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HATCHING RESPONSES OF TEMPORARY POOL INVERTEBRATES TO SIGNALS OF ENVIRONMENTAL QUALITY

MATTHEW SPENCER* AND LEON BLAUSTEIN
Community Ecology Laboratory, Institute of Evolution, University of Haifa, Haifa 31905, Israel

ABSTRACT

Many temporary pool invertebrates survive dry periods as diapausing eggs. Theory predicts that the proportion of diapausing eggs that hatch when the pool fills with water should vary with signals of likely reproductive success, if such signals are available. Reproductive success in temporary pool invertebrates is influenced by the presence of predators and desiccation. We studied hatching responses of temporary pool invertebrates to the presence of fire salamanders (*Salamandra salamandra* L., an important predator in temporary pools), and to manipulations of nutrients. Nutrient manipulations may mimic the increase in conductivity associated with high evaporation and risk of desiccation, but might also affect food availability or modify signals associated with the presence of *Salamandra*. Fewer eggs of the conchostracan *Cyzicus* sp. hatched in the presence of *Salamandra*, and in pools to which nutrients had been added. Other taxa (bdelloid rotifers and chydorids) did not show unambiguous hatching responses to the presence of *Salamandra* or nutrients. We discuss these results in the light of simple models for optimal hatching fractions. Large crustaceans such as *Cyzicus* are particularly likely to show strong hatching responses to signals of environmental quality. However, we also expect to find such responses in many other crustaceans.

INTRODUCTION

Many organisms survive seasonally adverse conditions as resistant resting stages such as diapausing eggs, seeds, and cysts. These resting stages emerge to become active stages at the start of the "growing season", during which conditions are potentially suitable (emergence is used here as a general term including hatching, germination, and excystment). However, the suitability of conditions in any given season is unpredictable. If conditions are good, the active stages may produce a new yield of resting stages. If conditions turn out to be bad, the active stages may die without producing any new resting stages. If all the resting stages of a given genotype emerge in a bad season, that genotype will be lost from the local population. On the other hand, if some resting stages do not emerge, and are able to survive until at least the next season, a single bad season will not lead to local extinction of the

*Current address: Department of Biochemistry, University of Cambridge, Tennis Court Road, Cambridge, CB2 1QW, England. E-mail: ms379@mole.bio.cam.ac.uk
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genotype. Cohen (1966) formally showed that when the reproductive success of the active stage is uncertain, and dormant stages may persist until the next season of suitable conditions, there is a single optimal emergence fraction per season that will maximize the long-term average growth rate of a genotype. This optimal emergence fraction is always less than one if there is a non-zero probability of zero reproductive success (and may be less than one in other circumstances). In apparent agreement with this qualitative prediction, prolonged dormancy of resting stages and emergence fractions less than one have been found in organisms ranging from annual plants (e.g., Pake and Venable, 1996) to freshwater crustaceans (e.g., De Stasio, 1989; Simovich and Hathaway, 1997).

Cohen's work has provided the foundation for a large body of theory on dormancy, life history strategies, and the maintenance of genetic diversity (e.g., Templeton and Levin, 1979; Venable and Lawlor, 1980; Bulmer, 1984; Ellner, 1985a,b; Brown and Venable, 1986, 1991; Venable and Brown, 1988; Rees, 1993, 1994; Ellner and Hairston, 1994; Ellner et al., 1998, 1999). Almost all of this theory has been based on the assumption that resting stages do not have any information about the likely quality of the environment in any given season (beyond the trivial sense in which resting stages only emerge during the growing season). However, there are limited observations that resting stages can adjust their emergence fractions according to signals associated with good or bad conditions. For example, germination rates of the seeds of desert annual plants are higher in years in which subsequent conditions lead to higher yields (Pake and Venable, 1996). Evans and Cabin (1995) showed that there were allozyme differences between seeds of mustard (*Lesquerella fendleri*) that germinated in arid habitats and seeds that remained dormant. They suggested that these differences may have been associated with differences in water requirements. The presence of herbivorous zooplankton reduces the excystment rate of the resting cysts of several species of freshwater algae (Hansson, 1996; Rengefors et al., 1998). If resting stages are able to detect signals indicating the likely quality of the environment, responding to these signals by adjusting the emergence fraction is a better strategy than maintaining the single emergence fraction giving the highest long-term average growth rate (Cohen, 1967; Venable and Lawlor, 1980). In order to understand the evolutionary causes and consequences of long-term dormancy, it is therefore important to know how much information resting stages are able to obtain about the environment into which they may emerge.

In northern Israel, there are many small rock pools (areas from <0.1 m^2 to a few tens of square meters, depths almost always <0.5 m) which hold water only during the wet season (usually between November and March). These pools often contain a wide range of invertebrates, mainly crustaceans, insects, and flatworms (Spencer et al., 1999). Many of these species, including all the crustaceans, survive the dry season as diapausing eggs in the sediment, hatching when the pools fill with water in autumn. Their reproductive success during the wet season is likely to be heavily influenced by two factors: the presence of predators and the risk of desiccation. The dominant predators are larvae of the fire salamander (*Salamandra salamandra* L.). *Salamandra* larvae are generalist predators (Degani, 1996), often arrive in pools within 24 hours of filling (L. Blaustein, personal observation), and have been shown to cause large reductions in the abundance

of many invertebrates (Blaustein et al., 1996). Rainfall in northern Israel is unpredictable, and many temporary pools dry and fill several times during the wet season. More transient pools tend to support fewer aquatic species (Spencer et al., 1999), and high densities of dead aquatic organisms can often be found in pools that have recently dried (M. Spencer, personal observation).

The diapausing eggs of invertebrates might be able to detect both the presence of predators and the risk of desiccation. Larval *Salamandra* may betray their presence by chemical cues, and their early arrival in pools makes it plausible that resting stages could detect these cues before emerging. Blaustein (1997) found that the negative effects of caged *Salamandra* on the abundance of crustaceans were similar in magnitude to the effects of uncaged *Salamandra*, even though the caged *Salamandra* were unable to consume crustaceans. One possible explanation is that fewer crustacean eggs hatched in the presence of *Salamandra* due to the release of a chemical signal. Chemical communication has been shown to be important in many other contexts in freshwater systems (Dodson et al., 1994). High evaporation rates are a major cause of desiccation in temporary pools and lead to an increase in conductivity (Williams, 1987). High conductivity reduces the fraction of eggs that hatch in many freshwater branchiopods (Hutchinson, 1967; Brown and Carpelan, 1971; Brendonck, 1996). However, conductivity may have other, sometimes contradictory, effects. The presence of *Salamandra* could increase conductivity (due to indirect effects on algal community structure, or to excretion of soluble waste products). If this were true, the effects of *Salamandra* on hatching fractions might vary with conductivity. On the other hand, high conductivity may be a result of nutrient inputs that can stimulate algal growth and provide more food for invertebrates. Thus in some conditions high conductivity may signal higher likely reproductive success.

We studied the hatching patterns of temporary pool invertebrates in artificial pools with and without larval *Salamandra* and nutrient additions (which altered conductivity). We also estimated the number of invertebrates present when pools were about to dry and *Salamandra* began to metamorphose at the end of the experiment. We used these data to estimate the likely differences in reproductive success between treatments. Temperature may also be a signal of the risk of desiccation or a direct stressor, so we examined the relationship between temperature (which varied naturally between pools) and hatching numbers, and between temperature and water depth at the end of the experiment. We predicted the following:

- The presence of *Salamandra* larvae, and high conductivity due to the addition of nutrients, would reduce the number of hatching invertebrates. These factors are likely to be associated with low reproductive success of invertebrates in natural temporary pools.
- There would be a negative association between temperature and the number of hatching invertebrates. High temperature may be an indicator of a high risk of desiccation or a direct stressor.
- The presence of *Salamandra* larvae would also reduce the number of invertebrates surviving to the end of the season, due to predation.
- The addition of nutrients would increase the number of invertebrates surviving to the end of the season, by increasing the amount of algal growth.

MATERIALS AND METHODS

EXPERIMENTAL DESIGN

We set up 24 artificial pools with or without *Salamandra*, and with or without nutrient additions, in a full factorial design with six replicates of each treatment combination. In each pool we added sediment collected from dry temporary pools (containing the diapausing eggs of temporary pool invertebrates). We also added a mesh-sided cage containing sediment from dry temporary pools. Invertebrates could hatch inside the cage without being eaten by *Salamandra*. We estimated the number of invertebrate individuals hatching inside the cages four times over a two-week period, and the number present in the pools outside the cages at the end of the experiment (when *Salamandra* began to metamorphose and the pools were close to drying).

SETTING UP THE EXPERIMENT

Pools were plastic tubs (0.6 m × 0.4 m, and 0.15 m deep), dug 7 cm into the ground to provide insulation. The pools were set out in a grid pattern on the University of Haifa campus on 13–14 January 1999, and allowed to collect rainwater until 20 January 1999, by which time they had accumulated about 10 cm of water. Treatments were assigned randomly with respect to spatial location. On 20 January, pools assigned to the *Salamandra* treatment each received three *Salamandra* larvae (mean mass 0.8 g, SD 0.4 g; mean length from snout to tip of tail 41 mm, SD 6 mm; collected from Secher Pool, a few kilometers from the experimental site). This is towards the low end of natural densities (M. Spencer and L. Blaustein, personal observations). On 21 January, we placed a cage in one corner of each pool. We made each cage from a cylindrical translucent polyethylene bottle (diameter 120 mm, height 215 mm), standing upright and open at the top, with a 75 × 140 mm window of 50-μm Nitex plankton netting in the side. Diapausing eggs and newly-hatched crustaceans were usually about 100 μm in smallest dimension, so would be unable to pass through the mesh. The same day, pools with nutrient additions each received 10 mL of 20:20:20 powdered NPK inorganic plant fertilizer (providing two potassium ions to two phosphate ions to one each of ammonium and nitrate), of which 0.5 mL was placed inside each cage. We think that the addition of fertilizer should provide a reasonable analogue of the general increase in salt concentration that occurs as water evaporates from a pool. The resulting conductivities cover most of the range found in natural pools. All pools also received 78 g dry weight litter, of which 3.5 g was placed inside each cage. Litter was collected from under *Pistacia lentiscus* bushes around the University of Haifa, and contained (by mass) 60% *P. lentiscus* leaves, 1% *Pinus halipensis* needles, 2% grass stems, and 37% other material including twigs, seeds, and other plant leaves. *P. lentiscus* is the commonest vegetation around natural rock pools, so the litter we collected should have a similar composition to that falling into natural pools. We added 500 mL sediment (measured as dry volume) to each pool, of which 23.5 mL was placed inside each cage. This was sufficient to provide a 2-mm layer across the base of the pool, similar to that found in many natural pools. Sediment was collected from dry temporary pools on Mt. Shechanya, Galilee Mountains, on 28 September 1998,

and was thoroughly mixed. The pools from which sediment was collected are inhabited by *Salamandra* (M. Spencer and L. Blaustein, personal observations). We did not quantify the initial abundance of diapausing eggs in the sediment in each experimental unit. Variation in the number of diapausing eggs added to each pool will therefore tend to increase variation in the number of hatching invertebrates. However, because this variation is random with respect to treatments, the Type I error rate (the probability of wrongly concluding that there is a treatment effect) will be unaffected, while the Type II error rate (the probability of wrongly concluding that there is no treatment effect) will be increased. Thus our conclusions will tend to be conservative with respect to the presence of treatment effects. We also added about 100 cm^3 limestone rocks inside each cage and 2000 cm^3 limestone rocks in the rest of the pool. Rocks commonly occur in natural pools and may provide shade and refuge from predators. These quantities provided equal concentrations of fertilizer, leaf litter, sediment, and rocks inside and outside cages. To ensure mixing of water inside and outside cages, we lifted each cage out of the water every day, allowed the contents to drain out through the mesh window, and returned the cage to the pool, where it refilled with water through the mesh.

SAMPLING INVERTEBRATES IN CAGES

On 24, 27, and 31 January and 3 February 1999 (the cage sampling period), we sampled crustaceans inside the cages. On each date, we lifted the cage out of the water at an angle so as to retain water inside the cage, swirled to ensure that the contents were well mixed, and poured the water and suspended material through a 50-μm filter. We then rinsed animals trapped on the filter into 95% ethanol, and counted them under a dissecting microscope. On the first three dates, we left a depth of 20 mm water in the bottom of the cage to avoid removing too much sediment. On the last date, we poured out all the water to ensure a complete take of hatching crustaceans. We stopped sampling the cages after 3 February, when differences in flow rates between nutrient treatments became apparent (see below). In preliminary laboratory trials, most hatching occurred within a week of hydration, so a two-week sampling period should be long enough. We summed the total number of invertebrates over the four cage samples, as numbers were low.

FLOW RATES OUT OF CAGES

We first observed noticeable growth of periphyton on 1 February, and by 2 February the rate at which water drained from cages was obviously lower in the high nutrient treatments than the low nutrient treatments. On 4 February, one day after the final samples from cages, we measured the volume of water that flowed through the mesh in each cage in the 5 s after removal from the pool, as an index of the likely flow rate. Flow rates out of cages were much higher in low nutrient (mean 24 mL s^{-1}, SE 12) than in high nutrient pools (mean 3 mL s^{-1}, SE 3; $F_{1, 20} = 42.64$, $p < 0.0001$; two-way ANOVA, with a natural log transformation to ensure positivity of predicted values and to reduce heteroscedasticity), but the difference between pools with *Salamandra* (mean 12 mL s^{-1}, standard error 4) and without *Salamandra* (mean 15 mL s^{-1}, SE 4) was very small ($F_{1, 20} =$

1.20, $p = 0.29$), and there was no evidence of an interaction ($F_{1, 20} = 0.08$, $p = 0.78$). Reduced flow rates made it less likely that conditions inside the cages reflected conditions outside the cages. Any effects of nutrient treatments on hatching rates are therefore confounded with possible consequences of differences in mixing rates between nutrient treatments. We considered cleaning the mesh, but did not do so for two reasons. First, algal growth only became a problem two days before the end of the cage sampling period. Second, cleaning the mesh would have released a flush of dead algal cells into the water column, with unknown effects on the rest of the system.

PHYSICOCHEMICAL CONDITIONS IN CAGES

Each time we sampled the cages, we also measured pH, temperature, and conductivity inside and outside the cages, using Hanna Instruments HI 9025 and HI 9033 meters (Hanna Instruments, Ronchi di Villafranca, Italy). Measurements were usually taken between 9 am and 12 noon. On sunny days, temperatures were positively related to the order in which pools were sampled. We used the residuals from least-squares regression relationships between order of measurement and temperature, rather than the raw temperature measurements, as a predictor variable in analyses of invertebrate counts. pH and conductivity did not show obvious relationships with order of sampling, so we used the raw measurements for these variables. We averaged pH, residual temperature, and conductivity measurements over the dates on which cages were sampled. To check that conditions were similar inside and outside cages, we examined the mean differences (inside–outside) in pH, conductivity, and temperature over the four dates on which samples were taken from inside cages. We tested for variation in pH, conductivity, and temperature between treatments using factorial ANOVAs. Overall, pH, temperature, and conductivity were similar inside and outside cages, although temperature was generally slightly lower inside than outside. The mean differences between measurements inside and outside were: for pH, 0.01 (SE 0.01); for temperature, –0.29 °C (SE 0.04); and for conductivity, 4.03 mS cm^{-1} (SE 2.38). The only significant treatment effect on differences between measurements of physicochemical parameters taken inside and outside cages was that the mean difference in pH was higher in low nutrient than in high nutrient pools (low nutrient pools: mean difference 0.04, SE 0.01; high nutrient pools: mean difference –0.01, SE 0.01; $F_{1, 20} = 7.47$, $p = 0.01$).

SAMPLING POOLS

We continued to measure pH, conductivity, and temperature outside the cages at approximately weekly intervals until the end of the experiment. We also recorded the depth of water in the pools. We ended the experiment on 7 March 1999, when the first *Salamandra* began to metamorphose. All pools were expected to be dry within a week due to hot weather and lack of rain. We compared pH and conductivity (means outside cages during the cage-sampling period and over the whole experiment) between treatments using two-way ANOVAs, with a natural log transformation to reduce heteroscedasticity. To find out whether temperature during the cage-sampling period was a reliable predictor of risk of desiccation, we estimated Kendall's τ_b (a nonparametric measure of association) between residual temperature inside cages and depth at the

end of the experiment (Gibbons, 1993). We also investigated whether conductivity during the cage-sampling period was a reliable predictor of risk of desiccation, after taking into account the effects of treatments. We first estimated the residual mean conductivity in each pool over the cage-sampling period (back-transformed residuals from a two-way ANOVA on natural log mean conductivity). We then estimated τ_b between these residual conductivity values and depth at the end of the experiment.

At least one *Salamandra* survived to the end of the experiment in 11 out of the 12 pools to which they were introduced. One *Salamandra* survived in one pool, 2 in six pools, and 3 in four pools. In the remaining pool, all *Salamandra* died for unknown reasons between 16 and 22 February. We included this pool in the *Salamandra* treatment as it contained *Salamandra* for most of the experiment. The results were qualitatively similar, although estimated *Salamandra* effects were larger, if we excluded this pool. We removed dead *Salamandra* from pools, but we did not replace them with new individuals, as the density of *Salamandra* naturally decreases over the season. *Salamandra* is also protected in Israel, and we had a permit to use only a limited number of individuals in this experiment.

Cyzicus sp. (an unidentified species: C. Dimentman, personal communication) was the only species that was abundant both in the cages during the cage-sampling period, and in the pools at the end of the experiment. On 7 March, we swept a small aquarium net (10×15 cm, mesh size about 250 μm) five times through each pool (covering the whole area each time) and counted the *Cyzicus* caught. Most were of reproductive size and had formed copulating pairs. Thus, the number of *Cyzicus* can be used to estimate treatment effects on likely reproductive success. We are confident that these counts are reliable, as they were consistent with less intensive samples taken before and after this date. We may underestimate the difference in reproductive success between pools with low and high nutrients, as some low nutrient pools appeared to contain relatively more small individuals. We also checked under the rocks and cage in each pool, in case *Cyzicus* tended to hide in these places when *Salamandra* were present, but they did not appear to do so.

ANALYSIS OF INVERTEBRATE COUNTS

We analyzed invertebrate counts using generalized linear models (McCullagh and Nelder, 1989). We assumed Poisson errors and a log link function. We corrected for overdispersion using an empirically estimated dispersion parameter. We initially fitted maximal models containing both main effects, their interaction, and residual temperature (measured inside the cages for hatching counts within cages, or outside cages for counts at the end of the experiment). We then sequentially deleted parameters until removing any of those remaining would cause a significant increase in deviance at an α of 0.05, using approximate *F*-tests: this gives the minimal adequate model (Crawley, 1993). We did not delete main effects when interaction terms were significant. Other reasonable methods of analysis (for example, analysis of variance on untransformed or natural log $(x + 1)$ transformed data) gave qualitatively similar conclusions, so we do not present them here. We present the results as back-transformed parameter estimates with normal approximate 95% confidence intervals, from both maximal and minimal ad-

Table 1

Interpretation of parameter estimates for the general linear models used to analyze invertebrate counts. The table gives the predicted count in pool *i*, for each treatment combination. Symbols: μ, intercept; α, *Salamandra* effect; β, nutrient effect; γ, *Salamandra* × nutrient interaction; δ, residual temperature coefficient; t_i, residual temperature in pool *i* (°C). The back-transformed parameter estimates in Table 2 are thus exp(μ) for the intercept, exp(α) for the *Salamandra* effect, and so on

	Nutrients added	No nutrients added
Salamandra present	$\exp(\mu + \alpha + \beta + \gamma + \delta t_i)$	$\exp(\mu + \alpha + \delta t_i)$
Salamandra absent	$\exp(\mu + \beta + \delta t_i)$	$\exp(\mu + \delta t_i)$

equate models. Presenting the results in this way is more informative than stating *p* values, as it allows the reader to distinguish between the size of effects and the precision with which they are estimated (Harlow et al., 1997). Table 1 explains the interpretation of parameter estimates. All statistics were done using JMP Version 3.2.2 (SAS Institute, Cary, NC).

RESULTS

TREATMENT EFFECTS ON PHYSICOCHEMICAL CONDITIONS

We found no evidence for effects of *Salamandra* on physicochemical conditions, or for interactions between *Salamandra* and nutrients. Mean pH during the cage-sampling period was not significantly different between low nutrient pools (mean 7.70, SE 0.01) and high nutrient pools (mean 7.68, SE 0.01; $F_{1,20} = 0.62$, $p = 0.44$). However, over the whole experiment, mean pH was significantly lower in low nutrient pools (mean 8.14, SE 0.02) than in high nutrient pools (mean 8.76, SE 0.06; $F_{1,20} = 93.71$, $p < 0.0001$). Over the cage-sampling period, mean conductivity was significantly lower in low nutrient pools (mean 237 mS cm^{-1}, SE 6) than in high nutrient pools (mean 520 mS cm^{-1}, SE 24; $F_{1,20} = 224.17$, $p < 0.0001$). Mean conductivity over the whole experiment was lower in low nutrient pools (mean 305 mS cm^{-1}, SE 10) than in high nutrient pools (mean 449 mS cm^{-1}, SE 26) ($F_{1,20} = 29.17$, $p < 0.0001$), although the difference between treatments was smaller than over the cage-sampling period. Conductivity generally declined over the course of the experiment, probably because salts became sequestered in algae or bound to sediment.

PHYSICOCHEMICAL PREDICTORS OF DESICCATION RISK

There was a significant negative association between mean residual temperature inside cages during the cage sampling period and depth in the final week of the experiment ($\tau_b = -0.43$, $N = 24$, $p = 0.005$). There was also a significant negative association between residual mean conductivity inside cages during the cage sampling period and depth in the final week of the experiment ($\tau_b = -0.49$, $N = 24$, $p = 0.002$).

INVERTEBRATE COUNTS

Three taxa hatched in sufficient numbers to examine inside cages: the conchostracan *Cyzicus* sp., bdelloid rotifers, and chydorids. Other taxa which were found occasionally in the cage samples included ostracods, cyclopoid and calanoid copepods, *Ceriodaphnia*, and ceratopogonid larvae. We did not examine the hatching responses of these rare taxa, but this does not affect the interpretation of our results for more abundant taxa. By the end of the experiment, the pools were dominated by calanoid copepods and ostracods, but *Cyzicu*s was also found in nine pools.

The number of *Cyzicus* hatching in cages (Fig. 1a, Table 2a) in pools with *Salamandra* was about 0.4 times the number hatching in cages in pools without *Salamandra*. The number hatching in cages in high nutrient pools was about 0.6 times the number hatching in cages in low nutrient pools, although the upper 95% confidence limit was close to 1. There was no evidence for an interaction between *Salamandra* and nutrient treatments. Each 1 °C increase in residual temperature was associated with an approximate doubling of the number of *Cyzicus* hatching in cages. The data are about as variable as we would expect, given that they are counts of small numbers of discrete individuals (a Poisson distribution would give a dispersion parameter of 1; we estimated a dispersion parameter of about 0.8, indicating a little less within-treatment variability than expected). Thus we can reasonably conclude that the differences between means are not simply a consequence of a few outlying data.

The number of *Cyzicus* counted at the end of the experiment in pools with *Salamandra* was only about 0.03 times the number counted in pools without *Salamandra* (Fig. 1b, Table 2b). In fact, we detected *Cyzicus* in only one out of twelve pools containing *Salamandra*, but eight out of twelve pools without *Salamandra*. The high frequency of zeros does not cause any problems for our analysis, as this is exactly the situation for which Poisson models are designed. All parameters other than the effect of *Salamandra* could be removed from the model without significantly increasing the residual deviance. However, residual deviance was very high. The estimates for the *Salamandra* effect and the *Salamandra* by nutrient interaction were perfectly correlated in the maximal model, inflating the standard errors of these parameters. We present estimates from the model without the interaction term (the removal of which caused only a very small increase in deviance). The association between numbers of *Cyzicus* hatching in cages and observed in pools at the end of the experiment was positive but not significantly different from zero ($\tau_b = 0.17$, $N = 24$, $p = 0.32$).

Bdelloid rotifers in cages (Fig. 1c, Table 2c) showed a significant interaction between *Salamandra* and nutrient treatments. There were relatively high numbers of bdelloid rotifers in low nutrient pools without *Salamandra* and high nutrient pools with *Salamandra*. Higher residual temperatures were associated with higher numbers of bdelloid rotifers, although the lower 95% confidence limit was close to 1. Residual deviance was high. The minimal adequate model for chydorids hatching in cages (Fig. 1d, Table 2d) contained no terms other than the intercept. Residual deviance was high, and the relationship between means and variances would have fitted a quadratic

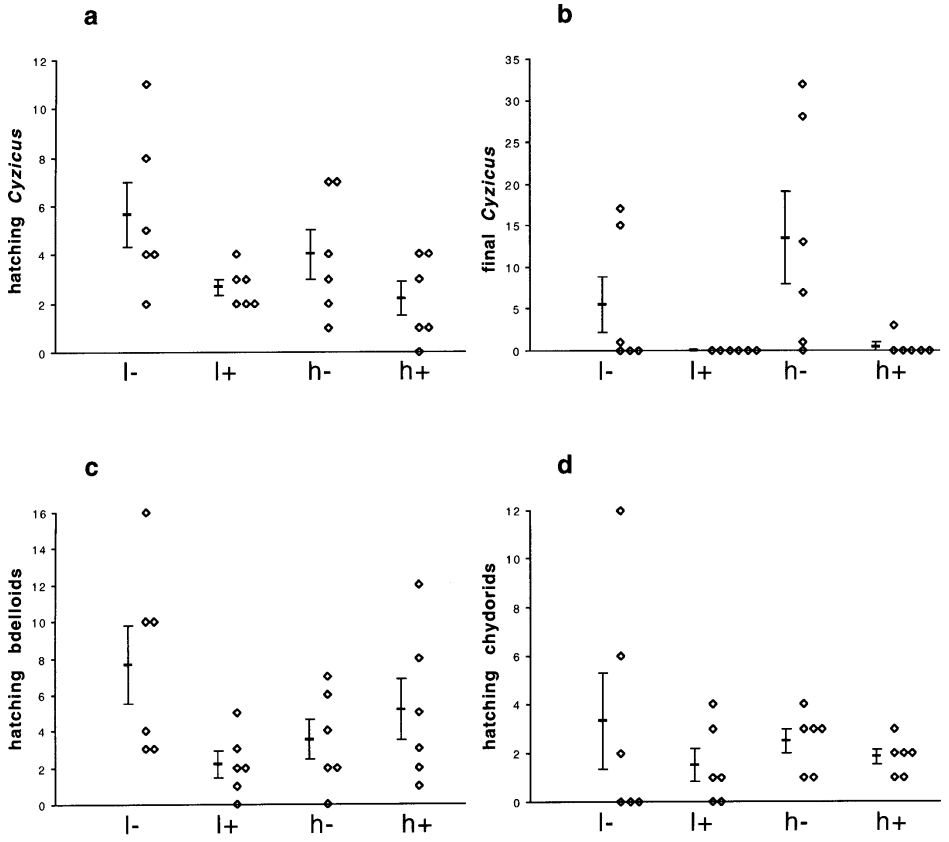

Fig. 1. Numbers of (a) hatching *Cyzicus* in each cage; (b) final *Cyzicus* in each pool; (c) hatching bdelloid rotifers in each cage; and (d) hatching chydorids in each cage. Each diamond is the count in a single replicate of a treatment combination, the bold horizontal bar is the mean for that treatment combination, and the error bar is ± one standard error. Numbers in cages are pooled over four samples (see Methods). Symbols: l, low nutrients; h, high nutrients; -, *Salamandra* absent; +, *Salamandra* present.

better than a linear model. Negative binomial errors might have been more appropriate for chydorids. However, the data do not suggest strong treatment effects.

DISCUSSION

More *Cyzicus* hatched in the absence than the presence of *Salamandra* (Fig. 1a). As there was no interaction between *Salamandra* and nutrients for *Cyzicus*, we can be

Table 2

Models for invertebrate counts. Back-transformed parameter estimates (which are multiplicative effects) and back-transformed normal approximate 95% confidence intervals (in parentheses) are shown for both maximal and minimal adequate models. In the latter, a back-transformed estimate of 1 indicates a term which was removed from the model. For *Cyzicus* at the end of the experiment, there was a perfect negative correlation between the estimates for *Salamandra* effects and the *Salamandra* by nutrient interaction, resulting in extremely large standard errors for these parameters. We therefore present estimates with the interaction term excluded

(a) *Cyzicus* hatching. Maximal model: residual deviance 18.14 with 19 df, dispersion parameter 0.83. Minimal adequate model: residual deviance 18.27 with 20 df, dispersion parameter 0.81

Term	Maximal model	Minimal adequate model
Intercept	6.49 (4.76, 8.86)	6.34 (4.76, 8.45)
Salamandra	0.38 (0.22, 0.67)	0.41 (0.27, 0.63)
Nutrients	0.58 (0.35, 0.94)	0.61 (0.41, 0.91)
Salamandra × Nutrients	1.19 (0.52, 2.69)	1
Residual temperature	1.99 (1.31, 3.04)	2.00 (1.31, 3.03)

(b) *Cyzicus* abundance at end of experiment. Maximal model: residual deviance 141.87 with 19 df, dispersion parameter 6.99. Without interaction term: residual deviance 143.93 with 20 df, dispersion parameter 6.86. Minimal adequate model: residual deviance 181.53 with 22 df, dispersion parameter 8.48

Term	Maximal model	Minimal adequate model
	(without interaction)	
Intercept	4.05 (1.38, 11.90)	9.50 (5.55, 16.24)
Salamandra	0.03 (0.002, 0.68)	0.03 (0.001, 0.74)
Nutrients	2.99 (0.97, 9.24)	1
Salamandra × Nutrients	not estimated	not estimated
Residual temperature	0.50 (0.20, 1.28)	1

(c) Bdelloid rotifer hatching. Maximal model: residual deviance 44.76 with 19 df, dispersion parameter 2.13. The minimal adequate model was identical

Term	Maximal model (and minimal adequate model)
Intercept	8.71 (5.67, 13.37)
Salamandra	0.24 (0.09, 0.59)
Nutrients	0.38 (0.17, 0.82)
Salamandra × Nutrients	5.38 (1.60, 18.05)
Residual temperature	1.86 (1.05, 3.29)

(d) Chydorid hatching. Maximal model: residual deviance 47.20 with 19 df, dispersion parameter 2.26. Minimal adequate model: residual deviance 56.15 with 23 df, dispersion parameter 2.90

Term	Maximal model	Minimal adequate model
Intercept	3.75 (1.92, 7.32)	2.29 (1.46, 3.60)
Salamandra	0.38 (0.11, 1.27)	1
Nutrients	0.64 (0.23, 1.79)	1
Salamandra × Nutrients	1.68 (0.32, 8.86)	1
Residual temperature	1.73 (0.74, 4.03)	1

confident that this *Salamandra* effect is not an artifact of differences in flow rates between nutrient treatments. Furthermore, Blaustein (1997) also found that the presence of caged *Salamandra* reduced the number of *Cyzicus*. By the end of the experiment, there were significantly more *Cyzicus* in pools without *Salamandra* than pools with *Salamandra* (Fig. 1b; Table 2b). Some of this difference is probably due to differences in hatching rates (although this would not have to be so, because the sediment samples inside and outside cages are independent, and hatching rate inside cages makes no contribution to the *Cyzicus* population outside the cages). However, most of this difference is probably due to consumption of *Cyzicus* by *Salamandra*.

We can estimate the effect of *Salamandra* on the active stages of *Cyzicus*. We assume that the proportional effect of *Salamandra* on *Cyzicus* hatching in cages over the cage sampling period is the same as the proportional effect on the total number of *Cyzicus* hatching outside the cages. The effect of *Salamandra* on active *Cyzicus* is then the effect at the end of the season divided by the effect on hatching. We assume that our estimates of the sizes of these effects are independent, as we have no information on their covariance. From the minimal adequate models (Table 2a,b), the effect of *Salamandra* on active *Cyzicus* is 0.03/0.41 = 0.06 (we give two decimal places, but calculations were done with higher precision), with a normal approximate back-transformed 95% confidence interval of 0.002 to 1.84. Thus, consumption by *Salamandra* may reduce *Cyzicus* survival, but we cannot estimate this effect precisely. *Cyzicus* have been found in the gut contents of *Salamandra*, but do not form a major part of the diet (Degani, 1996). Large *Cyzicus* are only rarely eaten in laboratory trials when *Salamandra* also have access to smaller crustaceans (L. Blaustein, unpublished data). However, juvenile *Cyzicus* may be much more vulnerable to *Salamandra*, as they swim slowly and lack the strong carapace that may protect adults. It seems plausible that a reduction in *Cyzicus* hatching in the presence of *Salamandra* could be an adaptive response to a signal indicating low likely reproductive success. Adult *Cyzicus* are relatively rare in field samples from pools containing *Salamandra*, yet juveniles frequently hatch from sediment samples collected from these pools. (L. Blaustein, personal observation). Our results suggest that two effects may contribute to this pattern: a reduction in hatching rate in the presence of *Salamandra*, and consumption of those *Cyzicus* that do hatch.

Both residual conductivity and residual temperature during the cage-sampling period were correlated negatively with depth at the end of the experiment. Thus both these variables contained information about the risk of desiccation. We expected that higher temperature or conductivity would be associated with reduced hatching, if organisms could use this information optimally (the risks of desiccation and predation may also interact, if decreasing water volume concentrates predators; Hairston et al., 1985). However, temperature was positively rather than negatively correlated with the number of hatching *Cyzicus* (Table 2a). This also argues against the role of temperature as a direct stressor. Perhaps eggs develop faster at higher temperatures, so that increasing temperature increased the proportion of total hatch which occurred during the cage-sampling period. The residual conductivity and temperature signals might also be weaker in most natural pools than in this experiment, as we added sediment containing

invertebrates only after the pools had held water for several days. Evaporation might have affected temperature and conductivity in the period between placing the pools in the field and adding sediment. If these signals were usually weak in natural pools, we might not expect organisms to respond to them.

Pools to which nutrients were added had higher conductivity, and fewer *Cyzicus* hatched in cages in these pools (Fig. 1a). Physicochemical conditions were similar inside and outside cages, and only pH showed any systematic change in differences between inside and outside measurements among treatments. However, it is possible that the effect of nutrients on hatching *Cyzicus* was an artifact resulting from differences in flow rates between nutrient treatments. The absence of a strong association between the numbers of *Cyzicus* in cages during the cage-sampling period, and in pools at the end of the experiment, is due mainly to the difference in responses to nutrients (Table 2a,b). In cages, there was a significant negative effect of nutrients, while in pools at the end of the experiment, the effect of nutrients was positive but not significantly different from 1 (i.e., no effect). High conductivity can therefore be an ambiguous indicator of environmental quality: it may indicate that the desiccation risk is high (reducing expected reproductive success), or that nutrient enrichment has occurred (increasing expected reproductive success). Furthermore, conductivity may only be a good indicator of desiccation risk if evaporation is the main way in which water is lost from pools. This is true for our experiment, but in natural pools water may also be lost by percolation through the bed of the pool.

Bdelloid rotifers showed an interaction between *Salamandra* and nutrient treatments (Fig. 1c, Table 2c), although this might be an artifact of differences in flow rates. In low nutrient pools (where flow rates were higher), fewer rotifers were counted during the cage-sampling period in pools with *Salamandra*. It is possible that small *Salamandra* eat rotifers, although they have not been recorded in gut contents (Degani, 1996, from 21 individuals; M. Spencer, personal observation, from four individuals). We have some reservations about these results. Firstly, bdelloid rotifers are small enough to pass through the 50-μm mesh from which cages were made, although we do not know how often they actually did so during the experiment. Secondly, the generation times of bdelloid rotifers are on the same order as the length of time over which we sampled the cages, so we can only estimate a combined effect on hatching, survival, and possibly fecundity. As with *Cyzicus*, increasing temperature increased the number of rotifers counted during the cage-sampling period. None of the predictor variables we examined explained a significant amount of the deviance in numbers of chydorids in cages, although the high dispersion makes it more difficult to detect small effects.

It is clear that the presence of *Salamandra* can affect hatching or early development in *Cyzicus*, and possibly also in bdelloid rotifers. There are several possible mechanisms to explain these phenomena (Blaustein, 1997). The most obvious is that a substance produced by *Salamandra* provides a signal that predators are present, reducing the hatching rate of eggs. The skin secretions of amphibians include amines, steroids, alkaloids, peptides, and proteins (Clarke, 1997), all of which could indicate to other organisms the presence of an amphibian predator. Our results suggest that predation by *Salamandra* on

juvenile *Cyzicus* may be important, so responding to cues indicating the presence of *Salamandra* would be advantageous to *Cyzicus*. However, this seems less plausible for bdelloid rotifers, which are smaller than most of the prey taken by *Salamandra*.

A substance produced by *Salamandra* might kill eggs before they hatch, or juvenile invertebrates just after hatching. Amphibian skin secretions have antimicrobial properties, and some species (including *Salamandra salamandra*) also produce repellent or toxic substances for protection against predators (Clarke, 1997). However, it seems unlikely that such a chemical would reach a high enough concentration to kill about 60% of *Cyzicus* eggs, which are by necessity resistant to a wide range of adverse environmental conditions. On the other hand, some rotifers are known to produce autotoxins which reduce population growth rate and survival (Kirk, 1998). If one of the many chemicals produced by *Salamandra* happened to have similar properties to a rotifer autotoxin, the presence of *Salamandra* could reduce rotifer numbers.

Salamandra might also affect the abundance of another organism such as an alga or bacterium. This other species might produce substances that kill *Cyzicus* eggs or juveniles, or reduce the hatching proportion. Substances produced by diatoms can inhibit the development of marine copepod eggs (Ianora et al., 1995), although this has only been demonstrated at higher concentrations than are likely to occur in nature. *Salamandra* can affect the abundance of both algae and bacteria, probably by altering the abundance of grazers or the recycling of nutrients (Blaustein et al., 1996). However, these indirect effects are unlikely to be strong soon after a pool has filled with water. When the pool has only recently filled, the abundance of grazers is likely to be low even in the absence of *Salamandra*, and many of the potential grazers may be the very species whose hatching is affected by *Salamandra*. This also makes it unlikely that the response to *Salamandra* is simply a response to changes in pH or conductivity resulting from the indirect effects of *Salamandra* on algae and bacteria (especially as we did not detect such changes in this experiment). Furthermore, theory suggests that organisms should use those signals having the highest correlations with reproductive success (Cohen, 1967). Thus, even though indirect effects may give some information about the presence of predators, responding to a unique chemical produced by the predator is likely to have greater fitness benefits.

A MODEL FOR HATCHING FRACTIONS

If, as seems possible, *Cyzicus* eggs are modifying their hatching in response to a chemical cue, we should consider what kinds of organisms are likely to show such a trait. The theory we present in the next section leads to three simple and testable predictions that may serve as a guide to future work on this problem. We will restrict our question to a closed population in which active stages may only survive and reproduce during a discrete season, and in which diapausing eggs may survive many seasons. A simple linear model for population growth is:

$$X_{t+1} = X_t [(1 - H_t)V + H_t Y_t] \quad (1)$$

(Cohen, 1966), where X_t is the population size of diapausing eggs at time t, H_t is the proportion of diapausing eggs hatching at time t, V is the proportion (assumed constant) of non-hatching diapausing eggs surviving from time t to $t + 1$, and Y_t is the number of new diapausing eggs produced per individual hatching at time t. Consider a case where there are two possible values for reproductive success, Y_1 and Y_2 (a necessary assumption to obtain an analytical solution for the optimum hatching proportion). There are k possible values of a signal carrying some information about the likelihood of these two values at the time of hatching, each associated with a hatching proportion H_k. The expected long-term average growth rate $E(r)$ is:

$$E(r) = \sum_k P_{1k} \log [V + H_k (Y_1 - V)] + \sum_k P_{2k} \log [V + H_k (Y_2 - V)] \quad (2)$$

(Cohen, 1967), where P_{ik} is the probability of the combination of signal k with reproductive success i. When both Y_1 and Y_2 are greater than V, the optimal value of H is 1 for all values of k (because a hatching organism always does better than a non-hatching organism). Similarly, when both Y_1 and Y_2 are less than V, the optimal value of H is 0 for all k. However, when $Y_1 < V < Y_2$, the optimal value of H for a given signal k (which we refer to as H_{kM}) is different for different signals. H_{kM} can be found from the partial derivative of eq 2 with respect to H_k:

$$H_{kM} = -V\left[\frac{P_{1|k}}{Y_2 - V} + \frac{P_{2|k}}{Y_1 - V}\right] \quad (3)$$

where any value of H_{kM} greater than one or less than zero is taken as one or zero, respectively. $P_{i|k}$ is the conditional probability of reproductive success i given signal k. When there are only two signal values, the conditional probabilities of reproductive success i and j are $P_{i|k}$ and $(1 - P_{i|k})$ respectively. The ratio (A) of any two optimal hatching proportions H_{1M} and H_{2M} is:

$$A = \frac{H_{1M}}{H_{2M}} = \frac{P_{1|1} (Y_1 - Y_2) + Y_2 - V}{P_{2|2} (Y_2 - Y_1) + Y_1 - V} \quad (4)$$

when $1 > H_{2M} > H_{1M} > 0$ (by definition, $H_{2M} \geq H_{1M}$). A is zero when H_{1M} is zero, one when both H_{2M} and H_{1M} are one, and H_{1M} when H_{2M} is one but H_{1M} is less than one. A corresponds to a back-transformed parameter for effects on numbers of hatching individuals estimated from our experiments (Table 1). A is always less than or equal to one, so a large effect of signal state on optimal hatching fraction corresponds to a small A. What are the conditions which will tend to make A small? We assume that both $P_{1|1}$ and $P_{2|2}$ are > 0.5, so that both signal states contain positive information about likely reproductive success. We also assume that the cost of detecting signals is negligible. If this is not so, we would only expect responses to signals when the benefits are greater than the costs of detection, and this is more likely when the difference between optimal hatching fractions is large. Although we do not have estimates for any of the parameters in the model, analysis (Appendix) yields the following general conclusions:

1. Organisms with high resting stage survival are more likely to show large responses to signals of likely reproductive success, other things being equal (Fig. 2a,b). That an increase in resting stage survival increases the response to a signal makes sense, because higher survival in the resting state increases the probability that an individual will be exposed to more than one set of environmental conditions.
2. The more information either signal gives about likely reproductive success, the larger the response (Fig. 2c,d). This result also makes sense, because increasing either of the conditional probabilities increases the likelihood that there will be a difference in reproductive success between the environmental states following signals 1 and 2. Furthermore, if one signal state already contains a lot of information, the benefit of increasing the amount of information in the other signal state is small.
3. Organisms with relatively low reproductive success in either state (Y_1 or Y_2), or in which the difference in reproductive success between states is large, are more likely to show a large response (Fig. 2d,e). Increasing either Y_1 or Y_2 increases the geometric mean reproductive success, and the higher this mean, the more likely it is that hatching is better than not hatching, and the less need there is to discriminate between signals indicating the likely reproductive success at any given time. If Y_2 and Y_1 are reproductive success in the absence and presence of a predator, respectively, then for fixed Y_2, this shows that increasing the effect of the predator on reproductive success increases the optimum response to signals indicating the presence of the predator. We do not consider density dependence, but we expect that a negative relationship between the number of juveniles and per capita reproductive success would reduce the difference between Y_1 and Y_2, and thus reduce the hatching response to the signals indicating the presence of the predator.

To summarize, we expect to find large responses to signals indicating likely reproductive success when egg survival is high, the signal contains reliable information, the difference in reproductive success between environmental states is large, and reproductive success is low even in "good" conditions. The *Cyzicus–Salamandra* interaction may meet these conditions. The only field estimates of annual survival in crustacean resting eggs of which we are aware are >0.98 (for a calanoid copepod; Hairston et al., 1995). The wide range of chemicals produced by amphibians makes it likely that there are specific and sensitive indicators of the presence of *Salamandra.* Comparing the effects of *Salamandra* on *Cyzicus* numbers in cages during the cage-sampling period, and in pools at the end of the experiment, suggests that the reduction in reproductive success associated with the presence of *Salamandra* may be large, although our estimate is imprecise. *Cyzicus* probably has relatively low reproductive success even in the absence of predators because its long development time generally allows only a single generation in temporary pools in Israel (L. Blaustein, personal observation; C. Dimentman, personal communication). In contrast, smaller crustaceans such as ostracods, cladocerans, and copepods may have many generations in which to multiply before a pool dries, and we predict that these species will show smaller hatching responses than *Cyzicus* to the presence of predators, other things being equal. However, the scarcity of reports of hatching responses to predators is probably because they have rarely been investigated, rather than because they do not occur.

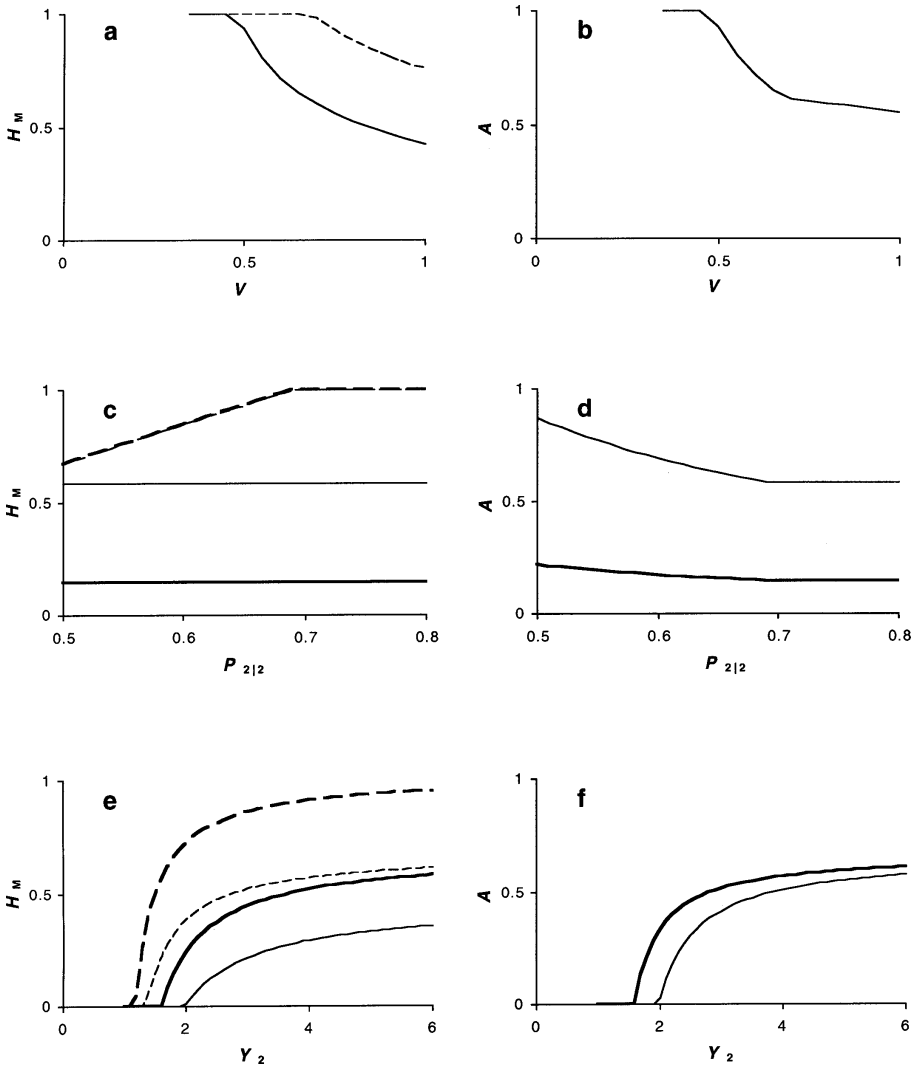

Fig. 2. Relationships between optimal hatching fractions (H_{2M} given a signal indicating "good" conditions, e.g., the absence of a predator; H_{1M} given a signal indicating "bad" conditions, e.g., the presence of a predator), the ratio of these hatching fractions ($A = H_{1M} / H_{2M}$), and the parameters of a simple model predicting optimal hatching fractions (eq 3). In **(a)**, **(c)**, and **(e)**, solid lines are H_{1M} and broken lines are H_{2M}. **(a)** and **(b)**: Effects of V, the survival of dormant stages, with $P_{1|1} = P_{2|2} = 0.6$ (the conditional probabilities of reproductive success Y_1 given signal 1, and of Y_2 given signal 2, respectively), $Y_1 = 0.3$, $Y_2 = 5$ (reproductive success in environmental states 1 and 2, respectively). **(c)** and (**d**): Effects of $P_{1|1}$ and $P_{2|2}$. Light lines: $P_{1|1} = 0.55$; bold lines: $P_{1|1} = 0.8$ (H_{2M} is identical in either case). $V = 0.85$, $Y_1 = 0.3$, $Y_2 = 5$. (**e**) and (**f**): Effects of Y_1 and Y_2. Light lines: $Y_1 = 0.1$; bold lines: $Y_2 = 0.35$. $V = 0.85$, $P_{1|1} = 0.6$, $P_{2|2} = 0.6$.

There is a large body of theory relating to the evolution of life history strategies in organisms with prolonged dormancy (see Introduction). Almost all of this theory assumes that resting stages have no information on environmental conditions (for exceptions, see Cohen, 1967; Venable and Lawlor, 1980). If the resting stages of many species are able to detect signals of environmental quality, most of this theory will be quantitatively inaccurate.

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APPENDIX

Here, we present analyses of eq 4 supporting the results in Fig. 2 and the Discussion.

1. Organisms with high resting stage survival are more likely to show large responses to signals of likely reproductive success, other things being equal (Fig. 2a,b). When $1 > H_{2M} > H_{1M} > 0$, the partial derivative of A with respect to V is:

$$\frac{\partial A}{\partial V} = \frac{(Y_1 - Y_2)(P_{2|2} + P_{1|1} - 1)}{[P_{2|2}\,(Y_2 - Y_1) + Y_1 - V]^2} \tag{5}$$

The denominator of eq 5 is always positive. The first term in the numerator is negative for all cases of interest because a difference in hatching response between different signals only occurs when $Y_1 < V < Y_2$ (Cohen, 1967). The second term in the numerator is positive because we have assumed that the signal provides positive information, such that both $P_{2|2}$ and $P_{1|1}$ are greater than 0.5. Thus the whole expression evaluates negative. When H_{2M} is one, $A = H_{1M}$, and continues to decrease with increasing V.

2. The more information the signal gives about likely reproductive success, the larger the response (Fig. 2c,d). When $1 > H_{2M} > H_{1M} > 0$, the partial derivative of A with respect to $P_{1|1}$ is:

$$\frac{\partial A}{\partial P_{1|1}} = \frac{Y_1 - Y_2}{P_{2|2}\,(Y_2 - Y_1) + Y_1 - V} \tag{6}$$

The numerator is negative for all cases of interest, and rearranging eq 3 shows that the denominator must be positive for a positive H_{2M}, so the whole expression evaluates negative. When H_{2M} is one, A is H_{1M} , and still decreases with increasing $P_{1|1}$. When $1 > H_{2M} > H_{1M} > 0$, the partial derivative of A with respect to $P_{2|2}$ is:

$$\frac{\partial A}{\partial P_{2|2}} = \frac{[P_{1|1}(Y_1 - Y_2) + Y_2 - V](Y_1 - Y_2)}{[P_{2|2}\,(Y_2 - Y_1) + Y_1 - V]^2} \tag{7}$$

The denominator is always positive, and $Y_1 < Y_2$ for all cases of interest. Rearranging eq 3 shows that the first term in the numerator must be positive for positive H_{1M} , so the whole of eq 7 is always negative for cases of interest. We can also take the second partial derivative of either eq 6 or eq 7 with respect to the other conditional probability when $1 > H_{2M} > H_{1M} > 0$, to obtain:

$$\frac{\partial^2 A}{\partial P_{1|1}\partial P_{2|2}} = \frac{\partial^2 A}{\partial P_{2|2}\partial P_{1|1}} = \frac{(Y_1 - Y_2)^2}{[P_{2|2}\,(Y_2 - Y_1) + Y_1 - V]^2} \tag{8}$$

which is positive. This implies that if one signal state already contains a lot of information, the benefit of increasing the amount of information in the other signal state is small.

3. Organisms with relatively low reproductive success in either state (Y_1 or Y_2), or in which the difference in reproductive success between states is large, are more likely to show a large response (Fig. 2d,e). When $1 > H_{2M} > H_{1M} > 0$, the partial derivatives of A with respect to Y_1 and Y_2 are:

$$\frac{\partial A}{\partial Y_1} = \frac{(Y_2 - V)(P_{2|2} + P_{1|1} - 1)}{[P_{2|2}\,(Y_2 - Y_1) + Y_1 - V]^2} \tag{9}$$

$$\frac{\partial A}{\partial Y_2} = \frac{(V - Y_1)(P_{2|2} + P_{1|1} - 1)}{[P_{2|2}\,(Y_2 - Y_1) + Y_1 - V]^2} \tag{10}$$

In both eq 9 and eq 10, the denominator is always positive, the first term in the numerator is positive for all cases of interest (because $Y_1 < V < Y_2$), and the second term in the numerator is positive for all cases of interest (because $P_{2|2}$ and $P_{1|1}$ are greater than 0.5 if the signal contains positive information), so the whole expression evaluates positive. If H_{2M} is one, A is H_{1M} and increases with increasing Y_1 and Y_2.