LIFE HISTORY VARIATION IN RECENTLY ESTABLISHED POPULATIONS OF WESTERN MOSQUITOFISH (*GAMBUSIA AFFINIS*)

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ABSTRACT.—We report life history characteristics for 4 recently established populations of western mosquitofish (*Gambusia affinis*). Mosquitofish from thermally stable habitats, Bonham and Garrett, were characterized by maturity at large sizes, high fat reserves, and large embryos. In contrast, females from a thermally unstable habitat, Wabuska, matured at small sizes and had low fat reserves and small embryos. Females from Parker, a site with no appreciable thermal input, matured at intermediate sizes and had low fat reserves as well as large embryos. These populations shared a common ancestor in 1937; therefore, these results suggest either phenotypic plasticity or rapid evolution.

Key words: *translocation, rapid evolution, western mosquitofish, life history traits, plasticity, temperature, novel environments,* Gambusia affinis.

Evolutionary ecologists have focused much attention on the response of organisms to novel environments (Kettlewell 1973, Stearns 1983a, Reznick et al. 1990, Meffe 1991). In such conditions new phenotypic variants may emerge. Indeed, many examples of evolution in the wild involve situations in which populations experience novel ecological conditions (Antonovics et al. 1971, Kettlewell 1973, Endler 1980, Boag and Grant 1981, Stearns 1983a, 1983b, Reznick et al. 1990, Stockwell and Mulvey 1998, Stockwell and Weeks 1999). Observed variation also may be due to phenotypic plasticity (Bradshaw 1965, Caswell 1983, Trexler 1989), which may or may not be adaptive (Weeks and Meffe 1996). The prospect for populations to experience novel environmental conditions has become more common due to human-induced environmental change (Hoffman and Parsons 1991) and translocation of populations to new environments (Stockwell 1995).

Because they have been introduced widely, live-bearing fishes (Poeciliidae) provide a good group with which to examine population responses to novel environmental conditions. For instance, mosquitofish (*Gambusia* spp.), which are native to the southeastern United States, have been introduced worldwide for mosquito control (Courtenay and Meffe 1989). Mosquitofish occupy a variety of habitats, from ice-covered lakes to thermally altered waters (Krumholz 1948, Meffe 1991, Stockwell 1995). Thermal springs are perhaps one of the more novel environments into which mosquitofish populations have been introduced, because thermal water sources are virtually absent throughout their native geographic range (Berry et al. 1980).

The wide variety of habitats occupied by various poeciliid species is reflected in considerable interpopulation variation in life history characteristics (Reznick and Endler 1982, Stearns 1983a, Trendall 1983, Trexler 1989, Trexler and Travis 1990, Meffe 1991, Haynes and Cashner 1995, Hubbs 1996, Reznick et al. 1996b). Life history traits have received much attention because of their presumed fitness effects (for reviews see Roff 1992, Stearns 1992).

Herein we report life history characteristics of 4 recently established populations of western mosquitofish (*G. affinis*) in northern Nevada. These populations shared a common ancestor approximately 60 yr ago, but occur in habitats with different thermal characteristics. Thus, life history differences identified among them could be indicative of phenotypic plasticity, rapid evolution, or both.

STUDY SITES

Mosquitofish were first introduced into Nevada near Fallon in 1934 (Miller and Alcorn

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1946, La Rivers 1962). These fish descended from nonnative populations in California that were in turn founded from native populations in Texas (Stockwell et al. 1996). During the 1930s fish were introduced from Fallon to numerous springs and wells throughout northwestern Nevada (Fig. 1). In 1937 mosquitofish from Fallon were stocked at Garrett Ranch (Black Rock Desert). By 1940 mosquitofish had been transplanted from Garrett Ranch to Parker Ranch (northern Smoke Creek Desert) and from Parker Ranch to Bonham Ranch (southern Smoke Creek Desert; Jack Bonham, Jimmy Parker, and Betty Paschall, personal communication). By 1940 mosquitofish had been transplanted from Fallon to Wabuska Hot Springs by Wally White (Vernon Mills, Churchill County Mosquito Abatement District; Raymond Alcorn, Nevada Department of Wildlife, personal communication). These Nevada mosquitofish populations are at least 50 linear km apart, preventing natural gene flow.

These sites differ in thermal and chemical characteristics (Table 1). Flow at Bonham, Garrett, and Parker ranches is maintained by artesian wells drilled in the early 19th century (Sinclair 1963, Glancy and Rush 1968, Garside and Schilling 1979). Temperature and conductivity are constant at all 3 sites. Temperatures at Garrett and Bonham are relatively high compared to Parker (Table 1). Specific conductance is highest at Bonham, intermediate at Garrett, and low at Parker (Table 1).

Hot springs historically existed at Wabuska, but numerous wells are also present in this area (Garside and Schilling 1979). Beginning in 1984, habitats at Wabuska were supported by surface discharge from a geothermal plant (Grace Townsend, TADS Enterprises, personal

TABLE 1. Summary of environmental characteristics for 4 Nevada study sites.

Population	Temperature (°C)	Specific conductivity (μmhos cm^{-1})
Bonham	34–36	4150
Garrett	34	1410
Parker	28	266
Wabuska[a]	12–40	1700

[a]See Figure 2 for details on temperature fluctuations.

communication). Although conductivity is relatively constant at this site, intermittent well inflow causes large temperature fluctuations (Table 1). For example, during plant operation water temperatures range from 25°C to 40°C, but during winter temperatures can drop as low as 12°C during plant shutdown. These temperature fluctuations affect all areas inhabited by fish, and ambient temperatures persist until reactivation of hot wells.

The periodicity of such temperature changes is not available, but data on geothermal plant operation provide insights regarding thermal characteristics at Wabuska. The 1st geothermal plant in Nevada was commissioned at Wabuska in 1984. From 1984 through 1987 the plant operated near capacity (Grace Townsend, TADS Enterprises, personal communication). We obtained power production data for the Wabuska geothermal plant for 1988–1995 (Don Townsend, TADS Enterprises, Reno, NV). The plant operated at or near capacity during all months in 1988. However, between 1989 and 1995 relative power production was erratic (Fig. 2). It is likely that water temperatures were also erratic during this time.

METHODS

During April and May 1993, we collected fish by dip net and preserved them in 5% formalin. To estimate female size distribution, we measured standard length (SL) to the nearest 0.01 mm for up to 100 females arbitrarily selected from each collection. All female fish were measured from collections with fewer than 100 females.

Life history data were obtained from dissections of a stratified sample of females from each collection. Females were grouped into 1-mm size classes, and 3 individuals per size class were dissected following techniques outlined by Reznick (1981). Contents of the digestive
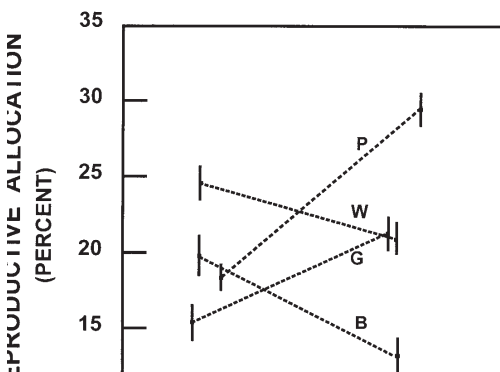

Fig. 1. Introduction history of mosquitofish populations at Nevada study sites.
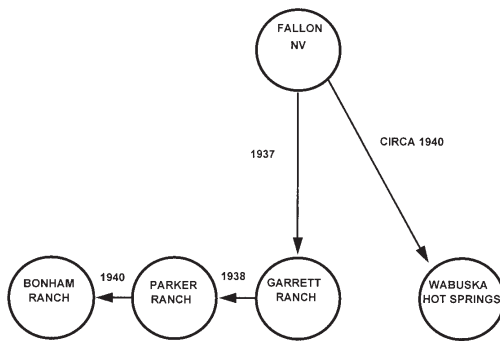
Fig. 2. Relative monthly power production for 1988–1995 at Wabuska Geothermal Plant, Nevada. Monthly production was scored relative to the highest observed amount of power produced during that particular month. For instance, the highest production during January was observed in 1988; all other January production values were scored relative to this score.

tract were removed and discarded. Embryos were counted and evaluated for developmental stage following Reznick (1981): no development (stage 1), un-eyed (stage 2), early-eyed (stage 3), mid-eyed (stage 4), late-eyed (stage 5), very late-eyed (stage 6). Somatic and reproductive tissues were oven-dried at 56°C for 18–24 h and weighed to the nearest 0.1 mg (gross dry weight). Minimum size at maturity represents the smallest size class in which 2 of 3 females were mature (Reznick 1981).

Fat extraction was accomplished by placing fish carcasses in scintillation vials filled with approximately 20 mL of anhydrous ether. Ether was replaced after 24 h and discarded at 48 h. Fish were dried overnight at 56°C and reweighed (net weight; Reznick and Braun 1987). Fat content was computed as a percentage of mass allocated to fat:

$$(gross - net)/gross * 100$$

Reproductive allocation was computed as the percentage of total dry mass contained in reproductive tissues. Embryo weight was determined by dividing total embryo weight by number of embryos. This was necessary because of the high measurement error encountered when embryos were weighed individually.

Analyses

Data were analysed using a 2-way ANOVA (fat content, reproductive allocation) or ANCOVA (embryo weight) to test for main and interactive effects of site and sample date; both were treated as fixed effects. Each monthly collection was also analyzed separately with ANOVA or ANCOVA. Because female size can influence reproductive characteristics, it is typically included as a covariate in analyses (Reznick 1981, Meffe 1991). Because embryo weight changes during development (Reznick 1981), analyses of embryo weight were restricted to eyed embryos (stages 3–6), and developmental stage was used as a covariate for comparing embryo size among populations. The assumption of homogeneity of slopes was met for the covariates of embryo weight: embryo developmental stage and female size. In cases where the covariate had no significant effect, it was removed from the model.

Tukey's HSD test was used to test for pairwise differences among groups for all ANOVA and ANCOVA analyses. Plots of residuals were visually inspected to assure that residuals met the assumptions of normality in the analysis of variance. We maintained experimental-wise error rate at $\alpha = 0.05$ with a sequential Bonferroni test (Sokal and Rohlf 1995).

We do not report brood size data because the ANCOVA assumption of homogeneity of slopes could not be met. Meffe (1991) addressed this problem by regressing brood size on female size and then comparing predicted brood size for females of an "average" size. However, because female size varied substantially among populations, selection of an "average" female was problematic. Brood size data are reported elsewhere (Palmquist and Stockwell 1995). In general, Wabuska and Parker females had the largest broods and Bonham the lowest brood sizes (Palmquist and Stockwell 1995).

RESULTS

At least 59% of females sampled from each collection were pregnant (Table 2-A, 2-B), indicating that the reproductive season was well underway by April. Female size was influenced by DATE ($F_{[1,720]} = 51.551$, $P < 0.001$), SITE ($F_{[3,720]} = 79.629$, $P < 0.001$), and DATE × SITE interaction ($F_{[3,720]} = 10.607$, $P < 0.001$). Fat content was significantly affected by DATE ($F_{[1,317]} = 44.189$, $P < 0.001$), SITE ($F_{[3,317]} = 106.380$, $P < 0.001$), and DATE × SITE interaction ($F_{[3,317]} = 12.415$, $P < 0.001$). Reproductive allocation was not significantly affected by DATE ($F_{[1,320]} = 4.960$, $P = 0.027$), but significant effects were observed for SITE ($F_{[3,320]} = 22.092$, $P < 0.001$) and DATE × SITE interaction ($F_{[3,320]} = 31.034$, $P < 0.001$). Embryo weight was affected by DATE ($F_{[1,168]} = 4.713$, $P = 0.031$), SITE ($F_{[3,168]} = 18.602$, $P < 0.001$), DATE × SITE ($F_{[3,168]} = 3.999$, $P < 0.001$), and by the covariates of FEMALE SIZE ($F_{[1,168]} = 10.025$, $P < 0.002$) and EMBRYO STAGE of development ($F_{[1,168]} = 12.139$, $P < 0.001$).

Significant interaction effects were observed for female size and fat content probably because these variables decreased from April to May, but the relative magnitude of this decrease (slope) was not similar (not parallel) among sites. Embryo weight decreased from April to May for Bonham, Parker, and Garrett populations, but did not change in the Wabuska population.

The DATE × SITE interaction for reproductive allocation was due to a change in site rankings between months (Fig. 3). In April, Wabuska females had significantly higher reproductive allocation than either Garrett or Parker females. However, in May, reproductive allocation for Wabuska females was significantly lower than Parker females and similar to Garrett females (Fig. 3). Because of this relationship, no further analyses of reproductive allocation were undertaken.

Female size varied significantly among the 4 sites in April and May (Table 2). Wabuska females were significantly smaller in April than females from the other 3 populations (Table 2). Bonham females were significantly larger than

TABLE 2. Life history characteristics of Nevada mosquitofish populations in April (2-A) and May (2-B) 1993.[1]

	Population			
	Bonham	Garrett	Parker	Wabuska
2-A) APRIL				
Female size (mm SL)	33.74 ± 0.62^a	26.51 ± 0.69^b	27.45 ± 0.37^b	22.16 ± 0.37^c
$F = 99.592$, $P < 0.001$	($n = 73$)	($n = 56$)	($n = 100$)	($n = 99$)
Pregnancy rates (percent)	94.29	60.42	88.14	81.25
	($n = 35$)	($n = 48$)	($n = 59$)	($n = 48$)
Minimum size maturity (mm SL)	26	21	19	18
Fat content (percent)	16.49 ± 1.51^a	21.90 ± 1.01^b	9.66 ± 0.47^c	5.68 ± 0.62^d
$F = 59.441$, $P < 0.001$	($n = 33$)	($n = 29$)	($n = 52$)	($n = 39$)
Embryo weight (mg)	1.84 ± 0.11^a	1.77 ± 0.12^a	1.90 ± 0.09^a	1.08 ± 0.03^b
$F = 30.970$, $P < 0.001$	($n = 11$)	($n = 8$)	($n = 31$)	($n = 32$)
2-B) MAY				
Female size (mm SL)	26.47 ± 0.89^g	25.35 ± 0.58^g	25.68 ± 0.67^g	20.10 ± 0.35^h
$F = 19.999$, $P < 0.001$	($n = 100$)	($n = 100$)	($n = 100$)	($n = 100$)
Pregnancy rates (percent)	58.93	63.38	90.00	84.91
	($n = 56$)	($n = 71$)	($n = 60$)	($n = 53$)
Minimum size maturity (mm SL)	22	20	22	16
Fat content (percent)	11.32 ± 0.68^g	14.43 ± 0.72^h	7.63 ± 0.41^i	6.64 ± 0.39^i
$F = 44.300$, $P < 0.001$	($n = 32$)	($n = 41$)	($n = 54$)	($n = 45$)
Embryo weight (mg)	1.55 ± 0.09^g	1.68 ± 0.08^g	1.43 ± 0.07^g	1.08 ± 0.08^h
$F = 8.389$, $P < 0.001$	($n = 18$)	($n = 21$)	($n = 31$)	($n = 26$)
Covariates:				
female size: $F = 7.110$, $P = 0.009$				
developmental stage: $F = 12.249$, $P < 0.001$				

[1]Data for female size, fat content, and embryo weight are presented as mean ± standard error of the mean, and sample sizes are given in parentheses. Data were analyzed by month. Means sharing a letter were not significantly different.
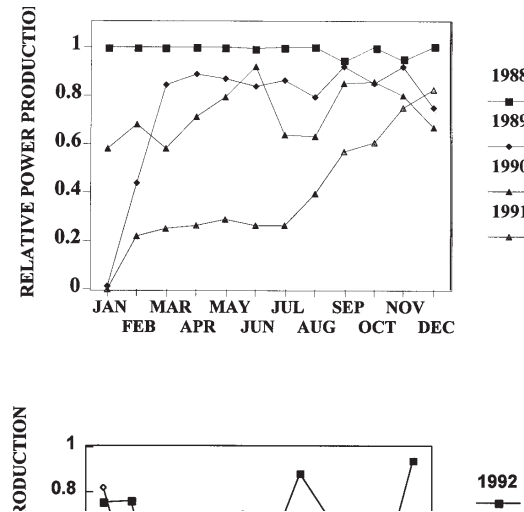
Fig. 3. Reproductive allocation (mean ± $s_{\bar{x}}$) by month for the 4 study populations (B = Bonham, G = Garrett, P = Parker, W = Wabuska). Dotted lines illustrate the DATE × SITE interaction.

females in the other 3 populations, but females from Parker and Garrett did not differ significantly in size (Table 2-A). In May, Wabuska females were once again smaller than females from the other populations. No significant differences were detected among Bonham, Garrett, and Parker populations (Table 2-B).

Minimum size at maturity during April and May was smallest for Wabuska females and largest for Bonham females (Table 2-A, 2-B). Parker females matured at relatively small sizes in April but moderate sizes in May. Garrett females matured at moderate sizes during both months (Table 2-A, 2-B).

Fat content varied significantly among populations during April and May (Table 2-A, 2-B). Garrett females had highest mean fat content in both months. Bonham females had higher fat content than either Parker or Wabuska females in both months (Table 2-A, 2-B). In April, Parker females had significantly higher fat reserves than Wabuska females, but these populations did not differ during May (Table 2-A, 2-B).

Embryo size varied significantly among sites during April and May (Table 2-A, 2-B). Female size and embryo stage of development were significant covariates in May but not April (Table 2). During both months Bonham, Garrett, and Parker embryo weight did not vary significantly from each other, but all were significantly larger than Wabuska embryos (Table 2-A, 2-B).

DISCUSSION

Striking life history differences were observed among Nevada mosquitofish populations that shared a common ancestor less than 60 yr ago. These sites varied in both water chemistry and temperature. Both environmental factors have been shown to influence life history characteristics of mosquitofish (Stearns and Sage 1980, Vondracek et al. 1988, Brown-Peterson and Peterson 1990, Meffe 1991).

In this study life history characters seem to be more closely associated with thermal conditions than with specific conductance. For example, Bonham and Garrett females had similar life history traits: maturity at large sizes, relatively high fat reserves, and large embryos. These sites have similar thermal conditions but differ considerably in specific conductance. Also, Wabuska and Garrett females had very different life history traits, despite the fact that they experience similar specific conductance.

Wabuska females, which occupied the most unpredictable thermal habitat, had the most distinctive life history characters: maturity at small size, low fat reserves, and small embryos. Wabuska females were exposed to fluctuating thermal environments where water temperatures ranged from 12° to 40°C.

Life history characters for the Wabuska population were similar to those observed by Meffe (1991), who found life history characters of eastern female mosquitofish (*G. holbrooki*) to be correlated with water temperature fluctuations. Females at both Par Pond, South Carolina (Meffe 1991), and Wabuska are exposed to variable thermal environments, and both populations exhibit similar life history tactics. This may indicate a generalized response of mosquitofish to thermal fluctuations.

The association between water temperature and maturity at small sizes may reflect phenotypic plasticity. Shifts in temperature are likely to influence food availability as well as metabolism in mosquitofish (Vondracek et al. 1988, Meffe 1991). Further, Vondracek et al. (1988) reported that size of maturity in mosquitofish is reduced for animals raised at low temperatures.

However, 2 results are consistent with the hypothesis that life history traits of Wabuska females are evolutionary responses to a harsh environment. First, mosquitofish at Wabuska were significantly smaller than females from the other 3 populations. Because age and size have been shown to be correlated (Reznick et al. 1990), these data suggest that Wabuska females did not live as long as females from other sites. Alternatively, these data may simply reflect relatively lower growth rates of Wabuska females due to low food availability. Second, Wabuska fish had very low fat content. Collectively, these factors suggest that Wabuska was a comparatively harsh environment. Such harsh conditions may lower both growth rate and average life expectancy of Wabuska mosquitofish, which should select for maturity at a smaller size (Gadgil and Bossert 1970, Roff 1984, 1986, Stearns and Koella 1986). Thus, our results may reflect rapid life history evolution. Evolution in response to temperature fluctuations would have been extremely rapid because mosquitofish at Wabuska would have experienced this type of envrironment for only 4 yr (1989–1993; 12–16 generations; Fig. 2).

In contrast to other life history traits, reproductive allocation was not clearly associated with thermal characteristics. Strong DATE × SITE interactions for this variable suggest this trait is plastic or that resources may vary in time and space. If resource distribution is unpredictable early in the season, plastic responses of reproductive allocation could allow females to respond quickly to local conditions.

We hypothesized that observed life history differences are responses to thermal environments. However, these life history traits may be associated with factor(s) that covary with temperature (Meffe 1991). Others have reported similar associations between life history characteristics and specific environmental factors such as predation (Reznick and Endler 1982, Reznick et al. 1990, Belk and Hales 1993) and fluctuating habitats (Stearns 1983a). However, determining the actual mechanism(s) responsible for the observed life history phenotype requires detailed ecological information and carefully designed field experiments (Reznick et al. 1996a).

The data reported here are consistent with those from other studies that reported interpopulation variability in poeciliid life history characters (Reznick and Endler 1982, Stearns 1983a, 1983b, Trexler and Travis 1990, Haynes and Cashner 1995, Hubbs 1996, Reznick et al. 1996b). Rapid life history evolution has been reported in Trinidadian guppies (*Poecilia reticulata*) and recently founded populations of western mosquitofish in Hawaii (Stearns 1983a, 1983b, Reznick et al. 1990). Hubbs (1996) observed extensive variation in life history traits among populations of *G. affinis* in Texas, but traits were not correlated with geography or environmental variables. Interestingly, populations in Nevada are derived from 2 wild populations in Texas that were introduced to California in 1922 (Stockwell et al. 1996). However, the early founding population in California appears to have experienced a genetic bottleneck during population establishment (Stockwell et al. 1996). Furthermore, fish were not introduced to Nevada until 1934, which was 12 yr after their initial introduction to California (36–48 generations). It seems unlikely that observed differences in Nevada represent historical differences in the native Texas populations; however, we cannot exclude this possibility.

Our data are of particular interest because life history traits are associated with thermal characteristics of their respective habitats and because the introduction history of these populations is known. This raises the possibility that rapid evolution has occurred in these recently established populations. Indeed, Stockwell and Weeks (1999) report a genetic basis for 2 of these life history traits, indicating that rapid life history evolution has occurred in these recently established populations.

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