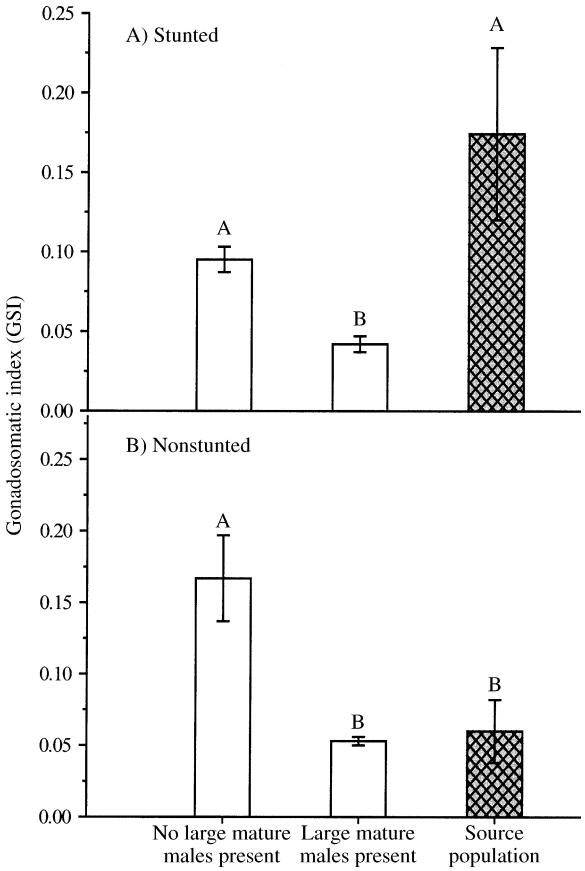

FIG. 1. Mean gonadosomatic indices of experimental males in the treatment ponds with and without large mature males (open bars) and of their cohorts collected during the resampling of the source populations at the end of the experiment (shaded bars). The top panel shows results for males collected from the stunted population, and the bottom panel shows results for males collected from the nonstunted population. Error bars represent ±1 SE. Different letters over error bars represent significant differences between groups (ANOVA; $\alpha = 0.05$).

TABLE 1. Final sizes of juvenile bluegill from the two source (nonstunted and stunted) populations in the experimental ponds (half with large mature males, half without).

Treatment	Males		Females	
	Total length (mm)	Total mass (g)	Total length (mm)	Total mass (g)
Source population				
Stunted	104 (0.8)	19.3 (0.6)	103 (0.7)	19.4 (0.3)
Nonstunted	106 (0.6)	21.1 (0.5)	105 (0.7)	19.6 (0.5)
P value	0.12	0.04	0.14	0.92
Social structure				
Large males present	102 (0.6)	18.0 (0.4)	102 (0.72)	18.0 (0.3)
Large males absent	108 (0.7)	23.0 (0.5)	106 (0.6)	21.6 (0.4)
P value	0.13	0.08	0.25	0.14

Notes: Data are means (with 1 SE in parentheses). *P* values were generated with split-plot ANOVA procedure. Data were log transformed to meet assumptions of ANOVA.

of experimental males in the treatment without large males initiated maturation during the experiment, compared to only 13% in the treatment with large males, reiterating the strong influence of large, mature males on timing of maturation of juvenile males. There was no concomitant source-population influence on gonad score; experimental males from the stunted (1.4 ± 0.06) and nonstunted (1.6 ± 0.07) populations had similar ($F_{1,4} = 1.27$, $P = 0.32$) scores.

Growth rates

At the end of the pond experiment, slight differences in growth rates were apparent between the experimental males originating from the two source populations. Although there was no difference in final total length of fish, males from the nonstunted population were heavier at the end of the experiment than males from the stunted source population (Table 1). There was no significant influence of social structure on length or mass of males (Table 1), nor was there a significant interaction between the genetic and environmental factors in the model for either length or mass ($F_{1,4} > 1.26$, $P > 0.32$). Additionally, no difference in growth of female bluegill collected in the initial sampling of the two source populations was apparent at the end of the experiment (Table 1).

Experiment vs. source population comparison

We compared the maturity status of experimental males to those of the same size cohort collected from each source population at the end of the experiment. Males from each source population showed similar maturation rates (GSIs) to their cohorts in the experiment when the social structure of the experimental treatment matched the social structure of the source population (Fig. 1). For example, juvenile males (TL $= 107.9 \pm 2.01$ mm, $n = 22$) collected at the end of the experiment from Lake Paris (stunted; no large, mature males present) exhibited high GSIs, similar to their experimental cohorts in treatments without large males present (Fig. 1A). Likewise, juvenile males (TL $= 106.9 \pm 4.7$ mm, $n = 22$) collected from Lincoln Trail Lake (nonstunted; large, mature males present) exhibited low GSIs, similar to their cohorts in experimental treatments with large, mature males present (Fig. 1B). The results from this final comparison confirm that juveniles have different maturation trajectories in the stunted and nonstunted source populations, suggesting that the maturation trajectories of juveniles in the experimental populations were a result of the treatments experienced.

DISCUSSION

Life-history variation is common and trade-offs between growth and maturation are well documented for a variety of organisms. Understanding the mechanisms associated with population-specific variation, however, can be complicated by the potential role of genetic differences among populations. Our study is unique in that it examines genetic and environmental influences in a common environment, allowing assessment of the relative strength of each factor in shaping individual life histories. This approach is necessary to understand how genetic differences among populations might influence their responses to selective pressures in the environment. We document that there is indeed a genetic component to growth rates and maturation schedules of bluegill, but that their life histories are quite plastic and exhibit a strong response to the social structure of the population. The practical implication of this finding is that stunting may not always be an ecological condition, but rather the result of a strategic life-history decision to mature early when social conditions permit (also see Jansen 1996).

Regardless of their origin, experimental male bluegill responded facultatively to environmental cues in

making decisions regarding timing of maturation; in general, juveniles delayed maturation in the presence of large, mature males and initiated gonad development in their absence. Social interactions can have a marked influence on the life histories of individuals, and social inhibition of maturation is seen in diverse taxa (see Huntingford and Turner 1987 for review). Among fish, many poeciliids exhibit male-dominated social control of maturation (e.g., Borowsky 1978, 1987, Bushman and Burns 1994). In certain wrasse species, social interactions influence the ability of females to reverse sex (Sale 1980, Warner 1984), which ultimately has a tremendous influence on an individual's reproductive success (Warner 1984). Comparisons of individuals used in the present experiment with their cohorts from each original source population confirm the importance of this mechanism in bluegill, and suggest that similar social-influence mechanisms are likely regulating maturation rates of bluegill in nonexperimental populations. As with other species (e.g., Borowsky 1978, Bushman and Burns 1994), size of mature males appears to be an important determinant in these social interactions, as juveniles were not inhibited by the small parental males in the stunted source population.

In our experimental ponds, differences in population-specific growth rates and GSI were small but statistically significant; males from the nonstunted population gained more mass and exhibited higher GSIs than males from the stunted population. Because no difference in growth was apparent between females from the two sources, the difference in mass of males was either an artifact of the experiment or a sex-specific phenomenon. The variation in mass gain and GSI of males from the different source populations may reflect genetic differences between the populations. In previous studies investigating population- or stock-specific life-history parameters in species such as rainbow trout (*Oncorhynchus mykiss* Walbaum; Reinitz et al. 1979, Wangila and Dick 1988), chinook salmon (*Oncorhynchus tshawytscha* W.; Ricker 1981, Heath et al. 1993), and channel catfish (*Ichtalurus punctatus* R.; Silverstein et al. 1999), variable growth and maturation schedules have been attributed to genetic differences. These studies demonstrate the potential role genetic differences can play in explaining variation in life-history traits. These variable growth and maturation rates could also reflect maternal effects or prior conditioning of bluegill before addition to the experimental ponds. In any case, differences in weight gain and GSI of males from the two source populations were minor, and individuals from both source populations had sufficient plasticity to respond to environmental cues. As such, the strength of the source-population effect on timing of maturation was small relative to the influence of the social environment.

To maximize lifetime reproductive success, fish have likely evolved the ability to manipulate maturation schedules in response to environmental cues (e.g., Jennings and Philipp 1992). Our data provide evidence of the relative importance of social interactions and genetic influences on maturation schedules in male bluegill, demonstrating that individuals from isolated populations respond similarly to social cues when placed in a common environment. As such, we suggest that plasticity in maturation rates of juvenile male bluegill is not an isolated phenomenon, but rather a common one. Plastic maturation schedules would benefit fish by providing some insurance of reproductive success in a variable environment (Garvey et al. 2002). For example, in environments in which adult mortality is high, early maturity might be favored (e.g., Fox 1994). Because of trade-offs between growth and maturation, however, early maturation will likely also result in a smaller, stunted body size that might reduce competitive ability in other environments. Because of the direct relationship between body size and reproductive success in bluegill (Gross 1982), the ability of a juvenile male to assess future reproductive success before making energetically expensive maturation decisions is likely critical for optimization of fitness (Borowsky 1973). This pattern of plastic maturation schedules influenced by environmental cues may be common; similar studies will be necessary with other species to fully understand the relative contributions of genetic and environmental variation to individual life-history strategies, and how that variation influences populations.

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