

Drosophila: Where the Wild Flies Are

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Drosophila melanogaster is a human commensal and dietary generalist. A new study in its ancestral range in Africa finds that wild *Drosophila melanogaster* are specialists on marula fruit — fruits cached in caves by Pleistocene humans.

In the mind of a modern biologist, the natural habitat of the fruit fly *Drosophila melanogaster*, the genetic workhorse of biology, is in a plastic vial containing banana food. By now, thousands of generations of flies have lived in this artificial environment since the appearance of the first white-eyed mutants with which the secrets of heredity were unlocked by Thomas Hunt Morgan and his students [1]. Along with the white-eyed mutant, scientists have generated thousands of other mutant stocks and dissected in fine detail its development, physiology and behavior, leading to major discoveries in human biology [2]. In stark contrast to its biology, the natural history of *D. melanogaster*, particularly its evolutionary origins, has remained enigmatic [3]. Outside of fly rooms, *D. melanogaster* can be found in kitchens, orchards, vineyards and trash heaps all around the world, hovering around overripe fruit or glasses of wine and revealing its status as a human commensal. But, where did wild *D. melanogaster* live before it became associated with humans, what did they eat and when did the wild-to-domestic shift take place? In a new study in this issue of *Current Biology*, Susan Mansourian, Marcus Stensmyr and colleagues [4] identify the host plant of wild *D. melanogaster* in its ancestral, wild habitat in southern Africa, characterize its host-finding mechanism and propose a hypothesis on how the shift to human commensalism took place.

Drosophila's Ancestral Host and Home

The ease of rearing *D. melanogaster* led to the widely held view that it is a generalist in the wild. Yet, the breeding habits of *D. melanogaster* as a generalist contrast

with findings that it has a specific egg-laying preference for oranges [5]. Within the genus *Drosophila*, *D. melanogaster* is a member of the *melanogaster* subgroup [6]. With the exception of the cosmopolitan species *D. melanogaster* and *Drosophila simulans*, the members of the group are found only in Africa, and some are specialists: *Drosophila sechellia* is a specialist of toxic noni fruit, *Drosophila erecta* is a seasonal specialist on screw-pine fruit and a population of the generalist *Drosophila yakuba* on Mayotte Island is a specialist on noni fruit [6,7].

Guided by previous work on the egg-laying preference of *D. melanogaster* for citrus fruit [5] and its ancestral range in southern Africa [8], Mansourian and colleagues [4] searched for the ancestral host of wild *D. melanogaster* populations in the Matobos national park in southwestern Zimbabwe. The authors identified the marula fruit (Acacardiaceae: *Sclerocarya birrea*) as a potential candidate ancestral host due to its similar physical and chemical features with citrus fruit. Indeed, they found that wild *D. melanogaster* is primarily present on ripe and rotting fruit from the marula tree and it strongly prefers these fruit over other locally abundant fruit (Figure 1). In addition, in laboratory experiments, the authors [4] showed that wild flies display a strong egg-laying preference towards marula over orange. Interestingly, in contrast to *D. simulans*, wild populations of *D. melanogaster* were found where marula trees were present, during the spring months, but not in any other location with similar vegetation in Matobos. This distribution of wild *D. melanogaster* and the seasonal presence of the fruit suggest that *D. melanogaster* is a host specialist in its ancestral range and is in fact a seasonal

specialist like its closely related species *D. erecta* [6]. Overall, this finding overturns a century of dogma by finding that in its ancestral range, *D. melanogaster* is not a generalist, as it is in its global range, but is rather a specialist for marula fruit.

Olfactory Pathways of Host Specialization

Flies rely heavily on their sense of smell, and we have an excellent understanding of the molecular and neuroanatomical organization of the fly olfactory system [9]. Given this knowledge, Mansourian and colleagues [4] asked which volatile cues guide *D. melanogaster* to marula, and how it detects these volatiles. They found that the two main volatile cues produced by marula act synergistically to guide *D. melanogaster* to marula. B-caryophyllene (a semi terpene) is a compound similar to limonene, the characteristic odor of orange, and acts only as an egg-laying stimulant through activation of the Or19a olfactory pathway [5]. On the other hand, ethyl isovalerate (an ester), a compound absent in oranges, acts both as an attractant for locating the marula fruit and as an egg-laying stimulant. Mansourian and colleagues [4] show that ethyl isovalerate activates the Or22a olfactory pathway, an olfactory circuit that is repeatedly targeted by adaptation during host specialization events in drosophilids [10,11]. Overall, the dissection of the olfactory neuroethology of *D. melanogaster* to its host plant showcases the importance of natural history in the study of an innate behavior.

Given the role of Or22a in the detection of the ethyl isovalerate from marula, the authors also looked for signs of local genetic adaptation at the tandemly duplicated genes *Or22a* and *Or22b*. First,





Figure 1. *Drosophila melanogaster* on marula.
 Photo: Marcus Stensmyr.

they found what others found: some flies had two separate genes at this locus, called *Or22a/Or22b*, and some flies had a single chimeric gene, called *Or22ab*. By comparing population genetic differentiation in the odorant receptor gene family and genome-wide differentiation between ten African populations and one European population, they found that this gene region was strongly differentiated between population pairs, whereas most of the other *Ors* exhibited little population structure. These patterns might reflect the fact that the fusion variant *Or22ab* is ancient and existed well before the species expansion in Africa.

Chimeric genes are thought to be associated with rapid adaptation in *Drosophila* [12]. Although duplicate genes are also indicated as key players in adaptive evolution, they are not typically substantial drivers for adaptation in the short term. Full-length duplicate genes typically carry the same promoters, UTRs, and cellular targeting signals, which create redundancy. Chimeric genes, on the other hand, are able to change expression patterns and function immediately, which allows for rapid evolution. In conjunction with the discovery of *Or22ab* tuning to odor of marula, *Or22ab* chimeric gene could have played a significant role in adaptive evolution in wild *D. melanogaster*.

The case of this newly formed chimeric receptor also raises the question how it is accommodated in the olfactory system of the fly. The fly olfactory system is organized based on a simple 1–1 rule: one odorant receptor is expressed in one olfactory sensory neuron [13]. An exception to this rule are recently duplicated receptors, such as the *Or22a* and *Or22b* receptors [14], expressed in a single OSN. It is therefore intuitive to presume that the chimeric *Or22a/b* receptor has a straightforward neuronal housing option, as it would be housed in the same OSN with the parental receptors. This hypothesis remains to be tested.

Marula — a Vehicle to Commensalism?

The marula tree is widespread in southern Africa. Marula fruit are part of the local human diet and also play an important role in the economy turned into jam, beer, wine and the popular liquor Amarula. The marula trees are also lore for safaris, as travellers are promised to see drunk elephants feasting on fermenting marula fruit (though this is actually unlikely [15]). The use of marula in the local diet likely traces back thousands of years, as archaeological excavations found seeds of marula in caves where the ancestors of the San people, historically indigenous hunter-gatherer groups, once lived [16]. The San people gathered fruit and honey

that they cached in their caves, as we now know from their elaborate and exquisite cave paintings.

Prompted by these observations, the authors asked whether the marula could have acted as the vehicle for the transition to a commensal lifestyle in *D. melanogaster*. By placing traps with fermenting fruit in caves, they managed to catch wild *D. melanogaster* but not *D. simulans*. This behavioral difference between the two closely related species is in agreement with previous observations: *D. melanogaster* would readily enter houses while *D. simulans* would not [17]. Although it is impossible to know whether the behavior of *D. melanogaster* mirrors its behavior in the past, it provides a plausible hypothesis on how the wild-to-domestic habit started. It is conceivable that *D. melanogaster* first evolved to become a commensal species through its shared desire with humans for the marula fruit and through further adaptation with humans, spread throughout Africa and eventually left to become the cosmopolitan species it is today.

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Ecology: Luck, Scarcity, and the Fate of Populations

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An animal's choice of diet plays a large part in determining whether it will find food during a period of searching. This has profound implications for the likelihood of reproductive success or starvation and many other important questions in ecology.

Energy is the fundamental currency of life [1]. Many organisms obtain their energy by consuming others; thus, consumption is one of the most important — and most studied — interactions for ecological and evolutionary dynamics and the focus of some of the earliest mathematical models in ecology [2,3]. Early models of consumer–resource or predator–prey interactions were often powerful, general, simple and deterministic. Since then, awareness of the importance of luck has increased, exposing how chance events like finding food, or encountering predators or bad weather, can play an important role in determining the fates of individuals and populations [4–6]. Despite this, standard results that many ecologists take for granted — such as the ecological drivers of diet breadth and specialisation, and insights into the stability of predator–prey interactions — lean heavily on a small number of early deterministic models. In a recent paper in *Current Biology*, Rory Wilson and

colleagues [7] show the link between diet and chance, highlighting the profound effects of diet in determining the fates of individuals and populations in changing environments.

As a foundation for their analyses, Wilson and colleagues [7] make use of recent advances in biologging, an area of development within which they have long been at the forefront. They used data from four different species (domestic sheep, Magellanic penguins, cheetahs and Andean condors), multiple individuals of which had been fitted with triaxial accelerometers and magnetometers as components of ‘daily diaries’ used to monitor many aspects of animal movement and behaviour [8]. As their names suggest, triaxial accelerometers record acceleration in three planes, whilst magnetometers indicate orientation. When analysed carefully [9], data from these devices can be used to infer characteristic patterns of movement associated with many behaviours, and so to reconstruct the activities and feeding

behaviour of animals during periods of monitoring. In addition, the penguins were fitted with Hall sensors, an ingenious device used to measure jaw-angle and, thereby, to reveal the frequency of food ingestion [10]. Using this technology, the team were able to determine how long individuals of the focal species spend looking for each consecutive item of food before they can eat.

Ecologists working on herbivores are often interested in their bite rates in different habitats [11], whilst carnivore ecologists often pay close attention to the frequency with which their subjects make kills [12]. However, the idea of comparing these rates among species with very different diets is novel. By doing so, Wilson and colleagues [7] show that sheep, which feed almost continuously on low-value vegetation, had fairly linear increases in cumulative intake with time, and very little difference between individuals. At the other end of the spectrum, Andean condors are scavengers that might search for days for