



GERM BANKING: BET-HEDGING AND VARIABLE RELEASE FROM EGG AND SEED DORMANCY

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ABSTRACT

Many species produce eggs or seeds that refrain from hatching despite developmental preparedness and favorable environmental conditions. Instead, these propagules hatch in intervals over long periods. Such variable hatch or germination tactics may represent bet-hedging against future catastrophes. Empiricists have independently recognized these approaches in diverse species. Terms such as seed banking, delayed egg hatching, and embryonic diapause have been used to describe these tactics, but connections between fields of study have been rare. Here we suggest a general term, germ banking, to incorporate all previous terms, unifying many seemingly disparate biological strategies under a single definition. We define the phenomenon of germ banking and use several biological examples to illustrate it. We then discuss the different causes of variation in emergence timing, delineate which constitute germ banking, and distinguish between germ banking and optimal timing of diapause. The wide-ranging consequences of germ banking are discussed, including modification of the age structure of a population, the alteration of microevolutionary dynamics, the migration of alleles from the past, the maintenance of genetic and species diversity, and the promotion of species coexistence. We end by posing questions to direct future research.

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IMAGINE an organism that generates numerous propagules and leaves them to the whims of the environment, vulnerable to predation, desiccation, damage, or myriad other injuries. Many of these propagules do not hatch when developmentally prepared and environmental conditions are suitable. Instead they emerge in installments over long periods. For some of these propagules, time spent dormant can exceed the cumulative duration of all other phases of the life cycle.

How could such life cycle delays be adaptive in the context of evolutionary processes that favor alleles or individuals that maximize copies of themselves (Livdahl 1979)? The argument against life cycle delays is as follows. Suppose there are two alleles: one leads to immediate emergence and the other to delayed emergence. If a population is growing and no catastrophes occur, then an allele expressing immediate emergence will produce more copies of itself over the same time period than an allele expressing delayed emergence. All else being equal, the allele expressing delayed hatch will decline in frequency and may disappear from the gene pool. Under this scenario, organisms that express immediate hatching are favored over those with considerable life-history delays and should predominate across most taxa. However, this is not the case. Early life developmental delays are known to occur in distantly related clades (see Table 1), which suggests multiple, independent origins.

Terms chosen to designate early life developmental delays include installment hatching, delayed egg hatching, asynchronous germination, embryonic diapause, egg banking, propagule banking, cyst banking, seed pooling, and seed banking (Table 1). Since each of these terms is taxon-specific, we introduce the general term, germ banking, to embrace all of them.

WHAT IS GERM BANKING?

We define germ banking as adaptive variation in emergence timing among offspring from a single clutch, leading to bet-hedging against future environmental stochasticity. Germ banking is most likely to occur in highly fecund organisms that do not engage in pa-

rental care (i.e., express r-selected life-history patterns *sensu* MacArthur and Wilson 1967) and occupy environments that are subject to rapid, biphasic, unpredictable environmental fluctuations (e.g., vernal pools, treeholes, desert playas, arid areas) for part or all of their life cycle. Because their young may be vulnerable to sudden environmental change, parents may experience intense selective pressure to ensure that their entire reproductive effort is not exterminated by calamity (Cohen 1966, 1970). For example, seeds of desert plants that germinate after a rainfall enter a highly variable environment. The next rainfall may occur next week or next year. An entire cohort can be lost if rains sufficient to support growth and seed production fail to occur. In such a scenario, alleles that result in variation in germination timing of seeds from a single clutch may be favored by natural selection because they protect parents from catastrophic reproductive failure by spreading risk over time. Staggered emergence increases the chance that at least a fraction of a parent's offspring will survive to adulthood and produce offspring themselves.

GERM BANKING AS A FORM OF BET-HEDGING

In order to spread the risk of catastrophic reproductive failure over time, parents may stagger offspring emergence into ecologically risky life stages to enhance the probability that a fraction of them survive to reproduce (Ellner 1986; Hyatt and Evans 1998). This strategy is best exemplified by the adage, "don't put all your eggs in one basket," or as Daniel Bernoulli (1738/1954:30) stated more formally, ". . . it is advisable to divide goods which are exposed to some danger into several portions rather than to risk them all together." This sort of strategy has been defined by Seger and Brockmann (1987) and Philippi and Seger (1989) as diversified bet-hedging.

Seger and Brockman (1987) and Philippi and Seger (1989) describe bet-hedging as an evolutionary tradeoff between the mean and variance of fitness. Because population growth, and hence change in gene frequency, is a multiplicative process, variation in fitness reduces long-term (geometric mean) fitness

TABLE 1
Selected putative examples of germ banking.

Species (Phyla)	Citation	Habitat/ Environmental Condition(s)	Observed Dormancy Duration ¹	Taxon- Specific Term	Environmental Correlation ²
<i>Aedes</i> spp. (Insecta)	Gillett (1955a,b)	Treeholes/Drought	5 years	Erratic hatching	No
<i>Austofundulus myersi</i> (Teleostei)	Wourms (1972)	Vernal pools/Drought	18 months	Developmental arrest	No
<i>Ephydriaria ramsayi</i> (Porifera)	Harrison (1974)	Ponds/Drought	25 years ¹	None	No
<i>Brachionus plicatilis</i> (Rotifera)	Pourriot and Snell (1983)	Oceans/Resources	40 years ¹	Resting eggs	No
<i>Heterodera schachtii</i> (Nematoda)	Zheng and Ferris (1991)	Soil/Drought	10 years ¹	Delayed egg hatch	No
<i>Lepidium lasiocarpum</i> (Angiosperma)	Philippi (1993)	Deserts/Drought	3 years ²	Delayed germination	Yes
<i>Ambystoma barbouri</i> (Amphibia)	Moore et al. (1996)	Streams/Predation	60 days	Delayed hatching	Yes
<i>Dinococcus</i> spp. (Insecta)	Zwick (1996)	Streams/?	3 years	Stonefly seed bank	No
<i>Branchinecta sandiegensis</i> (Branchiopoda)	Simowich and Hathaway (1997)	Vernal pools/Drought	5 years	Cyst banking	No
<i>Pteridita portalis</i> (Insecta)	Danforth (1999)	Deserts/Host plant bloom	3 years ²	Be-hedging emergence	No
<i>Desmarestia ligulata</i> (Alga)	Edwards (2000)	Oceans/Winter and environmental quality	1 + years	Seed bank analogue	No
<i>Enteromorpha</i> spp. and <i>Pilayella littoralis</i> (Alga)	Loize et al. (2000)	Oceans/Winter and predation	?	Propagule banking	No
<i>Cyzicus</i> spp. (Branchiopoda)	Spencer and Blaustein (2001)	Vernal pools/Drought and predation	?	Resting stages	Yes
<i>Diaptomus sanguineus</i> (Copepoda)	Hairston and Kearns (2002)	Ponds/Drought	332 years	Egg banking	Yes
<i>Carrichena annua</i> (Angiosperma)	Shem-Tov et al. (2002)	Deserts/Drought	?	Seed banking	Yes
<i>Pseudophryne australis</i> (Amphibia)	Thumm and Mahony (2002)	Vernal pools/Drought	?	Delayed hatching	Yes
<i>Daphnia pulex</i> (Cladocera)	Càceres and Tessier (2003)	Lakes/Competition or predation	160 years ¹	Egg banking	No
<i>Argulus coregoni</i> (Branchiura)	Hakalahti et al. (2004)	Salmonids/Host Availability	1 + years	None	No

We list the species, citation, and environmental condition(s) potentially creating selective pressures, the maximum recorded length of dormancy, the taxon-specific term used by the author to refer to variation in offspring emergence, and whether a correlation was empirically observed between the pattern of emergence and the pattern of potentially catastrophic environmental conditions.

¹Some data were obtained from Càceres (1997).

² Similar species have been observed to remain dormant for 10+ years (Danforth 1999).

(Lewontin and Cohen 1969; Gillespie 1974; Hopper 1999). If the variation in reproductive success generated by a particular genotype is great, natural selection may favor alternative genotypes with reduced (arithmetic) mean fitness if they also express reduced variance of fitness. In other words, genotypes with reduced potential fitness (i.e., reduced intrinsic rate of increase), but also a reduced chance of reproductive failure, may be favored over genotypes that maximize reproductive output, but are also more susceptible to reproductive failure. Germ banking represents just such a strategy: a high intrinsic rate of increase, via immediate development, is sacrificed in favor of the risk-spreading properties of staggered development. This sort of diversified bet-hedging is a means of risk spreading that reduces the variance of the aggregate while increasing the variance of individual outcomes (Seeger and Brockman 1987).

EMPIRICAL CONFIRMATION OF GERM BANKING

Although there is a solid theoretical foundation for expecting variable emergence patterns to be bet-hedging, rigorous empirical documentation is necessary to confirm the phenomenon. Variable emergence patterns may not embody bet-hedging if: (1) dormant stages are not resistant to environmental degradation; (2) posthatching stages are not vulnerable to hazards that the dormant stage can endure; and (3) dormant periods do not constitute a significant fraction of the life span of individuals (see Box 1). For example, the microscopic gametophytic stage of the marine alga *Desmarestia ligulata* is analogous to a seed bank in that it appears to be the sole source of the macroscopic sporophytic stage each year. The gametophytic stage is metabolically active and sensitive to environmental conditions and physical damage (Edwards 2000), however, so whether it constitutes bet-hedging is questionable. In some cases, variable emergence patterns may be a result of phenotypic plasticity or allelic variation at loci controlling hatch timing. We discuss later the many sources of variation in hatch timing,

and distinguish between those that constitute germ banking and those that do not.

We further distinguish variable emergence patterns from germ banking by defining variation in hatch timing expressed by germ banking organisms as an adaptation produced by natural selection. To demonstrate that variation in hatch timing is adaptive, three criteria should be met: (1) variation in hatch timing must affect fitness or a component of fitness; (2) the hypothesis of adaptive variation must be confirmed by either manipulating the selective environment or the phenotypic trait itself; and (3) the mechanistic link between germ banking and fitness must be demonstrated (Sinervo and Basolo 1996). To our knowledge, no study has yet accomplished all three criteria.

GERM BANKING: SELECTED EXAMPLES

GERM BANKING IN A CRUSTACEAN

Compelling evidence of germ banking comes from aquatic crustaceans. One species of crustacean, the copepod *Diaptomus sanguineus*, has been the focus of intensive study (De Stasio 1989; Hairston et al. 1995). Pond sediments can contain very old (up to 332 years), viable, dormant eggs (Hairston et al. 1995). Approximately 10 to 50% of such buried, dormant eggs hatched after stimulation, but, because of the short duration of the hatching trials, actual viability may have been much higher.

Hairston and Olds (1984, 1987) describe remarkable variation in the production of dormant eggs by *D. sanguineus* from permanent versus temporary ponds in Rhode Island. All ponds become uninhabitable for the copepods at some point during the year, but the onset of the uninhabitable period varies both spatially and temporally (Hairston and Olds 1984). Permanent ponds are rendered uninhabitable by the feeding activity of planktivorous sunfish (Hairston et al. 1983). Temporary ponds contain no sunfish and are made uninhabitable by summer droughts (Hairston et al. 1983). In permanent ponds, the production of dormant eggs peaks in March, just prior to the annual increase in feeding activity of sunfish. In temporary ponds, the production of dormant eggs peaks

BOX 1

We have constructed a simple hypothetical key to determine when hatch time variation is significant and represents germ banking. This key explores the relationship between variance in hatch timing and development time (mean time from hatch to adulthood).

$\sigma_{ht} \ll dt$ Not germ banking
 $\sigma_{ht} = dt$ Probably not germ banking
 $\sigma_{ht} \gg dt$ Possibly germ banking

When the standard deviation (σ) of hatch timing (ht) is smaller than or equal to development time (dt), we suggest that variance in hatch timing results from stochastic environmental or physiological conditions. When the standard deviation of hatch timing is greater than development time, it may indicate that germ banking is occurring.

in June before the annual dry season (Hairston et al. 1983; Hairston and Olds 1984, 1987). Thus, in the four ponds studied, the authors establish that copepods avoid uninhabitable periods by producing dormant eggs. A reciprocal transfer study showed that the variation in production of dormant eggs has a genetic basis; copepods transferred to a new pond continued to produce subitaneous (i.e., immediately hatching) or dormant eggs according to the schedule of their native pond (Hairston and Olds 1984, 1987). Since neither the mothers nor their eggs responded to a change in their immediate habitat, the authors concluded that the two reproductive phenologies may represent divergent adaptations to different local conditions.

With regard to germ banking, the most striking aspect of these studies is that each population of *D. sanguineus* may be uniquely adapted to the nature and timing of an annual catastrophe. In permanent ponds, populations switch, rapidly and completely, from producing subitaneous eggs to dormant eggs at the end of March each year. In temporary ponds, the switch from subitaneous to dormant eggs is much more gradual and occurs from May to July. Two separate phenomena are acting simultaneously in copepods residing in temporary ponds. Copepods are germ

banking by producing a mixture of dormant and subitaneous eggs in each clutch. However, the relative proportions are shifting in favor of dormant eggs as the summer progresses. The second phenomenon is that diapause eggs are being produced in anticipation of winter. These diapausing eggs can all have the same hatching time. In this case, there is no germ banking. As models have predicted, the pattern of dormant egg production is a function of the annual variation in the onset of catastrophe (Hairston and Munns 1984; Taylor and Spaulding 1989). When variation is high, females should always make at least some dormant eggs; that is, they should germ bank. When variation is low, dormant egg production should begin at a constant period before the mean catastrophe date. In permanent ponds, variation is always low; sunfish activity is consistent from year to year. In temporary ponds, variation ranges from high during mid-summer (when risk of drought predominates) to low at the end of summer (when winter threatens). We will further distinguish between variable onset of diapause and germ banking in greater detail below.

GERM BANKING IN MOSQUITOES

Another putative example of germ banking comes from treehole mosquitoes. These mos-

quito species usually deposit eggs just above the water line in treeholes or artificial containers. In many mosquito species, the eggshell cuticle is infused with a wax that probably reduces the rate of water loss through the shell (Beckel 1953). Because of these characteristics, eggs are able to survive desiccation for up to four years (Breeland and Pickard 1967). Gillett (1955a,b) first reported that eggs from a single female do not necessarily hatch upon maturity, even when conditions are favorable for hatching. Instead, eggs hatch in installments over long periods and may forgo several opportunities to complete their lifecycles before eventually hatching. This behavior has been documented in *Aedes africanus* and *A. aegypti* (Gillett 1955a,b), *A. vexans*, *Ochlerotatus triseriatus*, *O. albopictus*, *O. geniculatus*, *O. cantator*, and *O. sierrensis* (Wilson and Horsfall 1970; Livdahl and Edgerly 1987; Andreadis 1990).

Both plasticity and genetic variation may contribute to variation in hatch timing in mosquitoes. Studies show that several environmental factors, such as predator abundance, resource availability, competition, and cohort structure, may be involved in hatch time variation (Livdahl et al. 1984; Livdahl and Edgerly 1987; Edgerly and Livdahl 1992; Edgerly and Marvier 1992; Edgerly et al. 1993; Dennehy et al. 2001). Other data show that at least part of the variation in hatch timing is genetically based (Gillett 1955b). Eggs reared in the absence of larvae show staggered hatching patterns that cannot be explained by the strength of stimulus, location of the egg, or other environmental conditions (Livdahl and Koenekoop 1985). Evidence for genetic differences comes from deviation in hatch responses between mosquito species (Novak and Shroyer 1978; Lounibos and Munstermann 1981), sympatric ecotypes (Saul et al. 1980), different laboratory strains (Schwann and Anderson 1980), geographic strains, and strains taken from treeholes and tires within the same region (Means et al. 1977). Thus far, this genetically-based variation in hatch fraction has not been correlated with the risk of reproductive failure, which could provide indirect evidence that the variation is adaptive.

Hence, the evidence for germ banking in

mosquitoes remains circumstantial. Many treeholes dry out during a severe drought, with the result that all larvae currently in an active stage of their life cycle perish. Staggered hatch timing would prevent the loss of all of a parent's offspring to any single drought. Treehole mosquitoes provide a system that is ripe for further investigation of germ banking.

GERM BANKING IN AN ANNUAL PLANT

A considerable body of research exists on delayed germination as a form of bet-hedging in annual plants. Variation in germination timing occurs in an especially conspicuous and fascinating manner in some plants with seed or fruit heteromorphism. For example, the annual plant *Heterotheca latifolia* produces two types of seeds: disc and ray achenes (see Figure 1). Although their masses are similar, disc achenes are covered with silky hairs and possess a well-developed pappus of capillary bristles that facilitates wind dispersal, whereas ray achenes have smooth, waxy coats and are poorly suited for dispersal. Disc pericarps are composed of significantly less lignified fibers (and hence half as much biomass) than ray pericarps, and their embryos weigh 60% more than the embryos of ray achenes (Venable and Levin 1985a; Table 2). Germination of disc achenes is rapid (beginning within two days of dispersal) and nearly complete in 39 days, whereas ray achenes germinate slowly (beginning 8-10 days after dispersal) and germination fraction does not exceed 50%, even after 99 days (Table 2). Since germination percentage depends upon the integrity of the pericarp, ray achene dormancy can be attributed to the structural resistance of its thick, lignified pericarp walls (Venable and Levin 1985a). Thus, fully developed embryos often fail to hatch upon favorable conditions and can remain dormant but viable for several years.

Variation in germination timing among the seeds produced by a single mother has a genetic basis in *Heterotheca*. The mother's genes dictate both the production and frequency of two morphs that differ in germination behavior over time and in response to environmental conditions (Silvertown 1984; Venable and

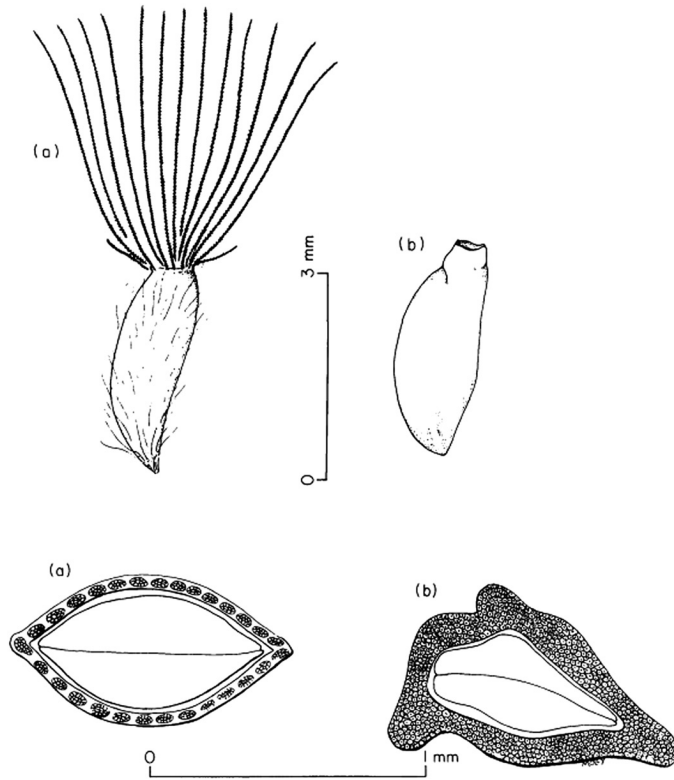


FIGURE 1. DISTINCT SEED MORPHS OF *HETEROOTHECA LATIFOLIA*

(a) Disc achene of *Heterotheca latifolia* and cross-section showing bundles of fibers in the pericarp; (b) ray achene and cross-section showing thick layer of fibers in the pericarp. Adapted from Venable and Levin (1985a) and used with permission.

Levin 1985a; Cheplick and Sung 1998; Donahue and Schmitt 1998; Imbert et al. 1999; Mandak and Pysek 1999). The proportions of *Heterotheca* achene types vary according to inflorescence size, plant size, and season (Venable and Levin 1985a,b).

The evidence of two germination and dispersal strategies in *Heterotheca latifolia* suggests two forms of risk spreading; one spreads risk through space, the other through time. Disc achenes are well suited for dispersal from the parent plant and rapid germination after the first available rain, thus allowing for swift invasion of open habitat. This strategy might prove ruinous, however, if the first available rain is followed by an extended drought, hence the risk-spreading ray achene. Some ray achenes will germinate sporadically following each rain, and therefore prevent the

loss of all offspring to any single catastrophe. Similar evidence for dual risk-spreading strategies comes from other heterospermic or heterocarpic species (Flint and Palmblad 1978; McEvoy 1984; Tanowitz et al. 1987; Kigel 1992; de Clavijo 1994, 1995; Imbert et al. 1997; Gibson 2001; El-Keblawy 2003; Dyer 2004). Seed heteromorphism is a rare, derived condition, but it is relatively more common among monocarpic (semelparous; i.e., annual or biennial) members of the Asteraceae and Chenopodiaceae (Imbert 2002).

Other studies have measured differences between seed morphs in plant traits, performance, or fitness components (Rai and Tripathi 1987; Venable et al. 1995; Imbert et al. 1997; Gardocki et al. 2000; de Clavijo 2001). Imbert et al. (1997) showed that the plants from heavier, more dormant seeds of *Crepis*

TABLE 2
*Summary of the differences between two seed morphs of *Heterotheca latifolia**

Seed Type	Morphology	Embryo Size	Germination	Seed Viability ¹
Disc	Pappus covered with silky hairs and pericarp has fewer lignified fibers.	Large	Rapid and synchronous	Reduced
Ray	No pappus. Seed coat waxy and smooth. Pericarp heavily lignified.	Small	Slow and variable	Increased

¹ = After longtime storage

sancta produced more reproductive biomass than plants from smaller, more dispersible seeds under conditions of competition (plant density treatments involving either conspecifics or other species).

Other evidence for germ banking in annual plants comes from variation among populations in the fraction of seeds germinating (in species without seed heteromorphism). Theory predicts that germination fraction should be positively correlated with mean annual precipitation (Cohen 1966; Augspurger 1979). Some studies have confirmed the predicted relationship (Hacker 1984; Kigel 1992; Philippi 1993; Clauss and Venable 2000; Figure 2), however, other studies have found mixed results (Hacker and Ratcliff 1989; Ehrman and Cocks 1996; Shem-Tov et al. 2002) or results contrary to this prediction (Jain 1982; Gutterman and Ednine 1988; Platenkamp 1991). Further, in two studies that did find the predicted positive correlation, the authors concluded that the pattern was due to maternal effects (Philippi 1993) or plasticity in germination behavior (Clauss and Venable 2000).

To summarize, these examples of germ banking have documented extended life span in, and staggered emergence from, a dormant germ stage. The genetic basis of variation in emergence timing has been demonstrated for three examples, and two examples (mosquitoes and annual plants) also show evidence of plasticity in emergence timing. In the crustacean and plant examples, variation in hatch behavior has been correlated with the degree of risk for emerging individuals. Still lacking are data on survival in the dormant stage, the fitness consequences of variation in emergence timing, and detailed stud-

ies of the nature of plasticity versus genetic variation in emergence timing.

SOME TROUBLESOME CONCEPTUAL ISSUES SOURCES OF VARIATION IN HATCH TIMING

Variation in hatch timing among propagules from a single clutch can result from several sources. We begin by decomposing phenotypic variation into three components: differences in genotype, environment, and their interaction. Such schemes are typical of analysis of variance (ANOVA) models of phenotypic variation (Lewontin 1974; Westcott 1986; Pigliucci 2001). One way that variation in hatch timing can be produced is through genetic variation (Jones and Nielson 1999). Offspring with different combinations of parental alleles may hatch at varying intervals due to differences in, for example, development rate, emergence thresholds, or other phenotypic characteristics. Such genetic polymorphisms are not considered bet-hedging (for discussion see Seger and Brockmann 1987; Hopper 1999; Soula and Menu 2003), and hence they do not constitute germ banking. Germ banking occurs when variation in emergence timing occurs within a single clutch despite identical alleles at loci controlling emergence timing.

Variation in hatch timing can also result when offspring within a single clutch experience different environmental conditions or cues for development or emergence (Schlichting and Pigliucci 1998; Pigliucci 2001; Gulden et al. 2004). The physical location of propagules can influence the temperature, light, oxygen, or moisture conditions that they experience, which in turn affect their development rate or propensity for emergence (Spencer and Blaustein 2001). For example, seeds or

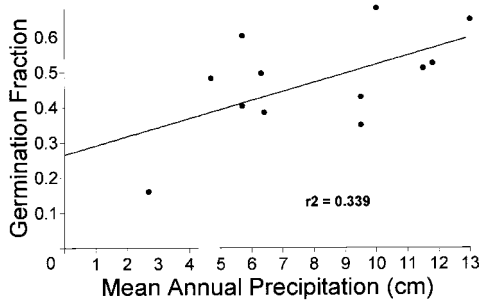


FIGURE 2. CORRELATION OF MEAN ANNUAL PRECIPITATION AND GERMINATION FRACTION

The germination fraction of the desert plant, *Lepidium lasiocarpum*, is regressed against mean annual precipitation in centimeters. The coefficient of determination (r^2) indicates what proportion of variation in germination fraction is explained by variation in precipitation. Data for *L. lasiocarpum* were obtained from T Philippi (1993) and used with permission.

eggs buried at different depths experience different microenvironments (Hairston et al. 1995; Mikheev et al. 2001). Clauss and Venable (2000) found that plasticity was an important source of variation in germination behavior among a series of populations of *Plantago insularis* along a precipitation gradient. Seeds from the drier sites had a higher intrinsic propensity for germination (in contrast to the predictions of Cohen and others), but in the wild, a lower fraction of seeds germinated at drier sites, simply because these seeds experienced less rain. A lack of rain predicts failure for seeds that germinate; hence not germinating in response to a lack of rain is a form of plasticity that is both predictive and adaptive. Variation in hatch timing that results from this sort of predictive, adaptive plasticity is not bet-hedging, or germ banking. Elsewhere, Pake and Venable (1996) found evidence of predictive germination in a guild of Sonoran desert winter annuals. In many species, germination fraction was higher in years of greater reproductive success.

On the other hand, nonpredictive plasticity may lead to variation in emergence timing, and thus give rise to bet-hedging, as demonstrated by Menu and Desouhant (2002). Additional studies of emergence behavior both in the wild and under controlled conditions are needed to identify the degree to which

variation in emergence timing is a result of plasticity (Adondakis and Venable 2004; Hakalahti et al. 2004) and whether plasticity is predictive. Because natural environments vary in a manner that includes both predictable and unpredictable elements, we should not be surprised to find evidence of both phenomena acting simultaneously (adaptive, predictive plasticity versus bet-hedging via non-predictive plasticity).

In some cases, plasticity in emergence timing on the part of offspring may facilitate a bet-hedging strategy on the part of parents (Van Dooren and Brendonck 1998). For example, female mosquitoes may vary the hatch timing of their offspring by laying their eggs vertically in a water-filled container. Eggs closer to the top of the container may be less likely to hatch than their lower-positioned siblings because they are less likely to be inundated with water. The pattern of egg laying on the part of the female mosquito thus represents a bet-hedging strategy, which is facilitated by the plastic hatching behavior of the eggs.

Maternal effects may also generate variation in emergence timing, including the effect of maternal genotype, maternal environment, and their interaction (Roach and Wulff 1987; Mousseau and Fox 1998). However, these three effects are invariant with respect to the offspring of a single clutch and hence cannot contribute to the phenomenon of germ banking. A mother's genotype is invariant for all of her offspring, and the environment that she has experienced is invariant amongst offspring produced in a single clutch, if they are produced at one point in time. Instead, variation in emergence timing among offspring produced by different mothers, due to the mothers' environment, represents a form of cross-generational plasticity that may even be adaptive (see Donahue and Schmitt 1998). Variation in emergence timing amongst offspring due to different maternal genotypes may contribute to the evolvability of variation in hatch timing.

Variation in emergence timing can also result from phenotypic variation among offspring. The case of seed heteromorphism makes this phenomenon particularly obvious (Figure 1). Morphological differences among

offspring relevant to hatching behavior can range from the obvious to the subtle. Hatch variation in mosquitoes can result from subtle variation among eggs in intrinsic factors such as shell thickness, wax content, or permeability (Beckel 1953; Breeland and Pickard 1967). The production of this sort of phenotypic variation may be random, that is, the result of developmental instability, as in adaptive coin-flipping (Cooper and Kaplan 1982; Kaplan and Cooper 1984; Walker 1986), or it may be expressed in a relatively stable, predictable manner, as in the case of ray versus disc achenes in *Heterotheca*. In either case, this sort of phenotypic variation constitutes diversified bet-hedging. It is worth noting that variation in emergence timing caused by phenotypic variation within a clutch falls into the error term in the classic ANOVA framework for phenotypic variation, which is not very useful.

Three important points emerge from this discussion. First, variation in emergence timing has many sources, including phenotypic plasticity, maternal effects, genetic differences, and genotype by environment interactions. Second, only those mechanisms that generate variable outcomes within a single clutch, despite identical alleles at loci controlling emergence timing and a lack of predictive cues, meet our criteria for germ banking (for similar definitions see Hopper 1999; Menu and Desouhant 2002). The essence of germ banking is to generate variation in emergence timing in the face of uncertainty (Walker 1986; Gutterman 2002; Meyers and Bull 2002; Roff 2002), with the result that not all offspring emerge, even under the most ideal of conditions for emergence and subsequent reproductive success. In Figure 3, we present a decision tree to distinguish whether variation in hatch timing represents germ banking. Finally, because any given environment has both predictable and unpredictable elements, we can expect to find mixtures and layering of the phenomena of bet-hedging and predictive plasticity.

GERM BANKING AND OPTIMAL TIMING OF DIAPAUSE

Although some attention has been devoted to the optimal timing of diapause in response

to variation in the onset of unfavorable conditions (Cohen 1970; Taylor 1980; Taylor and Spalding 1989; Frisch and Santer 2004), few recognize germ banking as a phenomenon separate and distinct from diapause. Perhaps this confusion results from lack of discrimination between predictable and unpredictable environmental catastrophes. Many insects produce diapause eggs in response to changing environmental cues, such as photoperiod or temperature. Essentially, this is a response to a predictable, but temporally variable, catastrophe (Rossiter 1998). The onset of winter (although not the date of the first frost) is inherently predictable. The fundamental "decision" is whether to squeeze in one more life cycle before winter arrives or to go into diapause and wait (Bradford and Roff 1993). As the probability of the onset of winter increases (shorter day length), so does the proportion of diapause eggs laid within a population.

By contrast, an organism practicing germ banking may deposit a clutch of delayed and immediate hatching eggs despite optimal conditions because of a truly variable probability of catastrophe. The critical distinction is that bet-hedging involves the production of a mixture of diapausing and subitaneous eggs within a clutch, whereas optimal timing of diapause involves a rapid shift from all subitaneous eggs to all diapausing eggs (see Bradford and Roff 1993, 1997a,b). That is, diapause relies on cues provided by the environment whereas germ banking occurs in the absence of environmental cues. Germ banking will occur in spite of favorable environmental conditions or before cues for success after hatching are available. Dormant egg production depends on the predictability of risk (Hairston and Munns 1984; Taylor and Spaulding 1989). When risk is unpredictable, females should always make at least some dormant eggs; that is, they should germ bank. When risk is predictable, a rapid shift to dormant eggs should occur before the mean catastrophe date. Of course, the distribution of risk is not a dichotomy, but rather a continuum that governs the speed of dormant egg production and the fraction of a clutch that should be devoted to dormant eggs.

An example of this distinction comes from

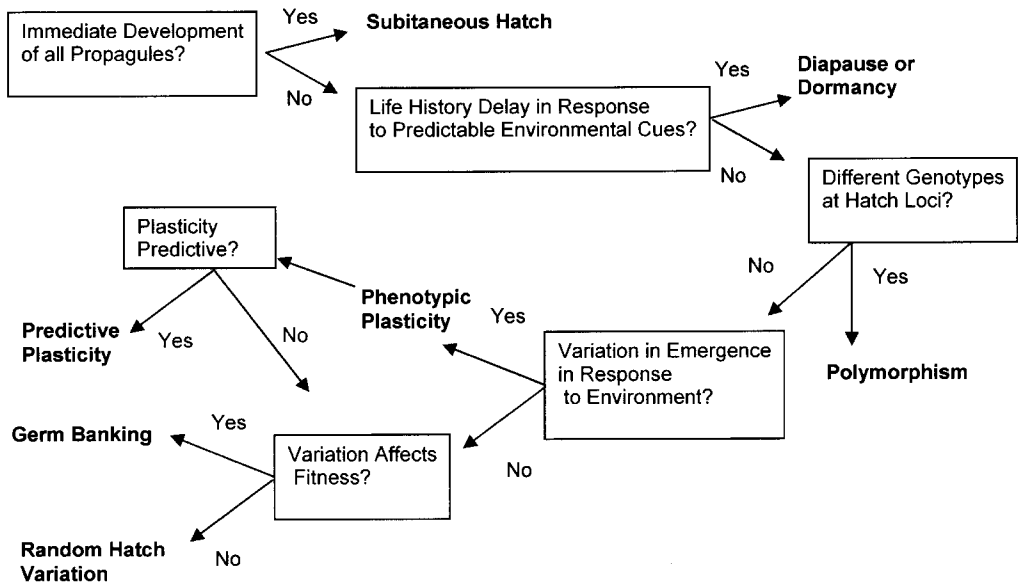


FIGURE 3. BEHAVIOR OF EGGS FROM A SINGLE CLUTCH
 A decision tree distinguishing various types of variation in hatch timing for eggs from a single clutch.

D. sanguineus (Hairston and Olds 1984, 1987; Hairston and Dillon 1990). Copepod populations from permanent ponds switch rapidly from producing immediately hatching eggs to dormant eggs at the end of March each year. This switch is a response to a predictable increase in the feeding activity of sunfish. Like winter, the onset of intense predacious behavior is, in this case, an inherently predictable event. Copepods not residing in resistant stages after March will likely be consumed. By contrast, the switch from subitaneous to dormant eggs in temporary ponds is much more gradual and occurs from May to July because the onset of drought is an inherently unpredictable event. During some years, temporary ponds may dry up in May while in other years they may not. Eventually each year, temporary ponds are subject to a predictable catastrophe as well: the onset of winter. Hence, at some point, copepods in temporary ponds stop germ banking and produce entirely diapause eggs.

For these reasons, germ banking and optimal timing of diapause represent separate and distinct biological phenomena. Until biologists recognize such, there will be contin-

ued confusion over the proximate and ultimate reasons for hatch delay and the correlates of life-history evolution. Nevertheless, one aspect of diapause timing does constitute germ banking: variable release from it. For example, variation in the length of diapause produces a mixture of univoltine and semivoltine life cycles in the *Odonata* (Corbet 1957; Lutz and Jenner 1964). Dragonflies often overwinter as larvae. Upon the arrival of spring, some larvae will continue their life cycle while others will remain in diapause for one more year and exit diapause the following spring.

CONSEQUENCES OF GERM BANKING

Germ banking can have important implications for alleles, individuals, populations, and communities. Germ banking can affect life-history traits following dormancy, the evolutionary dynamics of other traits, the persistence of alleles and populations over time, and the levels of biodiversity and composition of communities. Here we discuss some of the wide-ranging effects that germ banking can have in biological systems.

First, germ banking can have immediate consequences for individuals following dormancy. For example, Kroon and Veenendaal (1998) showed that for some spider mites, longevity, rate of oviposition, and total fecundity were negatively correlated with duration of dormancy. Fujii (1980) obtained a similar result in studies of the pear leaf miner *Bucculatrix pyrivorella*; the fecundity of individuals that did not enter dormancy was significantly greater than the fecundity of individuals that endured dormancy. In an invasive annual grass, Rice and Dyer (2001) found reduced growth, biomass, and competitive ability in plants grown from seeds that had delayed germination. In other cases, survival, longevity, and offspring fitness may be increased in germ banking individuals (Livdahl and Koenekoop 1985). These patterns suggest that dormancy is linked to other life-history traits through genetic, physiological, or allocational tradeoffs, in addition to the evolutionary tradeoff between the mean and variance of fitness. The costs and benefits of dormancy, in terms of other life-history traits, should be the subject of further investigation, including studies under both laboratory and natural conditions.

Modifications to the age structure of a population as a result of germ banking can have other important consequences for life-history evolution. For example, in *O. triseriatus* mosquitoes, individuals from the same egg batch may hatch at different times. As a result, first instar larvae may occupy treeholes with their fourth instar kin. Since larval cannibalism is common among treehole mosquitoes, staggered hatching times may have imposed selection for kin-recognition mechanisms and kin-biased behavior (Dennehy et al. 2001). On the other hand, one rationale for the evolution of germ banking is reduced sibling competition via staggered emergence (Ellner 1986; Venable and Brown 1988, 1993; Rees 1994; Lundberg et al. 1996; Dyer 2004).

Germ banking is also expected to have consequences for the microevolutionary dynamics of nondormancy traits (Templeton and Levin 1979; Brown and Venable 1986). In a constant environment, dormancy should slow the rate of approach to the equilibrium allele frequency (without affecting that equilibrium

value), more so as the mean and variance of the age distribution of emerging propagules increases (Templeton and Levin 1979). Hairston and De Stasio (1988) reported just this effect in the copepod *D. sanguineus*: evolution of the timing of diapause in response to the removal of an important predator was slowed by hatching of eggs produced before predator removal. In a variable environment, dormancy should magnify the evolutionary effect of good years (i.e., accelerate the spread of alleles that confer high reproductive success in years of high reproductive success), while dampening the evolutionary effect of poor years (Templeton and Levin 1979). Weakened selection against poorly performing genotypes is analogous to the effects of higher levels of ploidy (Frank 2001; Zeyl 2004), but instead of alternate alleles being stored on extra chromosomes, they are maintained in stasis until release from dormancy.

The idea that dormancy might lead to temporal substructuring of genetic diversity originates with Templeton and Levin (1979). They proposed that dormancy could lead to a temporal Wahlund effect: if propagules produced in different years differ in allele frequencies, they should have higher homozygosity than individuals produced after interbreeding among those propagules. A few empirical studies have documented higher homozygosity in the dormant germ stage relative to later life stages and considered a temporal Wahlund effect as a cause for this pattern (Tonsor et al. 1993; Alvarez-Buylla et al. 1996; Cabin et al. 1998; McCue and Holtsford 1998). This is probably a poor explanation because of the short-lived nature of the Wahlund effect (either spatial or temporal). In the face of repeated emergence and interbreeding of individuals produced in different years, the dormant germ stage should be temporally well mixed. Further, in the absence of selection, adults should be a random sample from the seed pool, and under these circumstances, cannot be expected to differ in genotype frequency from seeds. In fact, selection, either in the form of inbreeding depression or overdominance, is a more likely explanation for declining homozygosity throughout the life cycle. More formally, Vitalis et al. (2004) came to the conclusion

that the equilibrium inbreeding coefficient (F_{IS} ; a measure of the deviation of the observed frequency of homozygotes from Hardy-Weinberg expectations) should in fact be no different between the dormant stage and the adult stage, based on their analysis of joint demographic and population genetic models. Vitalis et al. (2004) also found that a temporal Wahlund effect due to dormancy is negligible except in very small populations ($N < 10$, not including dormant individuals).

By buffering changes in allele frequencies and storing alternate alleles, germ banking can prevent both the loss of genetic diversity and genetic differentiation among populations (Epling et al. 1960; Gottlieb 1974; del Castillo 1994; McCue and Holtsford 1998; Mahy et al. 1999). By removing a set of individuals from the effects of the current year's selection, an allele that is unfavorable in a poor year, but favorable in good years, may be retained in a germ banking population but lost in a population without germ banks (Templeton and Levin 1979). Another way that germ banks buffer changes in allele frequencies is that they increase the effective size of the population (Nunney 2002; Vitalis et al. 2004). By providing a "genetic memory," germ banking could lead to the reintroduction of genotypes that performed poorly in past years (De Stasio 1989; Hairston 1996). Further, populations that have formerly disadvantageous, but currently advantageous, alleles emerging from storage would approach fixation for these alleles faster than populations that have to wait for advantageous mutations to occur. Bennington et al. (1991), McGraw et al. (1991), and Vavrek et al. (1991) illustrated the potential for these phenomena when they documented the preservation of a "memory" of past selection in centuries-old, viable seeds of arctic plants.

Similarly, a germ banking organism is buffered against local and species extinction (e.g., Kalisz and McPeck 1992; Ripley et al. 2004), relative to a comparable nongerm banking organism. Since dormancy can exceed the active life span of some organisms, germ banking allows organisms to avoid catastrophes on a temporal scale that would be impossible for a similar, nongerm banking organism (e.g., severe, multiyear droughts).

Stochastic demographers have formalized this notion. Tuljapurkar and others have shown analytically that increased generation time ameliorates the negative effect of environmentally-driven variation in demography, increasing the long-term, average growth rate of a population experiencing a stochastic environment and the probability of population persistence (Tuljapurkar 1982; Orzack and Tuljapurkar 1989; Tuljapurkar and Wiener 2000). In a remarkable verification of this effect, Stöcklin and Fischer (1999) found that rates of local extinction in fragments of calcareous grasslands were higher for plants with shorter-lived seeds. Similarly, Piessens et al. (2004) found that plants with short-lived seeds were more sensitive to the extinction-promoting effect of patch isolation in heathland relics. Some controversy exists on whether germ banking genotypes can be selected for their extinction-avoidance properties. Prominent theorists have claimed that this scenario would entail group or species selection (e.g., Williams 1966). However, germ banking may be favored by selection occurring on multiple levels of the biological hierarchy (Wilson 1997). Germ banking can simultaneously have the consequence that parents are less likely to lose an entire cohort *and* that species are less likely to become extinct.

By buffering population extinction, germ banking may help explain the so-called paradox of the plankton (Hutchinson 1961). Hutchinson (1961) asked how it was possible that many species of phytoplankton—all competing for similar resources—can survive in isotopic or unstructured environments in apparent contradiction with the competitive exclusion principle. If each phytoplankton species is adapted to specific environmental conditions differently, and dormant propagules can persist among years, coexistence can occur via temporal niche-partitioning. In any given year, the prevailing conditions may favor one species over others, and during this year, the favored species may bank many dormant offspring in the sediment. Conditions during subsequent years may be unfavorable for this species, thus recruitment and survival may be low. Nevertheless, sufficient reserves present in the sediment would enable this

species to endure many years of low recruitment until favorable conditions return. In this manner, phytoplankton diversity would be maintained by periodic recruitment from dormant propagules.

The idea of species coexistence, via temporal niche-partitioning combined with environmentally-resistant life stages, was formalized by Chesson and others as the "storage hypothesis" (Chesson and Warner 1981; Chesson 1994; Chesson and Huntly 1997). The storage hypothesis requires that not all species perform equally well in a given year and that there is positive covariance between competition and environmental conditions (i.e., good environmental conditions lead to more competition), along with "subadditivity" (i.e., negative effects of competition are weaker in poor years than in good years). The pattern of subadditivity can be obtained via long-lived, environmentally-resistant life-history stages, such as dormant propagule stages, which limit the rate at which a population can decline in a poor year (Levins 1979; Chesson and Warner 1981; Chesson 1994; Chesson and Huntly 1997; Hairston and Kearns 2002). Empirical support for the storage hypothesis comes from studies with desert annuals (Pake and Venable 1995, 1996; Adonakis and Venable 2004) and copepods (Càceres 1997; Hairston and Kearns 2002).

The storage hypothesis has been applied to the problem of coexistence of competing alleles within a locus as well (Ellner and Hairston 1994; Sasaki and Ellner 1995; Ellner 1996; Ellner and Sasaki 1996; Turelli et al. 2001). Evidence for the storage effect in action at the level of alleles comes from the seed-banking desert annual *Linanthus parryae*, in which a blue-flowered morph is determined by a single dominant allele. Schemske and Bierzychudek (2001) showed that the relative and absolute fitness of the blue and white flower color morphs fluctuated among years in natural populations in the Mojave Desert. They suggest that the maintenance of the two color morphs may be due to storage of alleles in the soil seed bank (Schemske and Bierzychudek 2001).

CONCLUSIONS AND FUTURE DIRECTIONS

Germ banking research has consequences for many interesting biological phenomena,

such as migration from the past, bet-hedging, multilevel selection, temporal heterogeneity, and the maintenance of biodiversity and genetic variability. However, empirical evidence on the topic lags behind theoretical work. There are still few instances where the phenomenon of germ banking has been documented, that is, few studies have shown that adaptive variation in emergence timing not due to predictive plasticity or genetic polymorphism occurs within clutches. Future research would also do well to focus on the evolutionary and ecological consequences of germ banking. We pose these questions to direct future research:

- How long do dormant stages survive?
- What mechanisms allow for dormancy and germination/hatching?
- What are the relative contributions of genetic variation, plasticity, maternal effects, and phenotypic polymorphism to variation in emergence timing?
- How is the process of producing phenotypic polymorphism within clutches controlled? Is the process random, deterministic, or plastic?
- How does germ banking affect post-germination life-history traits? Are there costs or benefits of extended dormancy?
- What evidence is there that germ banking prevents local extinction or allows for species coexistence?
- What evidence is there that germ banking prevents the loss of genetic diversity, or otherwise affects microevolutionary patterns?

Much work also remains to understand the relationship between germ banking and other types of life-history delays. Dormancy occurs in various life stages in a variety of organisms. Insects, for example, can diapause as eggs, larvae, pupae, and adults (Denno and Dingle 1981; Butterfield et al. 1999). Recent research on diapause as a form of bet-hedging comes from a beetle with larval diapause (Menu and Debouzie 1993; Menu et al. 2000; Menu and Desouhant 2002). Some plants have an extended prereproductive period as

a plant rather than as a seed (e.g., *Agaves*; Young and Augspurger 1991). The causes and consequences of longevity or environmental insensitivity in different life stages remain to be fully explored. Orzack (1997) and Tuljapurkar and Wiener (2000) found that various factors can favor the evolution of one kind of life-history delay over another (developmental delay versus reproductive delay): if the costs of the two types of delay are not equivalent; if one type of delay is already present in the life history; or if the environment is highly variable and uncorrelated over time, or correlated over time. Orzack (1997) made a comparative analysis of four different types of life histories with delay: what he called "iteroparity," "diapause," "biennial," and "pre-reproductive delay" life histories. He concluded that the latter two life histories can be much more resistant to environmental fluctuations than the first two because, as he constructed them, these two life histories have at least one stage in which individuals can remain indefinitely. The relevance of the life histories that Orzack analyzed remains to be assessed.

There is also a need to further explore, both empirically and conceptually, the relationship between germ banking and a variety of other strategies for coping with environmental uncertainty. Some research exists on the evolution of diapause versus other forms of risk-spreading, including dispersal, offspring size, and adult longevity (Venable and Lawlor 1980; Venable and Brown 1988; Rees 1994; Wiener and Tuljapurkar 1994; Ellner et al. 1998). Meyers and Bull (2002) provide a framework for organizing the various forms of adaptive variation in response to environmental fluctuation. Multiple morphs co-occurring within a population embody population-level variation. Variation at the individual level includes adaptive variation among individuals in a population (diversified bet-hedging in its many forms, dispersal, developmen-

tal plasticity, and hypermutation) and within single individuals (i.e., plasticity and somatic mutation). Additional forms of variation within individuals are available to modular organisms such as plants, like the simultaneous production of leaves or flowers of different morphs (e.g., heterophylly and chasmogamous versus cleistogamous flowers; Lloyd 1984). Meyers and Bull (2002) further suggest that different strategies should be adopted according to the degree of environmental predictability, the relative scales of population growth and environmental change, and a third unspecified axis (see Figure 2 in Meyers and Bull 2002).

Understanding not only germ banking itself as a phenomenon, and its causes and consequences, but its relationship with other forms of life-history delay and other mechanisms for dealing with environmental uncertainty will provide fodder for much excellent research in the future. The results of this research have the potential to be relevant not only for evolutionary ecologists, but for those concerned with biodiversity conservation, evolution of disease, agriculture, and numerous other fields.

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