

they form juxtaposed pointillistic colour centres which, to our eyes, create the stimulus of the colour green (the same principle is used in many neo-impressionist paintings).

One further special feature of this structurally coloured system, and possibly the reason it evolved, is that only the blue colour component is significantly linearly polarised; linear polarisation is sometimes used for intra-specific signalling in Lepidoptera, so this system seems ideally designed to be cryptically green to, say, predator visual systems that do not see differences in the polarisation of light, while broadcasting linearly polarised blue signals to conspecifics.

A separate small family of swallowtails, the *Nireus* group that is indigenous to the Afrotropics, concurrently employs a fluorescent pigment and not one, but two forms of specialised photonic structure: a multilayer and a two-dimensional photonic crystal slab. These carefully control the emission direction of the fluorescent light and make the butterfly a much brighter object than it would be without them. This is the first known example in which fluorescent pigment and colour-producing or colour-controlling nanostructures are so closely tied together.

There are a vast number of other examples. Lepidopteran structural colour systems, and those in other orders too, truly exhibit a remarkable ability to control the flow of light and colour in so many ways and for so many purposes.

Why is this subject worth investigating? Textbooks tell us that a colour pattern is a slice in time; a frozen moment in the dynamic processes of development and evolution. Genetic information is translated into the manipulation of cell systems and cuticle assembly to give final patterns and appearances.

To understand these processes in Lepidoptera, we examine the biological components that

underpin their wing colours and patterns. We seek to know how changes in genes and development can control colour and pattern; how larval food plant quality affects male sexual quality indicators; how the forms and relative weighting of inter-specific and intra-specific selection pressures affect wing colour intensity, hue, polarisation and angular visibility.

A study of the biology of the wing colours and patterns of Lepidoptera is a study of evolution itself. Now, within this field, it is increasingly clear that structural colour, and the many ways in which it is produced, is a fundamental component.

From the perspective of technological photonics, these lepidopteran systems are amazingly elaborate. They feature self-assembled highly complex biological engineering for photonic purposes (amongst others) that, given the limited range of constituent materials, exhibit an ingenuity of design that easily surpasses all but a few of our best technological efforts. Technology is keenly interested in the ideas and design principles that such natural photonic systems, such as those in certain Lepidoptera, are able to offer.

Who knows how much photonics research time may be saved, or how many technological design solutions may be realised, simply by looking to nature's wing for inspiration?

Where can I find out more?

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Primer

The nature of *Drosophila melanogaster*

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*'The time has come,' the Walrus said,
'To talk of many things:
Of shoes - and ships - and sealing-wax -
Of cabbages - and kings -
And why the sea is boiling hot -
And whether pigs have wings.'*

Lewis Carroll, *Through the Looking-Glass*

Many biologists have dreamed of a research organism that can be studied from many, if not all, perspectives. The fruit fly, *Drosophila melanogaster*, may be just such an organism. Its genetics have been studied since the early 1900s, starting in Thomas Hunt Morgan's fly rooms at Columbia and Caltech. Since then, numerous studies have used fruit flies to uncover important aspects of evolutionary processes such as selection, migration and genetic drift. Concurrent studies using the fruit fly have unraveled fundamental processes of cell biology, neurobiology and development. Despite this impressive array of accomplishments, very little is known about *D. melanogaster*'s natural history and ecology in the wild.

A better understanding of this species' natural history can help direct research questions posed in the laboratory and the field. For example, such questions come to mind as: Does *D. melanogaster* overwinter and if so where? Is dispersal important to its natural history, and if so, when and how far do animals disperse? Do flies exhibit aggressive behaviour, sleep, group sex or homosexual courtship in nature? Is learning important in nature and if so how long do flies remember? Do flies

have different ‘personalities’ — are some bold and others shy, and how does this affect their fitness?

In this Primer, we shall consider why the natural history and ecology of *D. melanogaster* has been neglected relative to other aspects of its biology. We also summarize what is known about its ecology from evolution and population genetic studies done in the wild, and from lab studies using flies from nature. And, finally, we consider directions for integrating knowledge of the fly’s natural history and ecology with studies in behaviour and neurogenetics.

The fly’s emerging ecology

Why haven’t studies on the natural history and ecology of *D. melanogaster* progressed at the same pace as, say, studies on its genetics and development? *D. melanogaster* has a tropical origin and has dispersed and differentiated genetically in various climates ranging from temperate to neotropical. Few ecologists have been interested in this species of *Drosophila* because they assumed that localities are recolonized each year by source populations through human-mediated transport. However, the evidence has accumulated that does not support this assumption. For instance, temperate populations are known to have the ability to overwinter. Also, changes in the frequencies of genes or phenotypes with latitude have been frequently reported, suggesting long-term local residency.

These findings imply that *D. melanogaster* is adapted to local environmental conditions and that this will be reflected in changes in behaviour and life-history, for example, developmental time, fecundity, age at reproduction and life span. An even closer look at existing evidence suggests that this species has a rich ecology where local biotic factors, such as parasitoids and conspecifics, and abiotic factors, such as temperature and humidity, impose selective pressures

on the fly that lead to local adaptations. Indeed, adaptations in such complex environments can lead to changes in the genetic architecture of complex behaviours and life history traits. Nonetheless, the details of its ecology in the diverse environments in which it is found remain poorly understood.

It seems timely, then, to gain a deeper understanding of the natural history and ecology of *D. melanogaster*. This organism’s long history of genetic research provides us with mutations, of varying severity, in many genes. Additionally, we can analyze changes in gene expression at the genomic level to assess the fly’s response to genetic and environmental variation. These tools can be used to dissect local differences in the adaptations of flies to their natural environments. We can also address questions about how and why certain genes, gene networks or even genomes have evolved to affect particular phenotypes in specific environments. Furthermore, using a well-described model may be valuable for the elucidation of ecological principles. For instance, the experimental control of genetic variation is relatively easy in *D. melanogaster*, and an arsenal of physiological and behavioural assays are available to be applied to flies from wild populations.

Ecology of natural populations

Fly life

It can be said that *D. melanogaster* lives where it eats. Courting of adult females by males leads to copulation, fertilization of eggs and oviposition onto the food source. Other than having a clear preference for fermenting fruit, how females choose oviposition sites in nature is largely unknown. The embryos mature and hatch, and the larvae emerge and feed, moving within and between the broken pieces of fermenting fruit that make up their food sources. At this developmental stage, the fruit is their primary habitat and conditions can vary at a very fine scale. For instance, depending on the location and time of day, the fruit might be shaded by a tree or fully exposed to the sun.

The larvae go through three molts before they reach the minimum weight necessary to pupate. As larvae they are susceptible to parasitoid wasps such as *Asobara tabida* that lay single eggs inside fly larvae. The parasitoid larva hatches inside the fly larva, slowly consuming it from within. If the wasp larva survives, it will emerge from the fly’s pupal case.

D. melanogaster pupae can be found on the skin or surface of fruit. Pupae can also be found directly under fruit or even in the soil at a distance from fruit. The choice of pupation site depends in large part on the water content of the soil. In dry environments, larvae pupate closer to or on the fruit, while in wet environments they pupate away from the fruit. Presumably, the choice of pupation site is a tradeoff between the risks of desiccation and rotting from molds. Pupae are also susceptible to pupal parasitoids such as *Pachypoideus*.

In the morning, when it is relatively humid, adults emerge from their pupal cases, dry their wings, and await sexual maturity. Courtship and mating in *D. melanogaster* has been observed on food sources yet little is known about how they proceed in the wild. For example, we do not know if flies disperse to new food sources prior to or following mating and oviposition. Despite the fly’s close relationship with its food source, there are times when it ventures away from fruit. The reasons for such roaming remain unclear but may be due to changes in temperature, food quality, or biotic conditions such as interactions with conspecifics or exposure to threats such as parasitoids. The nuances of such space-use patterns in the wild require further clarification. Nevertheless, the close relationship between the fly and its food source has sparked a good deal of inquiry on habitat choice, dispersal and other food-related behaviours in natural *D. melanogaster* populations.

Out and about

Early studies on dispersal in *D. melanogaster* suggested flies are relatively stationary, moving only 10 meters or less daily [1]. Later studies, however, using laboratory mutants, suggested that their mobility might in fact be greater than previously expected, but dispersal over large distances is likely facilitated by human transport [2]. The magnitude of dispersal is species-specific in Drosophilids, suggesting some underlying genetic mechanisms for this behaviour that could correlate with habitat choice and resource use. In the wild, a species' propensity to emigrate and its subsequent 'decisions' regarding habitat choice are important aspects to consider. These processes not only play a large part in determining the character of an organism's environment, but may also lead to modifications of the environment. This happens because of attraction and subsequent interactions with conspecifics, prey or parasites.

Studies of food-related behaviour in *D. melanogaster* have provided an example of natural variation in fine-scale spatial-use patterns of larvae. Natural variation in foraging behaviours are due in large part to a single, major gene called *foraging* (*for*) which encodes a cGMP-dependent protein kinase (PKG) [3]. The *for* gene has two naturally occurring alleles called *for^R* (rover) and *for^S* (sitter). Rover larvae have longer foraging trails while feeding within and between food patches compared to sitter larvae. Adult rovers walk farther from a sucrose drop after feeding, have higher sucrose sensitivity and habituate to sucrose more rapidly than sitters.

The rover and sitter behaviour variants are maintained in nature in stable ratios, 70% rover:30% sitter, suggestive of some type of balancing selection. Variation in pupation distances from fruit in the field is also correlated to lab-based pupation distance measures. Sitters pupate on fruit whereas rovers pupate off fruit and in the soil. A natural selection experiment in the lab

showed that, in high-density lab conditions, rover larvae are preferentially selected, whereas in low densities sitters predominate. Intriguingly, although rover/sitter behaviour differences are attributable to a single major gene, *for*, the phenotypes are plastic when exposed to changes in food abundance and quality.

Building on the observed space-use patterns of rover and sitter adults, Judy Stamps and colleagues [4] approached important questions about adult space-use and habitat selection of *D. melanogaster* using natural populations from a mixed-fruit orchard. These researchers sought to mimic the more complex natural habitat a fly encounters in nature. The experimental habitats were built in rooms and used plastic leaves and brown wires to provide perches and hiding places for the animals. Moreover, light intensity and temperature were adjusted over the course of the day to reflect normal daily changes. To control for possible effects of these fluctuating variables on behaviour, they included measurements of temperature and humidity in their analyses.

Stamps *et al.* [4] showed that complex structural habitat features, such as leaves and branches, are likely important for the natural history of this species. That is, the presence or relative abundance of these features may be a sign of habitat quality for the fly. Newly emerged females preferred settling on structural features away from their natal food source. This suggested to the authors the existence of sex-specific adaptations for space-use that might be driven by predator, parasite and/or male avoidance. Interestingly, larval foraging distances were positively correlated to lateral movements of adult flies, possibly implicating *for* in phenotypic differences in the distances that adults fly from food sources.

Further inquiry showed that in female *D. melanogaster*, habitat choice is influenced by experience in natal habitat, a 'learning process' known as natal habitat preference

induction. By allowing females to have free choice of habitat types, after conditioning to a high-quality habitat for a day posteclosion, flies were found to overwhelmingly choose their natal habitat [5]. They also found that virgin females may be attracted by conspecific virgin females. These findings suggest that complex behaviours observable only in complex environments incorporate aspects of previously described behaviours, such as foraging and dispersal. So, these emergent behaviours may be genetically tractable when environmental variation can be controlled but made more realistic.

Stress

Many drosophilists are familiar with the studies reporting higher alcohol tolerance of wine cellar fruit fly populations at Chateau Tahbilk in Victoria, Australia, discovered by McKenzie and Parsons [6]. Numerous studies have demonstrated how ecological stresses, such as exposure to relatively higher concentrations of ethanol, can shape natural populations of *D. melanogaster*. Environmental variation in stresses such as temperature, starvation, desiccation and parasitoids can lead to natural variation in life histories and behaviour. For example, following colonization of the New World, *D. melanogaster* was exposed to much cooler temperatures than are found in its tropical home range. How, then, could flies cope with winter conditions? Were localities recolonized anew each year or had flies developed some physiological and/or behavioural changes in response to these novel conditions?

As early as the 1940s, P.T. Ives' [7] studies of wild *D. melanogaster* populations in North America suggested that flies overwinter in an adult reproductive diapause. More than 60 years later, we now know that *D. melanogaster* does in fact exhibit a reproductive diapause where adult females arrest the development of their ovaries with the onset of winter conditions.

This diapause varies with latitude, with 30% of isofemale lines from neotropical habitats expressing diapause compared to 90% from temperate habitats [8]. Several life-history traits differ between diapause and non-diapause lines. For example, diapause lines show higher survival under starvation stress, greater total body triglyceride content and distinct distributions of oocyte developmental stages in the ovaries following stress exposure. Thus, diapause incidence is an important feature of natural history likely to have multiple effects on behaviours in nature.

Like diapause, numerous genes and traits related to stress show patterns of latitudinal clines in *D. melanogaster* populations. Such clines were recently found to respond to climate change [9] as well as have parallel changes in altitudinal clines. Taken together, these findings suggest that *D. melanogaster* likely experiences strong local selection on complex traits. An example of concomitant changes in physiology and behaviour in response to stress may be found in geographical variation in heat shock proteins [10]. These important molecules are cellular responders to stressful conditions and are therefore crucial for survival. Furthermore, functional mutations in heat shock protein genes are known to be under selection in natural populations. Environmental stressors, such as high density, up-regulate heat shock proteins but are also known to influence foraging behaviour. Thus, local adaptations affecting changes in physiology and life history can also influence behaviour.

An interesting natural experiment is taking place on the slopes of Mount Carmel in Haifa, Israel [11]. Two opposite slopes, separated by only 100 meters at the bottom and 400 meters at the top, have very different abiotic and biotic characteristics in their landscapes. The 'African' south-facing slope has greater solar radiation, spatio-temporal heterogeneity and lower humidity than its 'European', north-facing counterpart. Variation in the DNA

sequences of *period*, a gene involved in circadian rhythms, was found between fruit flies collected from the two slopes. These findings are reminiscent of the latitudinal sequence differences first found in *period* from European and North African populations [12]. Thus, life history differences associated with adaptations to different climates may signify concurrent modifications in genes that affect behaviour and physiology.

Ecology, behaviour and neurogenetics

Knowledge of natural history and ecology can provide interesting perspectives on individual variation in behaviours studied in the lab. For instance, courtship in *D. melanogaster* was once thought to constitute a sequence of fixed action patterns. We now know, however, that many aspects of courtship can be modified by experience. In fact, the importance of social experience and signaling from conspecifics is becoming increasingly apparent to behavioural neurogeneticists [13]. We have noted the case where habitat choice can be affected by the presence of conspecifics; but pheromonal cues have been implicated in affecting the circadian clock as well as courtship in *D. melanogaster*. Similar observations have been made on the honeybee, *Apis mellifera*, where a developmental switch from the time-challenged worker to the more scheduled forager is associated with larger oscillations in *per* RNA. Lower densities in the hive can reduce the number of workers that develop into foragers. This suggests some interaction between social experience and molecular mechanisms for behaviour.

In the model nematode *Caenorhabditis elegans*, normal variation in aggregation behaviour while foraging has been shown to be due to variation at a single amino acid within a G-protein-coupled neuropeptide Y receptor, NPR-1 (reviewed in [3]). Variation in NPR-1 in *C. elegans* results in either solitary

or aggregate feeding behaviours. The influences of social experience and group effects may be as important a consideration as genetic background or sex when dissecting complex traits. It is valuable, then, to consider the biotic and abiotic elements of the environment that are important to a species' natural history. In this way, observations in more complex environments, such as those found in nature, promise to broaden our understanding of the factors that influence individual variation in behaviour.

Ecology and neurogenetics have been coupled to provide interesting insights into behaviour in various species. For instance, field observations of the prairie vole *Microtus ochrogaster*, noting the uncommon mammalian quality of monogamy, led to intriguing lab-based analyses [14]. Investigators have described how length polymorphisms in the promoter of the gene encoding the vasopressin V1a receptor lead to differences in its distribution in the brain and then influence pair-bonding behaviour. Others, trying to find the Zeitgeber (time cues) in scorpions, have described how the twilight transition of dusk and dawn is the most effective timing cue and is sensed by a network of photoreceptors [15]. Considering the biotic and abiotic elements that constitute an organism's ecology can shed light on how relatively simple behaviours studied in the lab combine to form complex composite behaviours essential for survival in nature. Understanding the ecological contexts of complex behaviours also allows for an assessment of their evolutionary significance. By dissecting behaviours that are important in nature, we might deepen our understanding of the structure of neural pathways that were formed by evolution.

Toward bridging ecology and neurogenetics

There are promising avenues for asking about how ecological context affects variation in individual behaviours of *D. melanogaster*. It is clear that

field and lab-based research can inform and complement one another. In general, we might consider: first, starting in the lab with well-described behaviours and then searching for their ecological relevance in the field; or second, starting in the field with well-described environments and populations and then searching for correlated variation in behaviours.

In the first approach, one might seek out the environmental heterogeneity that led to the evolution of specific behaviour variants known from the lab. It may be difficult to find parallels to some of the extreme behaviours produced through mutagenesis in the laboratory. However, hypomorphic mutations, modifiers or other 'small-effect' genes may exist for these behaviours in the wild, yet such inquiries are germinal.

In the second approach, variation in behaviour resulting from local adaptation can be dissected in the lab using wild-caught flies in genetically and environmentally controlled (semi-natural) conditions. These approaches are mutually inclusive and interactive and can be made more powerful with further ecological studies. Most excitingly, these approaches have the potential to lead to the discovery of new composite behaviours found only in nature. Because of space limitations, we consider only a few of the numerous and well-studied prospective behaviours for further inquiry in natural populations. Some of these behaviours were first described from behavioural screens in laboratory populations while others were observed first in natural populations of *D. melanogaster* or other *Drosophilids*.

There is a remarkable body of work that has explored the neuronal bases of learning and memory in *D. melanogaster* [16]. Olfactory-based learning was first discovered and described in the lab. This was done by inducing mutations in *dunce* which resulted in the lack of phosphodiesterase to degrade cAMP. Since then,



Figure 1. Examples of *Drosophila melanogaster* in a natural setting.

In nature, individuals might interact on fruit, leaves, branches, or grass. For example, at top right, a male courts female on a blade of grass. Or, at bottom right, two males posture prior to an aggressive interaction. (Photographs by Christopher J. Reaume.)

other genes with multiple pleiotropic effects, for example *rutabaga* and *amnesiac*, have been implicated in learning and memory in *D. melanogaster*. Learning ability is correlated to other well described behaviours that are under genetic influence in *D. melanogaster*, such as conditioned courtship, choice of oviposition substrate, and foraging behaviour. For instance *for*, and therefore PKG, has been found to affect habituation to a food source. Investigations into the genetic architecture of learning and memory are made even more intriguing in light of research that examines the ecological and evolutionary relevance of such traits.

A burgeoning field called 'cognitive ecology' is focused on understanding how environmental heterogeneity affects genetic variation for cognition. It also seeks to examine the evolutionary costs and benefits of learning and memory. Recent work by Mery and Kawecki (for example [17,18]) has shed much needed light on the evolutionary origin and ecological maintenance of learning-related behaviours in *D. melanogaster*. Their work suggests that learning ability can be selected for in response

to association of an ecologically relevant resource. For instance, learned avoidance of an oviposition site with an aversive chemical (quinine) resulted in improved learning and memory. However, improved learning may have fitness tradeoffs by lowering oviposition rate and thereby reducing reproductive productivity. These findings suggest, perhaps not surprisingly, that learning-related behaviours may be an integral part of an organism's natural history.

Much early work on the mating behaviour of *D. melanogaster* began with the pioneering studies of Herman Spieth on the Hawaiian species group (reviewed in [19]). Courtship behaviour in *D. melanogaster* is complex, requiring interacting genes that are expressed in different regions of the central nervous system [20]. Throughout development, genes such as *fruitless* and *doublesex* are involved in specifying sex as well as sexual dimorphisms in morphology and behaviour. Courtship is a composite behaviour incorporating several other simpler behaviours such as chasing, orienting, licking and copulating. Mutations in genes related to learning and memory (*dunce*, *rutabaga* and *amnesiac*)

and circadian rhythms (*period*) may affect several aspects of courtship behaviour in nature. Further examinations into the extent to which these genes affect natural variation in courtship behaviour in different ecological contexts are of interest.

Aggressive behaviour was first characterized in *D. melanogaster* following observations by Spieth in other lekking *Drosophilids*. Since then, numerous studies have attempted to distill the important natural history correlations with this behaviour (reviewed in [21]). For instance, investigators have asked if 'winning' an encounter provides increased access to females; or, if the result of an encounter can be predicted based on status, size, age or experience. Of particular importance, territorial behaviour in this species was shown, through artificial selection, to have heritable variation. Investigations are beginning to focus on the neurological and sex-specific aspects of aggression in *D. melanogaster*. Aggression is also seen in female *D. melanogaster*, but there appear to be no 'winners' as there are with males. Interestingly, females show plasticity in their aggressive behaviour in response to social experience and food resources. For example, females were more aggressive when held in isolation or while on food with yeast colonies. Females also showed a conditioned behaviour to rich food sources analogous to the conditioning found in learning mutants in courtship behaviour. The role of aggression for *D. melanogaster* in nature, however, remains to be investigated.

Final thoughts

Our understanding of the cellular mechanisms underlying behaviour has been vastly improved by the growing number of functional genetic techniques, candidate genes for behaviour, and descriptions of the neurogenetic aspects of behaviour in *D. melanogaster*. By integrating these data with studies on ecological patterns of natural behaviour

variation (and its relationship to environmental heterogeneity) we can begin to make important links between ecology and behaviour that may be applied across varied taxa [22]. We expect such integration to not only lead to the identification of new behaviours, such as those involving social interactions, but also to an understanding of how these behaviours are affected by temporal and spatial heterogeneity in the natural environment (Figure 1). Rewards abound for such pursuits with promises of gaining new insights into the evolution of complex behaviours and their underlying genetic architecture. Studying behaviour in wild populations may help us to identify genes and traits that are important for local adaptation and speciation. Key to such pursuits is assaying naturally derived populations with precisely described ecologies under highly controlled yet realistic lab conditions.

The prospects for attaining a complete understanding of the biology of an organism have never been as exciting as they are today. The little fruit fly, a nuisance in many of our kitchens, has facilitated the acquisition of knowledge on genetics, development, neurobiology, and behaviour — all of which were thought unimaginable before the turn of the 19th century. Where some might see an opportunistic human commensal, others will see a symbiont where food and habitat is traded for biological insights of remarkable breadth.

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