HABITAT EPHEMERALITY AND HATCHING FRACTIONS OF A DIAPAUSING ANOSTRACAN (CRUSTACEA: BRANCHIOPODA)

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ABSTRACT

Diapause allows aquatic organisms to survive periods of drydown in intermittent pools. However, often not all of the individuals hatch in response to a filling event. This prolonged diapause (diapause lasting through one or more favorable periods) is the likely consequence of several factors. We address the possibility that prolonged diapause in fairy shrimp in Southern California vernal pools is a bet-hedging adaptation to unpredictability in the duration of filling events. Under the simplest bet-hedging model of selection on prolonged diapause, the fraction of eggs hatching in any filling event should approximate the fraction of filling events lasting long enough for successful reproduction.

We quantified filling durations in seven pools of coastal San Diego County, California for all winter and spring events between 1983 and 1996. The distributions of filling durations did not differ significantly among pools, so selection should be similar across pools. When the 189 filling durations were combined into a single estimated probability distribution, approximately 28% of the filling events lasted 17 days or longer, the developmental time to first reproduction (under field conditions) in the fairy shrimp Branchinecta sandiegensis (Branchiopoda: Anostraca) inhabiting these pools. Previous laboratory hatching experiments determined a maximum hatching rate of 18% at 10°C, with lower hatching percentages at higher and lower temperatures.

INTRODUCTION

Southern Californian vernal pools are isolated ephemeral wetlands that may fill several times per year, but are dry for most of the year (Bauder, 1987; Zedler, 1987; Bauder and McMillan, 1998). Given the surrounding semiarid Mediterranean climate, these vernal
pools are patches of aquatic or mesic habitat in a matrix of xeric habitat, both spatially and temporarily (Ebert and Balko, 1987). A suite of plant and animal species exploit these ephemeral wet conditions (Zedler, 1987), including several species of endemic anostracan shrimp (Eng et al., 1990; Simovich and Fugate, 1992; Eriksen and Belk, 1999).

In general, species exploiting ephemeraly favorable habitats survive bad conditions by dispersal to more favorable sites, tolerance of stressful conditions, or diapause. Diapause is the only option for shrimp in these vernal pools. Dispersal to other pools is ineffective, as favorable and unfavorable conditions are highly synchronous among pools. Tolerance of stressful conditions allows some plants to survive through dry periods, but is not an option for obligate aquatic species such as shrimp. Diapause, a state of reduced metabolic activity relatively resistant to environmental conditions unfavorable to growth and reproduction, allows organisms to avoid unfavorable seasons and exploit episodic favorable conditions. Annual plants exist as dormant seeds through the dry summer and fall; aquatic species exist as diapausing individuals such as encysted eggs.

For these vernal pool shrimp, not all individuals break diapause and hatch when a pool fills. This prolonged diapause (some individuals remaining in diapause through one or more episodes of favorable conditions; Hanski, 1988) has the effect of preventing populations from being extirpated when a pool filling is of too short duration to allow completion of the life cycle and production of diapausing offspring.

Prolonged diapause may occur for several reasons. First, not all individuals may experience the appropriate cues for hatching, or favorable conditions, and thus the prolonged dormancy may be environmentally enforced. During a partial filling event, encysted eggs above the high-water mark do not hatch. In many plants, seeds that are buried too deeply do not germinate despite favorable moisture and temperature, but may subsequently germinate when brought to the surface (e.g., Roberts, 1964; Philippi, 1993a; Rees and Long, 1993). Similarly, in other aquatic systems, encysted eggs buried too deeply in the sediment do not hatch (e.g., De Stasio, 1989; Hairston et al., 1995).

Second, prolonged diapause may be an adaptive response to reduce sibling competition (Bulmer, 1984; Ellner, 1986; Philippi, 1993b), or localized competition in general via dispersal in time (Venable and Lawlor, 1980; Ellner, 1987). If density or the magnitude of competition vary over time, prolonged diapause may increase fitness by "dispersing" offspring from high-density to low-density times, even in completely predictable (but varying) environments (Ellner, 1985, 1987).

And third, prolonged diapause may be a bet-hedging adaptation maximizing the long-term mean fitness in unpredictable environments (Cohen, 1966; Hanski, 1988). Population growth is multiplicative, so natural selection should maximize the geometric mean fitness across generations or episodes (Lewontin and Cohen, 1969). A trait that slightly decreases the arithmetic mean fitness while greatly decreasing the variance of fitness across generations can increase the geometric mean fitness. Such traits are considered to be forms of bet-hedging (Slatkin, 1974; Philippi and Seger, 1989).

Prolonged diapause observed in ephemeral pool shrimp and other crustacean systems...
is often assumed to be prima facie evidence for bet-hedging adaptation, despite the existence of the other potential causes. In part, bet-hedging adaptation to environmental uncertainty is simply a seductive concept. But also, because bet-hedging involves maximizing fitness across a long sequence of random events, comprehensive (complete) tests of it are difficult or impossible in any system. Instead, even in the seed germination literature, only corollaries or specific qualitative predictions are developed and tested (e.g., Freas and Kemp, 1983; Philippi, 1993a, 1993b; Pake and Venable, 1996).

In previous work, Simovich and Hathaway (1997) collected Branchinecta sandiegogenensis cysts from soil samples from these pools and subjected them to repeated hydrations in the laboratory. They demonstrated that cysts that do not hatch during the first hydration in the laboratory will hatch under the same conditions in subsequent hydrations. Hildrew (1985) and Brendonck et al. (1998) report similar results with ephemeral pool anostracans in Africa. Therefore, while some cysts undoubtedly do not receive appropriate cues to hatch in the field, much of the observed prolonged diapause cannot be explained as being environmentally enforced.

Here, we test a prediction about bet-hedging per se. For our system, selection for prolonged diapause as a bet-hedging response to environmental unpredictability makes a quantitative prediction about hatching fractions: that they should approximately equal the probability of successful reproduction. Our logic in performing this test is not that of naive rejection or acceptance of bet-hedging; prolonged diapause in this system is almost certainly the result of a combination of all three factors listed above. Without much more information about the strengths of competition, quantitative partitioning is not possible, but we can do a qualitative test. If observed hatch fraction differs widely, then other factors must be contributing more than bet-hedging.

THE SYSTEM

San Diego vernal pools are ephemeral wetlands located largely atop the coastal mesas. These pools fill with late winter and early spring rains. Rainfall averages 25 cm per year but is extremely variable in amount (5-56 cm) (National Weather Service, 1997) and in spatial pattern. Pools are generally shallow (5-15 cm) but a few can be as deep as 30 cm. Depending on depth and precipitation, pools can fill for a few days to several weeks and may fill and dry numerous times within a season (Bauder, 1987; Ebert and Balko, 1987; personal observation). Branchinecta sandiegogenensis (Fugate, 1993), an endemic anostracan shrimp, dominates the early stages of these coastal pools. This species exhibits a compact life history: time from initial wetting to first reproduction is about 17 days at water temperatures within the seasonal range (10-20 °C), a few days faster at warmer temperatures, and slower at colder temperatures (Hathaway and Simovich, 1996). These shrimp are univoltine within a filling event: all eggs are encysted and must go through a period of diapause before hatching. Finally, Hathaway and Simovich (1996) determined a maximum hatching fraction of 28% for field-collected cysts hydrated under laboratory conditions.
COHEN'S MODEL OF BET-HEDGING

Cohen's model of bet-hedging diapause was developed for seed germination in desert annuals (Cohen, 1966, 1967). Translating the notation and biology to hatching of diapausing eggs, the number of eggs \(X_{t+1}\) following a filling cycle is:

\[X_{t+1} = X_t (1 - H_t) S_t + X_t H_t Y_t,\]

where \(X\) is the number of individuals (cysts) in the population, \(H_t\) is the fraction that hatch in episode \(t\), \(S_t\) is the survival rate of encysted eggs, and \(Y_t\) is the per capita yield (numbers of encysted eggs produced) for individuals that hatched in episode \(t\). The first term in the equation is survival of eggs that do not hatch, the second term is the production of new eggs from the fraction of eggs that do hatch. Natural selection should maximize the product of the growth rates across episodes, or, equivalently, the mean of the logs of the growth rates:

\[\mathcal{W} = \frac{1}{N} \sum_{t=1}^{N} \log ((1 - H_t)(S_t + H_t Y_t)).\]

One simple case Cohen explored analytically is where the survival rate of diapausing eggs \(S\) is constant and the year qualities are either good \((Y = Y_g)\) with probability \(p\) or bad \((Y = 0)\) with probability \((1-p)\). In this case the optimal hatching fraction is:

\[H_{opt} = \frac{Y_g - S}{Y_g} \cdot p\]

If the per capita egg production in good years \((Y_g)\) is moderately large, subtracting \(S\) (constrained to be \(\leq 1\)) has little effect, the optimal hatching is approximately \(p\), and the precise value of \(Y_g\) cancels out of the equation (Cohen, 1966).

Reproduction in \(B.\ sandiegensis\) is 0 for all pool durations less than the age at first reproduction, and then on the order of 10–20 eggs per day for a few weeks. Therefore, while \(Y_g\) is not constant for all good events, \(Y_g\) for durations with even one day of reproduction are moderately large, so \(p\) can be approximated as the fraction of durations longer than the time to first reproduction.

Because even adjacent vernal pools vary in size and depth, the probabilities of lasting long enough for successful reproduction \((p)\) might vary widely among pools. In that case, if dispersal among pools were extremely low, selection would be for different hatching fractions in different pools. With any appreciable inter-pool dispersal, the optimal hatching fraction would be a complex function of dispersal and source-sink dynamics between long- and short-duration pools.

POOL DURATIONS

As part of another project, the filling behavior of 37 vernal pool basins in the Kearny Mesa area of San Diego, California was monitored during the winter and spring months.
between 1983 and 1996 (Bauder, unpublished data). Water depth was measured within one day of each significant rainfall event, and subsequently every two or three days until the pool dried. We tabulated the duration of each filling event for the seven pools monitored in all years where B. sandieganensis is known to occur. Several pools had one or more years with no filling events; in 1988 one pool had eight separate filling events. Over these 14 years, the numbers of filling events ranged from 16 for one pool to 40 for another.

Difference among pools in filling durations were tested with Kruskal–Wallis non-parametric ANOVA. This tests for shifts in the central tendencies in distributions without assuming normality. For graphical presentation, the probability distributions of filling durations for individual pools were estimated by kerneling (Silverman, 1986). Each observed duration was replaced with a gaussian “bump” with area 1/N, the sum of those bumps estimates the probability distribution.

Despite the fact that some pools filled more than twice as many times as others over these 14 years, the distributions of durations did not significantly differ among pools (Kruskal–Wallis \( \chi^2 = 5.2, \text{ df = 6, } p = 0.522 \) ) (Fig. 1). The maximum durations ranged from 94 to 128 days across pools, the median durations ranged from 8 to 12 days. The fractions of filling events lasting at least 17 days varied from 13% (3/23) to 35% (10/28), well within the among-pool variation expected due to chance with these sample sizes (Likelihood Ratio \( \chi^2 = 6.1, \text{ df = 6, } p = 0.413 \) ).

Because the pools did not differ significantly in filling durations, the probability distribution for filling durations was tabulated from the combined 189 filling events (Fig. 2). For these pools in these years, 27.5% of the filling events lasted at least 17 days, long enough for the eggs to hatch and develop into reproductive adults. One-third of the pool fillings lasted at least 14 days, and 23% lasted 20 days, a plausible range of

![Fig. 1. Probability distributions of filling durations for each of the seven pools for all filling events between 1983–1996. While the numbers of events per pool range from 16 to 40, each probability distribution integrates to 1. The modal durations among pools range between 8–11 days.](image-url)
Fig. 2. Fraction of filling events lasting at least as long as the given duration, based on the combined 189 events from the seven pools. The vertical line marks the time to first reproduction for *B. sandiegonensis*; the horizontal line indicates the fraction of filling events exceeding that threshold.

DISCUSSION

The match between the fraction of filling events of sufficient duration for successful reproduction and the hatching fraction indicates that selection for bet-hedging per se could explain nearly all of the prolonged diapause in *B. sandiegonensis*. As noted above, this result does not constitute proof that selection for bet-hedging is important in this system.

The result that pools with quite different frequencies of filling, and quite different durations until drying for a given precipitation event, nonetheless have similar distributions of filling durations appears counterintuitive. However, following a heavy rainfall event, pool A lasts longer than pool B, but then a light rainfall event that fills pool A for a short duration does not fill pool B at all. A wet winter may fill pool B for two prolonged periods with a single drydown, but fill pool A for the entire winter.

Our results have two implications for conservation. Because roughly 90% of the vernal pool habitat in the state of California has been lost (Stone, 1990) and 97% of that in San Diego County (Baude, 1987), several vernal pool species including *B. sandiegonensis* are listed Federally as endangered or threatened (Federal Register, 1997). Continued development of vernal pool habitat requires mitigation, often the creation or restoration of other vernal pools via recontouring of soil, and inoculation with cysts from sacrificed pools. The existence of prolonged diapause in a cyst bank implies that the mere observation of hatched shrimp in an inoculated pool is not sufficient to indicate successful recreation: even a pool completely unable to support shrimp reproduction will continue to have eggs hatching from the cyst bank for several developmental times at field temperatures. These numbers are comparable to the 28% hatching observed under optimal laboratory conditions.
years. Detection of reproductively mature shrimp should be a bare minimum criterion for mitigation credit.

Finally, the similar distributions of filling durations among these pools suggests that creating pools with hydrology suitable for B. sandiegonensis may require care. If natural pools inhabited by B. sandiegonensis had widely varying distributions of durations, then most created pools should mimic some subset of natural pools. Whatever covariation in basin size and pool depth produced the similar distribution of filling durations across our range of natural pools might not be replicated automatically in created pools. To the extent that B. sandiegonensis hatching fractions are bet-hedging adaptations to the specific duration probabilities, created pools with substantially different distributions of filling durations might be unable to sustain populations.

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