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The Evolution of Ovoviviparity in a Temporally Varying Environment

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ABSTRACT: Environments that vary within a generation of an organism provide opportunities for adaptation if the level of variation is severe and predictable. We describe a model of evolution in such environments with genotypes that show trade-offs in viability and fecundity. One genotype develops rapidly and has superior viability but reduced fertility relative to the alternative genotype. Conditions that allow the evolution of the rapidly developing genotypes are explored. We show how the evolution of ovoviviparity and resource specialization in *Drosophila sechellia* shares many important features of this model. We suggest that our model may capture many of the evolutionary forces responsible for the evolution of niche specialization and ovoviviparity seen in *D. sechellia*.

Keywords: *Drosophila sechellia*, ovoviviparity, temporal variation, natural selection.

Introduction

The study of the evolution of life histories in animals has been an important cornerstone of evolutionary biology (Roff 1992; Stearns 1992). Empirical research in life-history evolution has typically focused on particular components of the life history. One important part of the overall life history that varies greatly among animals is the degree to which a mother provisions offspring before birth or egg laying. There are three broad modes of reproduction, although subdivisions of these are also recognized for Diptera (Meier et al. 1999): (i) viviparous animals produce live offspring; (ii) oviparous animals lay eggs shortly after fertilization, and the embryo then takes some period of time as an immobile egg to develop; and (iii) ovoviviparous animals allow eggs to develop internally for some time, and hatching then occurs shortly after the egg is laid. There is some disagreement over how much time can pass from the moment the egg is laid until it hatches for reproduction to qualify as ovoviviparity (Meier et al. 1999). In this article, we will treat the transition from oviparity to ovoviviparity as a continu-

ous sequence and thus will focus on the degree of ovoviviparity.

In their discussion of the evolution of viviparity in Diptera, Meier and colleagues (1999) noted that this mode of reproduction is often associated with coprophily (dung feeding) and feeding on ephemeral plants. They point out that this association may be due to evolution for reduced egg-to-adult development time in such environments. We suggest that similar arguments would apply to ovoviviparity, the transition between oviparity and viviparity.

Here we develop a model of selection in a temporally varying environment. In particular, we imagine a resource that decays within a generation of an organism. During that degradation process, it undergoes profound changes in its chemical and biotic composition. The model specifically examines the situation in which genotypes that take advantage of a resource early or late in the degradative process may experience trade-offs in fecundity and viability. Despite these trade-offs, we explore conditions that will permit a genotype to specialize in the early phase of the resource degradation. We conclude by reviewing some life history and ecology of *Drosophila sechellia*. We argue that the life history of *D. sechellia* may have been substantially affected by the evolutionary mechanisms developed here.

Common Themes in Dipteran Ovoviviparity and Viviparity

In *Drosophila*, aside from *Drosophila sechellia*, there are several other examples of ovoviviparity and viviparity associated with flower breeding. Hunter (1988, 1992) reports that seven out of 10 flower-breeding *Drosophila* in Bogota, Colombia, are viviparous. Relative to other species of *Drosophila*, these species have reduced numbers of ovarioles (Hunter 1988). In this region of Colombia, flowering occurs in many plants twice a year during the rainy seasons, December–January and April–May (Hunter 1988). Although the high-altitude environment makes the climate temperate and acts to prolong the duration of the life of a flower, these are still ephemeral resources. Hunter (1988) reports

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collecting dried flowers containing pupae that yielded live adults several days later. There is also likely to be competition in these flowers. *Drosophila chiasca* has been found in the same flowers as *Drosophila freilejoni*.

As we will see later, these flower-breeding *Drosophila* share many ecological and life-history traits with the more carefully studied model species, *D. sechellia*. However, before reviewing the specific ecology and life history of *D. sechellia*, we develop a general model for the evolution of ovoviviparity which may be applicable to many of the Dipteran species and possibly other groups.

Genetic Model

The model we develop here is similar to the model developed in Borash et al. (1998). In that model, the environment was assumed to change in a regular fashion within a generation, such that each genotype experienced a different viability in the early and late phase of the environmental transition. The main difference between the model developed here and that developed in Borash et al. (1998) is that the latter model considered only genotypic effects on the viability component of fitness, whereas our model assumes that fertility is also affected by this environmental transition. Each genotype, A_iA_j, has a fraction, v_{ij}, of its eggs that hatch rapidly and therefore develop to the adult stage faster, whereas the remaining $1 - v_{ij}$ eggs develop more slowly. Thus, v_{ij} can be thought of as the level of ovoviviparity. If $v_{ij} = 0$, the genotype is oviparous, and when $v_{ij} = 1$, the genotype is ovoviviparous. In the discussion below, we will often refer to differences in development time, which should be understood as times from egg laying to adult emergence and which are entirely due to different development periods before egg laying. Those eggs that hatch early have viability w_{eij}, whereas the later-hatching eggs have viability w_{lij}.

We will assume that w_{lij} will be low for all genotypes due to the deterioration of the environment, and w_{eij} will be low for oviparous genotypes but high for the ovoviviparous genotypes. This suggests a specific adaptation to the early and late environment of the ovoviviparous and viviparous genotypes. This certainly seems to fit *Drosophila sechellia* but may not fit the flower-breeding *Drosophila*. We will also consider the evolution of ovoviviparity in the absence of this adaptation.

Genotypes may also differ in fertility, which again varies according to development time. Thus, early-developing A_iA_j genotypes have fertility f_{eij}, and late-developing individuals have fertility f_{lij}. Here we assume that both males and females have a similar fertility affect, although we could also limit the fertility effects to just females and get the same results. This model assumes that viability and fer-

tility will trade off, so that genotypes with high viability in the early environment have low fecundity in the late environment.

We assume assortative mating by development time. Thus, early-developing individuals mate at random with all other early-developing individuals but not with late-developing individuals, and late-developing individuals mate at random with other late-developing individuals but not with early-developing individuals. Assortative mating will cause genotype frequencies in the whole population to depart from Hardy-Weinberg proportions, so we need to keep track of genotype frequencies. Accordingly, we let x_{ij} be the frequency of genotype A_iA_j. We now consider a locus with two alleles and let p'_1 be the frequency of the A_1 allele among the early-developing individuals and p''_1 be the frequency among the late-developing individuals, as follows:

$$p'_1 = \frac{[x_{11}v_{11}w_{e11}f_{e11} + (1/2)x_{12}v_{12}w_{e12}f_{e12}]}{\bar{w}'}, \quad (1a)$$

$$p''_1 = \frac{[x_{11}(1 - v_{11})w_{l11}f_{l11} + (1/2)x_{12}(1 - v_{12})w_{l12}f_{l12}]}{\bar{w}''}, \quad (1b)$$

and $\bar{w}' = (x_{11}v_{11}w_{e11}f_{e11} + x_{12}v_{12}w_{e12}f_{e12} + x_{22}v_{22}w_{e22}f_{e22})$, $\bar{w}'' = [x_{11}(1 - v_{11})w_{l11}f_{l11} + x_{12}(1 - v_{12})w_{l12}f_{l12} + x_{22}(1 - v_{22})w_{l22}f_{l22}]$. Genotype frequencies in the next generation are then computed from a weighted Hardy-Weinberg average among the early- and late-developing individuals. Let $\tilde{x}_{12}$ be the heterozygote frequency in the next generation, then

$$\tilde{x}_{12} = 2p'_1(1 - p'_1)E + 2p''_1(1 - p''_1)L, \quad (2)$$

where $E = \bar{w}'(\bar{w}' + \bar{w}'')^{-1}$, and $L = \bar{w}''(\bar{w}' + \bar{w}'')^{-1}$. The other genotypes are computed in a similar fashion.

To study the evolution of ovoviviparity, we let the A_1A_1 homozygotes be the more slowly developing, oviparous genotype. We might think of A_1 as the ancestral allele. Under this model, slower development is due to the additional time the egg takes to develop after being laid. The heterozygote is the faster-developing, ovoviviparous genotype. For this model, these assumptions imply that $v_{12} > v_{11}$. If we assume the population is fixed for the A_1 allele, then the important evolutionary analysis is to determine under what conditions the A_2 allele will increase when rare. The increase of the A_2, or "ovoviviparity," allele will be assured when

$$v_{12}w_{e12}f_{e12} + (1 - v_{12})w_{l12}f_{l12} > v_{11}w_{e11}f_{e11} + (1 - v_{11})w_{l11}f_{l11}. \quad (3)$$

We can simplify this inequality by assuming the genotypes show no overlap in development time (e.g., $v_{11} = 0$ and $v_{12} = 1$). In addition, we can simplify fitness by letting $w_{l11} = f_{l11} = 1$ and $w_{e12} = 1 + s$ and $f_{e12} = 1 - t$, where both s and t are positive. We assume fecundity is reduced

in the A_1A_2 genotype, because mechanisms of ovovivipar-ity, like egg retention, are likely to reduce fecundity. Then the conditions for the increase of the A_2 allele simplify to $(1 + s)(1 - t) > 1$. These conditions show that, as long as the fecundity penalty is not too severe, then the fast-developing genotype can increase when rare. These conditions might be more likely to apply to the flower-breeding *Drosophila* that have no special adaptation to the early environment; viability is superior in the early environment simply be-cause it has not degraded. We expect that the conditions for invasion of A_2 will be narrower if $v_{12} < 1$ and $v_{11} > 0$. If mating between early- and late-developing types occurs at random, the initial increase condition (equation 3) is un-changed.

We next used the system of equations (1) to explore the most interesting evolutionary scenario. In this simple model, we would consider the A_2A_2 genotype to be the ovovivipar-ity genotype, with increased survival and fecundity in the early environment, and the A_1A_1 genotype to be the ances-tral oviparity genotype, with low survival and fecundity in the early environment. Although the level of ovoviviparity is fixed for each genotype, we can ask what the course of evolution would be if the ovoviviparity genotype initially had a low level of ovoviviparity. To establish a genetically variable population, we used an example with overdomi-nance. As an example, we note that, in the "late" environ-ment of *D. sechellia*, females have one-third the fecundity of their sister species *Drosophila simulans* (R'kha et al. 1997), so we set $f_{l22} = 0.33$ and $f_{l12} = f_{l11} = 1$. We also suppose that viability for any genotype will be low in the late environment due to competition or dessication of the food resource relative to the viability of a genotype in the early environment. Thus, we set $w_{e22} = 1$ and let $w_{l22} = w_{l12} = w_{l11} = 0.2, 0.25, 0.3,$ or 0.35. In this special case, we also assume that the ovoviviparous genotype has spe-cial adaptations that allow it to survive in an otherwise toxic early environment (see the example below involving *D. sechellia*), thus $w_{e11} = 0$ and $f_{e11} = 0$.

In figure 1A, we see that increasing the level of ovo-viviparity (v_{22}) of the ovoviviparity genotype (A_2A_2) results in an increasing equilibrium frequency of the ovovivipar-ity allele. In fact, when the level of ovoviviparity is suffi-ciently high, there is no longer overdominance, and the ovoviviparity allele (p_2) is fixed. This is because we did not let the level of ovoviviparity change in the hetero-zygotes. If there were a second locus or loci that affected the level of ovoviviparity in the ovoviviparity homozy-gotes, how would this level evolve? We suggest that alleles that increase the level of ovoviviparity (e.g., v_{22}) would be favored, because the mean fitness of the population in-creases as the level of ovoviviparity (v_{22}) increases (fig. 1B). The strength of selection for the ovoviviparity allele also increases as the viability in the late environment decreases.
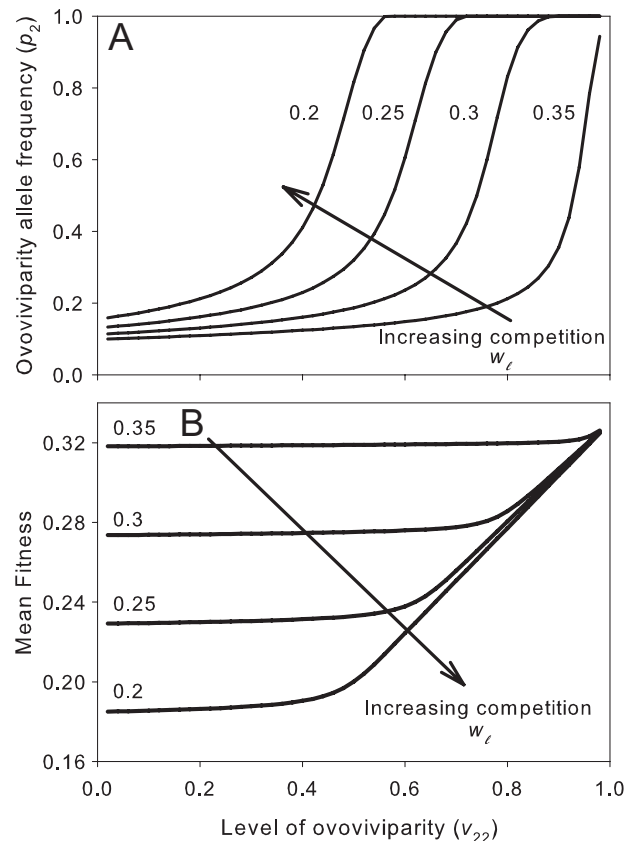
Figure 1: Predictions from the genetic model (eq. [1]). *A*, For a fixed set of fitness parameters, the equilibrium frequency of the ovo-viviparity allele (A_2) was computed for different levels of ovovivi-parity for the ovoviviparity homozygote (A_2A_2). Each line indicates the simulation results for a different value of late viability, which in-dicates the strength of competition. In general, the frequency of the ovoviviparity allele increases as the level of ovoviviparity increases and as the level of competition increases. *B*, Population mean fitness for each equilibrium point in *A*. Mean fitness increases as the level of ovoviviparity increases in the ovoviviparity genotype (A_2A_2). Model parameters that were kept constant are as follows: $v_{11} = 0.1$, $w_{e11} = 0$, $f_{e11} = 0$, $f_{l11} = 1$, $v_{12} = 0.1$, $w_{e12} = 1$, $f_{e12} = 0.33$, $f_{l12} = 1$, $w_{e22} = 1$, $f_{e22} = 0.33$, and $f_{l22} = 0.33$.

In other words, competition among and between species in the late environment or desiccation of the late environ-ment would be expected to help drive the evolution of ovoviviparity and specialization of the ovoviviparity geno-type on the early environment.

Case Study: The Evolution of Ovoviviparity in *Drosophila sechellia*

In this section, we review the evidence that suggests that the evolution of ovoviviparity in *D. sechellia* may have evolved as a means of avoiding competition and exploiting an unoccupied niche.

Phylogeny of D. sechellia

Drosophila sechellia is a member of the *Drosophila melanogaster* subgroup. It is most closely related to *Drosophila mauritiana* and *Drosophila simulans* (Jones 2005). There are claims to have broken this trichotomy, ultimately placing *D. mauritiana* and *D. sechellia* as sister species (Caccone et al. 1988). But more recent evidence suggests that *D. sechellia* speciated from the main *simulans* line before the split between *D. simulans* and *D. mauritiana* (Kliman et al. 2000), with the former split occurring 413,000 years ago and the latter split occurring 263,000 years ago. The genome of most *Drosophila* species are remarkably conserved, including overall genome size, number of genes, distribution of transposable element classes, and patterns of codon usage (*Drosophila* 12 Genomes Consortium 2007).

It is now well documented that *D. sechellia* is one of the least genetically diverse species of *Drosophila* (Legrand et al. 2009, 2011). Historical estimates of N_e are an order of magnitude less than the closest relatives of *D. sechellia* (Legrand et al. 2009). This type of evidence has added fuel to the hypotheses that the low level of fecundity in *D. sechellia* is a byproduct of population bottlenecks and small population size.

Drosophila sechellia *Show Reduced Fecundity Compared to Close Relatives*

Louis and David (1986) found that another difference between *D. sechellia* and other *Drosophila* species is the low female adult reproductive potential. Not only does *D. sechellia* produce far fewer ovarioles than *D. simulans* (R'kha et al. 1997), but it also produces uncharacteristically large eggs (Lott et al. 2007; Markow et al. 2009). These two traits are tied to fecundity, and it seems that producing fewer ovarioles and larger eggs can both be adaptive trait differences. In several studies, it can be seen that the egg width and length was found to be longer and wider in *D. sechellia* than in other species of *Drosophila* (Markow et al. 2009), and *D. sechellia* were also found to have the largest eggs in volume (Lott et al. 2007).

Markow et al. (2009) suggested that *D. sechellia* females will retain fertilized eggs in their reproductive tracts for long periods. Meier et al. (1999) found that a reduction in the number of ovarioles as well as an increase in egg size is associated with ovoviviparity in *Drosophila*.

R'kha et al. (1997) proposed two theories for *D. sechellia's* small ovariole number. The first is that, with the natural extinctions and recolonizations of the *D. sechellia's* host plant, the small ovarian size was fixed at some point due to random genetic drift. Second, *D. sechellia*, in their natural environment, must travel long distances to find fresh fruit to lay their eggs. If the flies have a smaller ovariole number, they will weigh less. This would be an advantage to long-range dispersal that is characteristic of *D. sechellia*.

Jones (2004) lays out three possible explanations for the reduced number of ovarioles and eggs produced by *D. sechellia* females. The first is that this is a direct response of adaptation to the local ecology of the Seychelles islands. Second, this may be a maladaptive byproduct of population bottlenecks. Finally, Jones suggests these phenotypes may be pleiotropically affected by genes involved in other adaptations. Jones (2004) tends to discount the first two hypotheses and says that the third hypothesis cannot be rejected on the basis of the available evidence. An argument similar to Jones's third hypothesis was also made by Legrand et al. (2009).

The Specialized Niche of D. sechellia *Varies over One Generation*

Drosophila sechellia is endemic to the Seychelles, a group of islands off the east coast of Africa. *Drosophila sechellia* has evolved to be a host specialist of *Morinda citrofolia* (Indian mulberry). This specialization is accompanied by some substantial physiological adaptation, because fresh *Morinda* fruit is toxic to most *Drosophila* species except *D. sechellia* (R'kha et al. 1991; Legal et al. 1994).

This toxicity is due to hexanoic and octanoic acids, the two major components of the host plant of *D. sechellia*. These organic acids promote oviposition in *D. sechellia* but inhibit oviposition in its sibling species (Amlou et al. 1998). When *D. sechellia* females are given a choice of oviposition sites, they choose to lay their eggs on *Morinda* fruit rather than cornmeal-sugar food (R'kha et al. 1991). *Drosophila sechellia* larvae also tend to pupate directly in their larval food, unlike cosmopolitan populations of their close sibling species, *D. simulans* (Erezyilmaz and Stern 2013).

The larvae of *D. sechellia* are highly resistant to octanoic acid. In contrast, close relatives of *D. sechellia*, *Drosophila simulans* and *Drosophila melanogaster*, are not resistant (Jones 2001). Some theories have suggested that evolution of tolerance to a new toxic food might be facilitated by a correlation to adult preference for that food by either pleiotropy or linkage. Hungate et al. (2013), in a study of genetic variation that affects tolerance of octanoic acid, found no support for a close genetic correlation.

Consistently, *D. sechellia* produce a small number of eggs (R'kha et al. 1991), roughly one-third the number produced by other *D. melanogaster* subgroup species. Is it possible that the strong smell of the *Morinda* fruit might be responsible for the low production of eggs in *D. sechellia*? R'kha et al. (1991) found no significant differences in *D. sechellia* egg production between females that had direct access to *Morinda* fruit and those that could smell the fruit behind a wire screen. However, *D. sechellia* are drawn to the *Morinda* fruit and can detect this resource at a distance of over 150 m. Ripe *Morinda* fruit has a high concentration

of esters that gives it a specific aroma. *Drosophila sechellia* have a larger proportion of neurons devoted to detecting these esters, in theory enhancing their ability to locate the *Morinda* fruit over longer distances than other *Drosophila* (Stensmyr et al. 2003; Ibba et al. 2010).

Natural microorganisms break down the toxic products of the *Morinda* fruit over several days, allowing other species to cohabitate on the *Morinda* fruit. Octanoic acid levels decrease as *Morinda* rots, and thus the suitability for other *Drosophila* species increases gradually. The high levels of toxicity decrease by 50% or more as the toxins break down during rotting (Legal et al. 1994). On the island of Mauritius, samples of fresh and rotten *Morinda* were placed in natural sites, and flies were later raised from them. Only one species of drosophilid was recovered from fresh *Morinda*, whereas nine species were recovered from rotten *Morinda*, including one member from the melanogaster subgroup, *D. mauritiana* (David et al. 1989). This important observation suggests that any insect capable of using fresh *Morinda* fruit as a larval substrate will experience little competition for this food, but only temporarily. As the fruit begins to rot, early colonizers lose the protection provided by *Morinda* toxins, and many additional species make use of the fruit. We believe this is an important fact that has not been fully appreciated by others trying to explain the evolution of niche specialization of *D. sechellia*.

Drosophila malerkotliana is a tropical generalist that is found in *Morinda* (Louis and David 1986). Direct competition on standard laboratory food revealed that *D. malerkotliana* is a vastly superior competitor to *D. sechellia* (Louis and David 1986). Although direct observation under field conditions has not been made, these results suggest that *D. sechellia* eggs laid at the same time as *D. malerkotliana* eggs would have a very low chance of survival. It is possible that *D. sechellia* that have a day or more head start on *D. malerkotliana* could nevertheless fend off smaller *D. malerkotliana* larvae and survive reasonably well, as has been observed with other species of *Drosophila* (Bakker 1961).

The idea that temporary resources are used by different temporal sequences of *Drosophila* is well documented for another habitat, figs (Lachaise and Tscas 1983). First, flowers mature, then fruit is formed, and finally this fruit decays. We find different species of *Drosophila* colonizing the figs over this developmental profile (fig. 2). We suggest that something similar happens in fresh and decaying *Morinda*, with *D. sechellia* being one of the only species colonizing fresh *Morinda*.

Drosophila sechellia *Are Ovoviviparous*

In a study of 11 species of *Drosophila*, Markow et al. (2009) found that *D. sechellia* eggs hatch in approximately 1.7 h, whereas the eggs of its close relative, *D. simulans*, take nearly 21 h to hatch (fig. 2). Given the widespread distribution of oviparity among the close relatives of *D. sechellia* (fig. 2), it is reasonable to assume that the appearance of ovoviviparity in *D. sechellia* is a recently evolved trait.

An Evolutionary Hypothesis

With the facts outlined, we now suggest a route by which the specialization of *D. sechellia* on *Morinda* fruit evolved. As noted by the observations of David et al. (1989), rotten *Morinda* fruit was probably a perfectly acceptable larval substrate for the ancestral lineage of *D. sechellia*. However, competition from other species, such as *D. malerkotliana*, for this resource was likely to be intense. Competition for natural resources in the wild has been documented in *Drosophila* populations, albeit not, to our knowledge, for *D. sechellia* (Grimaldi and Jaenike 1984). The use of less rotten samples of *Morinda* probably happened gradually, as suggested by R'kha et al. (1997), and we suggest that this occurred as a means of avoiding competition. In the initial phases of the evolution of ovoviviparity, the more rapidly developing genotypes most likely had only a slightly increased tolerance for octanoic acid relative to the slowly developing genotypes and thus could not start development at the peak of octanoic acid concentration but required some degradation from those peak levels. Therefore, the rapidly developing genotypes had only a short time to begin growth on the *Morinda* fruit before the arrival of other species that would leave strong larval competitors.

However, this adaptation to fresh *Morinda* would require both adaptations to tolerate the toxins in fresh *Morinda* and the ability of *D. sechellia* larvae to rapidly develop after eggs are deposited in the fresh *Morinda* to avoid the inevitable colonization and competition for this resource by other *Drosophila* species. One mechanism to accomplish more rapid development is for females to produce eggs that hatch rapidly (i.e., ovoviviparity). However, this then requires that female *D. sechellia* fertilize eggs internally and allow them to begin development before being laid on fresh *Morinda*. At this time, we do not know the precise mechanism by which *D. sechellia* achieves rapid hatching, although Lavista-Llanos et al. (2014) suggest one mechanism. A byproduct of this mode of reproduction is a reduction in the number of eggs that can be laid relative to *D. sechellia*'s close oviparous ancestor, *D. simulans*. Thus, our hypothesis is a specific example of the third hypothesis offered by Jones (2004).

In a food-limited environment, even a few hours head start in larval development can be important for the outcome of competition (Bakker 1961). Bakker showed that a 3-h head start for the competitively inferior Bar-eye genotype of *D. melanogaster* was enough to erase its competitive disadvantage with the wild type. A 6-h head start gave
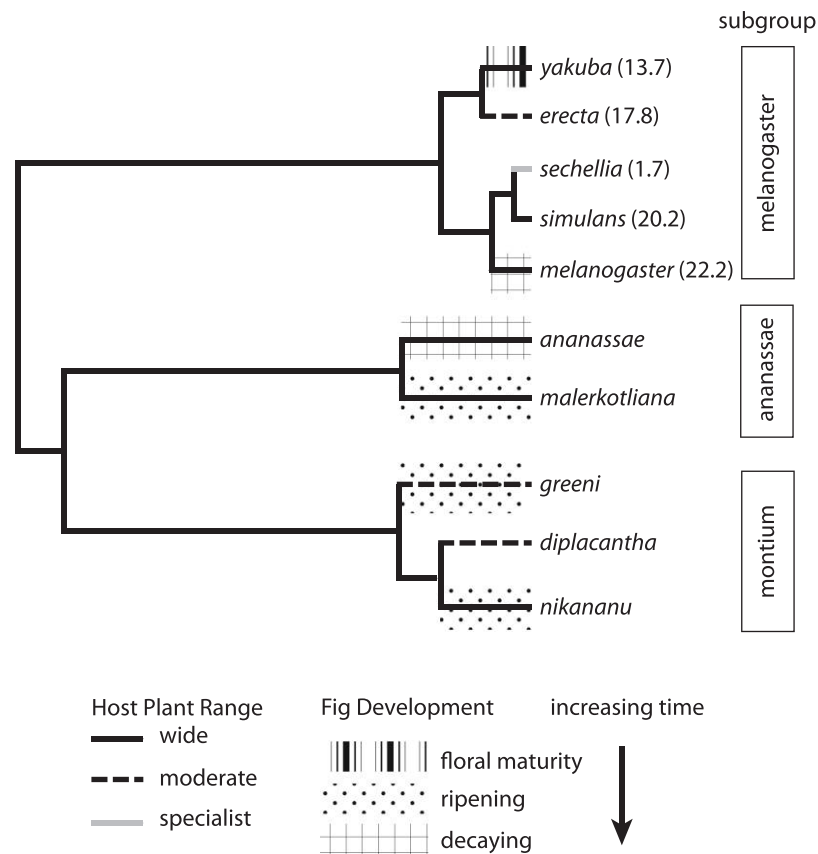
Figure 2: A cladogram of some African *Drosophila*. The tips of the cladogram are drawn in three types of lines that indicate the host-plant range of each species (Lachaise and Tscas 1983). Species with a wide host-plant range (solid black line) were found on greater than 10 host plants, species with a moderate range (dashed line) were found on two to 10 host plants, and specialist species (solid gray line) were found on a single host plant. Next to the name of each species are egg hatch times in hours (adapted from Markow et al. 2009). Several species also use figs as host plants. The temporal use of this host is also indicated by shading on the tip of the cladogram. The cladogram relies on information from the *Drosophila* 12 Genomes Consortium (2007) and Schawaroch (2002).

Bar-eye mutants a competitive advantage over wild type. Thus, even without an evolved resistance to fresh *Morinda* fruit, ovoviviparous *D. sechellia* would have a competitive advantage with other *Drosophila* species laying eggs at about the same time.

It is not unusual to find that eggs laid by *D. melanogaster* hatch in just several hours. This presumably happens when these females fertilize eggs but then retain them for some time. The theory we have described for the evolution of ovoviviparity in *D. sechellia* could be tested with a species like *D. melanogaster* by selecting for early egg hatch. The evolution of an ovoviviparous population of *D. melanogaster* would be consistent with the theory outlined here.

Discussion

Degradative succession is a process of species turnover seen in habitats that are temporary but undergo a repeat-able pattern of decay (Rose and Mueller 2006:448–449). For instance, human bodies left out of doors undergo a temporal transition of insect species that is sufficiently consistent that forensic entomologists can give approximate times of death by simply examining the insect fauna in the remains (Rose and Mueller 2006).

The model developed here has some similarities to earlier models of the evolution of egg size in fish. Sargent et al. (1987) suggest that increased parental care fosters the production of larger eggs, which also results in reduced fecundity but higher egg viability and shorter juvenile development time. If we consider egg retention as a form of Dipteran "parental care," then this model also suggests that parental care will result in reduced development time but will sacrifice fecundity.

In this article, we have developed a general model for the evolution of ovoviviparity that is specific for organisms utilizing ephemeral resources that degrade substantially

within the lifetime of a species utilizing them. Under such conditions, we suggest that adaptations that allow a genotype to begin development immediately after the mothers have located the resource will likely experience increased survival and fertility relative to genotypes that have longer developmental periods. Ovoviviparity is one mechanism to shorten the period of development after a resource has been identified and eggs deposited. In carefully controlled laboratory experiments involving *Drosophila*, a head start of hours in development has been shown to provide the early developers with a substantial competitive advantage (Bakker 1961).

Borash et al. (1998) pointed out that crowded laboratory cultures of *Drosophila* go through a dramatic and predictable decay within a single fly generation as resources are depleted, ethanol levels decrease, and ammonia levels increase. They suggested that this temporal variation may be responsible for a polymorphism in larval feeding rates among populations long adapted to these crowded conditions. In this article, we expand upon that idea to suggest that the decay of *Morinda* fruit may set in motion a series of events that have favored rapid development and tolerance to *Morinda* fruit toxins.

Ovoviviparity in *Drosophila sechellia* ensures that eggs will hatch almost immediately in the environment chosen by the female parent. If this is a fresh *Morinda* fruit, then these larvae will be in a virtually competitor-free environment until the fruit becomes substantially rotten. On the basis of development-time data from *Drosophila melanogaster*, this level of ovoviviparity would be expected to cut down the total larval development time by approximately 20%. We have suggested that ovoviviparity and tolerance to fresh *Morinda* toxins exhibited by *D. sechellia* are a consequence of changing biotic community in *Morinda* fruit as it decays.

The theory developed here suggests that, in *D. sechellia*, low fecundity, ovoviviparity, and resistance to Morinda toxins are all part of a coordinated adaptive process. Previously, the low fecundity of *D. sechellia* was thought to be a maladaptive by-product of population bottlenecks (R'kha et al. 1997). Although this nonadaptive explanation has not been falsified, the present theory has the virtues of tying together many of the unusual features of *D. sechellia* ecology and life history.

Recently, Lavista-Llanos et al. (2014) published evidence for a possible molecular mechanism of ovoviviparity and resource specialization. They noted that some populations of *D. sechellia* have genetic variants that produce defective dopamine regulatory protein Catsup. This defect leads to the arrest of oogenesis. Morinda contains high levels of 3,4-dihydroxyphenylalanine, which can compensate for this defect and is likely to result in ovovivparity and the production of large eggs. We might expect that a mutant with these effects would be rapidly removed from populations of *D. melanogaster* or *D. simulans*. However, in a population already undergoing adaptation to Morinda to avoid competition, it is expected that such a mutation would be tolerated and perhaps even accelerate the process of adaptation.

An open question is whether evolution in *D. sechellia* would continue and ultimately produce a viviparous life history, as has happened a number of times in other Diptera (Meier et al. 1999). Although most ideas about the evolutionary origins of reproductive strategies are difficult to test (Meier et al. 1999), the interesting possibility exists that, with *Drosophila* species, experimental programs could be performed that could test some of the critical components of these theories.

Acknowledgments

Literature Cited

Amlou, M., B. Moreteau, and J. R. David. 1998. Genetic analysis of *Drosophila sechellia* specialization: oviposition behavior toward the major aliphatic acids of its host plant. Behavior Genetics 28:455–464.

Bakker, K. 1961. An analysis of factors which determine success in competition for food among larvae of *Drosophila melanogaster*. Archives Néerlandaises de Zoologie 14:200–281.

Borash, D. J., A. G. Gibbs, A. Joshi, and L. D. Mueller. 1998. A genetic polymorphism maintained by natural selection in a temporally varying environment. American Naturalist 151:148–156.

Caccone, A., G. Amato, and J. R. Powell. 1988. Rates and patterns of scnDNA and mtDNA divergence within the *Drosophila melanogaster* subgroup. Genetics and Molecular Research 118:671–683.

David, J. R., S. F. McEvey, M. Solignac, and L. Tsacas. 1989. *Drosophila* communities on Mauritius and the ecological niche of *D. mauritiana* (Diptera, Drosophilidae). Journal of African Zoology 103:107–116.

Drosophila 12 Genomes Consortium. 2007. Evolution of genes and genomes on the *Drosophila* phylogeny. Nature 450:203–218.

Erezyilmaz, D. F., and D. L. Stern. 2013. Pupariation site preferences within and between *Drosophila* sibling species. Evolution 67:2714–2727.

Grimaldi, D., and J. Jaenike. 1984. Competition in natural populations of mycophagous *Drosophila*. Ecology 65:1113–1120.

Hungate, E. A., E. J. Earley, I. A. Boussy, D. A. Turissini, C. Ting, J. R. Moran, M. Wu, et al. 2013. A locus in *Drosophila sechellia* affecting tolerance of a host plant toxin. Genetics 195:1063–1075.

Hunter, A. S. 1988. High altitude flower-breeding *Drosophila* (Diptera: Drosophilidae). Pan-Pacifc Entomologist 64:299–312.

———. 1992. Flower-breeding *Drosophila* of Bogota, Colombia: new species (Diptera: Drosophilidae). Pan-Pacific Entomologist 68:192–199.

Ibba, I., A. M. Angioy, and B. S. Hansson. 2010. Macroglomeruli for fruit odors change blend preference in *Drosophila*. Naturwissenschaften 97:1059–1066.

Jones, C. D. 2001. The genetic basis of larval resistance to a host plant toxin in *Drosophila sechellia*. Genetical Research 78:225–233.

———. 2004. Genetics of egg production in *Drosophila sechellia*. Heredity 92:235–241.

———. 2005. The genetics of adaptation in *Drosophila sechellia*. Genetica 123:137–145.

Kliman, R. M., P. Andolfatto, J. A. Coyne, F. Depaulis, M. Kreitman, A. J. Berry, J. McCarter, et al. 2000. The population genetics of the origin and divergence of the *Drosophila simulans* complex species. Genetics 156:1913–1931.

Lachaise, D., and L. Tscas. 1983. Breeding sites in tropical African Drosophilids. Pages *in* M. Ashburner, H. L. Carson, and J. N. Thompson, Jr., eds. The genetics and biology of *Drosophila*. Vol. 3. Academic Press, New York.

Lavista-Llanos, S., A. Svatos, M. Kai, T. Riemensperger, S. Birman, M. C. Stensmyr, and B. S. Hansson. 2014. Dopamine drives *Drosophila sechellia* adaptation to its toxic host. eLIFE 3:e03785.

Legal, L., B. Chappe, and J. M. Jallon. 1994. Molecular basis of *Morinda citrifolia* (L.): toxicity on *Drosophila*. Journal of Chemical Ecology 20:1931–1943.

Legrand, D., M. I. Tenaillon, P. Matyot, J. Gerlach, and D. Lachaise. 2009. Species-wide genetic variation and demographic history of *Drosophila sechellia*, a species lacking population structure. Genetics 182:1197–1206.

Legrand, D., D. Vautrin, D. Lachaise, and M. L. Cariou. 2011. Microsatellite variation suggests a recent fine-scale population structure of *Drosophila sechellia*, a species endemic of the Seychelles archipelago. Genetica 139:909–919.

Lott, S. E., M. Kreitman, A. Palsson, E. Alekseeva, and M. Z. Ludwig. 2007. Canalization of segmentation and its evolution in *Drosophila*. Proceedings of the National Academy of Sciences of the USA 104:10926–10931.

Louis, J., and J. R. David. 1986. Ecological specialization in the *Drosophila melanogaster* species subgroup: a case study of *D. sechellia*. Acta Oecologica 7:215–229.

Markow, T. A., S. Beall, and L. M. Matzkin. 2009. Egg size, embryonic development time and ovoviviparity in *Drosophila* species. Journal of Evolutionary Biology 22:430–434.

Meier, R., M. Kotrba, and P. Ferrar. 1999. Ovoviviparity and viviparity in the Diptera. Biological Reviews of the Cambridge Philosophical Society 74:199–258.

R'kha, S., P. Capy, and J. R. David. 1991. Host-plant specialization in the *Drosophila melanogaster* species complex: a physiological, behavioral, and genetical analysis. Proceedings of the National Academy of Sciences of the USA 88:1835–1839.

R'kha, S., B. Moreteau, J. A. Coyne, and J. R. David. 1997. Evolution of a lesser fitness trait: egg production in the specialist *Drosophila sechellia*. Genetics 69:17–23.

Roff, D. A. 1992. The evolution of life histories. Chapman & Hall, New York.

Rose, M. R., and L. D. Mueller. 2006. Evolution and ecology of the organism. Pearson Education, Upper Saddle River, NJ.

Sargent, R. C., P. D. Taylor, and M. R. Gross. 1987. Parental care and the evolution of egg size in fishes. American Naturalist 129:32–46.

Schawaroch, V. 2002. Phylogeny of a paradigm lineage: the *Drosophila melangaster* species group (Diptera: Drosophilidae). Biological Journal of the Linnean Society 76:21–37.

Stearns, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Stensmyr, M. C., T. Dekker, and B. S. Hansson. 2003. Evolution of the olfactory code in *Drosophila melanogaster* subgroup. Proceedings of the Royal Society B: Biological Sciences 270:2333–2340.

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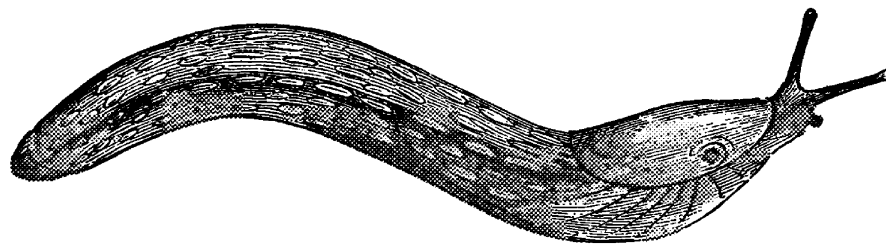
"*Arion fuscus* . . . is readily distinguished by its jaw which has no median beak-like projection to its cutting edge, but has rib-like processes on its anterior face, crenulating the margin. . . . It is of European origin and thus far has only been noticed in Boston and vicinity. It is not properly a cellar snail, but is found with the preceding species around kitchens and gardens." From "The Mollusks of Our Cellars" by W. G. Binney (*The American Naturalist*, 1870, 4:166–171).