evidence of reproductive isolation as a result of their differing seasonal preferences.

The researchers used nuclear and mitochondrial sequence data to check the phylogenetic relationships of the summer-developing processionary moths with their winter-developing counterparts. They also used microsatellite markers to compare the two populations and monitored adult flight behaviour to determine whether activity overlapped between the two populations.

The resulting mitochondrial and nuclear data gathered suggested that the individuals sampled from the Leiria summer population belong to the same species as the classical winter-developing populations of these moths, sampled from the same site and also Spain and France, ruling out the appearance of a cryptic processionary moth species at this site.

From analysis of all the data, the authors conclude that the summer-developing population at Leiria was established by a small number of individuals with early adult emergence and rapid larval development. "These individuals were 'instantly' reproductively isolated from the surrounding winter individuals", the researchers report. The "shift was not correlated with a change in host species, habitat or resource, as the summer larvae still feed on one-year-old needles (like the conspecific winter caterpillar), and on the same pine trees as the sympatric winter individuals."

This population of summer-developing moths "thus represents a unique opportunity to study the very first steps of sympatric speciation that could ultimately lead to sympatric, allochronic speciation," the authors believe.

Essay

Drosophila melanogaster's history as a human commensal

Andreas Keller

When W.E. Castle at Harvard and T.H. Morgan at the Columbia University started using a tiny fly for laboratory experiments in genetics they were probably unaware that the species had only been introduced to the United States a few years earlier. *Drosophila melanogaster*, now a widely popular organism in biological research, is a human commensal that owes its current cosmopolitan distribution largely to human activity. Since this became clear considerable progress has been made in understanding the historical biogeography of *Drosophila melanogaster* and its association with human activities. There are even first attempts to describe the ecology of populations not associated with human activities, which might shed light on the evolutionary history of the species.

There has been much speculation about the ancestral home range of *Drosophila melanogaster*, but today it seems clear that the species is native to equatorial Africa [1]. From there it spread to all major continents, and today the northernmost record is from Tampere, Finland [2] and the southernmost record from Tasmania [3]. The home range of closely related species is a strong indication that *Drosophila melanogaster* has an African origin. *Drosophila melanogaster* and eight sister species form the *Drosophila melanogaster* subgroup. Of these, *Drosophila yakuba* was discovered in the Ivory Coast in the 1950s [4]. In the 1970s and 1980s, five more species were discovered by Léonidas Tsacas and his coworkers. *Drosophila teissieri*, *Drosophila orena* and *Drosophila erecta* were all found on the African mainland [5–7], whereas *Drosophila mauritiana* is endemic to the island of Mauritius [8] and *Drosophila sechellia* was only found on some islands of the Seychelles archipelago [9]. The Seychelles archipelago and the island of Mauritius are both in the Indian Ocean off the coast of Africa. In the year 2000, another species in the *Drosophila melanogaster* subgroup, *Drosophila santomea*, was discovered on the island of São Tomé in the Atlantic Ocean near the West African coastline [10].

All these flies have so far been found only in the Afrotropical region. The other two members of the subgroup, *Drosophila melanogaster* and *Drosophila simulans*, are cosmopolitan, but because all of the closely related species are endemic to the Afrotropical region, it can be assumed that these two originated there, too. The discovery of species closely related to *Drosophila melanogaster* that are not human commensals opened the interesting possibility of studying their ecology in an attempt to learn how *Drosophila melanogaster* may have lived before it became associated with humans.

All species of the *Drosophila melanogaster* subgroup breed on fruits, yet they differ considerably in their ecology (reviewed in [1]). Little is known about the natural history of *Drosophila orena*, which has only been reported from a single collection in the West Cameroon mountains at 2100 m [6], or of *Drosophila santomea*, which was discovered only recently "in the remote, submontane, mist rainforests covering the higher rugged volcanic slopes of São Tomé" [10]. *Drosophila sechellia* and *Drosophila erecta* are predominantly found on the fruits of a single plant species, *Morinda citrifolia* and *Pandanus candelabrum*, respectively. *Drosophila mauritiana*, *Drosophila*

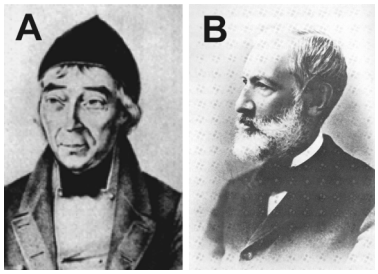

Figure 1. The entomologists who first described *Drosophila melanogaster*.

(A) Johann Wilhem Meigen (1764–1845) described a vast number of Diptera in the 19th century and is universally recognized as the father of Dipterology. Meigen was an amateur entomologist who received his doctor's diploma at the age of 83, eight weeks before his death. He described the species *Drosophila melanogaster* in 1830 in "Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten". His very brief description of the species translates to: "Head, thorax, and legs yellow; abdomen black. The halteres are white, the wings colorless. " (B) Joseph Albert Lintner (1822–1898) was the first to report the species, under the synonym *Drosophila ampelophila*, in the United States in 1875. Like Meigen, Lintner started as an amateur entomologist, but at the age of 45 he became the Zoological Assistant in the New York State Museum of Natural History in Albany and ultimately rose to the level of the New York State Entomologist. He received an honorary Ph.D. at the age of 62. In his first annual report on the injurious and other insects of the state of New York in 1882, he said (page 216), in referring to flies that were sent to him: "They proved to be identical with numerous specimens of *Drosophila ampelophila* in my collection, having the memorandum of 'bred from a jar of pickled plums, September, 1875'" [23]. (Reproduced with permission from the New York State Museum, Albany, NY, USA.)

yakuba and *Drosophila teissieri*, on the other hand, breed on a wide variety of fruits including mangos (*Mangifera indica*), figs (*Ficus lyrata*) and guavas (*Psidium guajava*) [1].

Drosophila simulans and *Drosophila melanogaster*, the two cosmopolitan species, also exploit a variety of different fruits and can also breed on anthropogenic food sources such as stale beer [11]. The first hint that *Drosophila melanogaster* breeds on fruits came in 1864, when it was reported from the raisin stores of Smyrna (now Izmir, Turkey; cited in [11]). Subsequently *Drosophila melanogaster* was, like many commensal species, reported to occur in a wide variety of habitats. It was found in a human grave in 1898 [12] and was bred from human excrement one year later [13]. More commonly though, it is reported in sources like canned fruits and pickles, decaying apples, cider mill refuse, fermenting vats of grape pomace and raspberry vinegar [13]. It was bred from potatoes, tomatoes and a variety of fruits [11].

All these food sources are domesticated fruits or other products of human activity. What food source *Drosophila melanogaster* used in its ancestral home range in equatorial Africa before it became dependent on these man-made sources is unclear. It may be that it used an entirely different fruit than the domesticated species on which it is now most commonly found. A fascinating discussion of the wild-to-domestic habit shift in *Drosophila melanogaster* can be found in Lachaise and Silvain [14]. Interestingly, a host-plant shift from a natural source to a domesticated fruit was shown for another fly, *Rhagoletis pomonella*, which originally infested hawthorn. A recently derived population of this species now breeds preferentially on apples that were introduced in the geographic range of the species. In the case of *Rhagoletis pomonella*, this host–plant shift was associated with, and perhaps causally related to, a shift in olfactory preferences [15].

Reports of *Drosophila melanogaster* breeding sites in natural habitats in Africa (reviewed in [1]) can help answer the question of what food sources *Drosophila melanogaster* originally used. The species is said to breed most successfully on bananas [11,14] and was reported to occur in a natural habitat with fruits of the banana species *Ensete giletti* [14]. Other host plants used as breeding sites of *Drosophila melanogaster* in the Afrotropical region include mangos (*Mangifera indica*), papaya (*Carica papaya*) and apple guava (*Psidium guajava*). A total of 25 plant species in the Afrotropical region have shown to host *Drosophila melanogaster* larvae. Sixteen of these are native plants, making them possible food sources for *Drosophila melanogaster* before its association with man [1].

Although all nine *Drosophila melanogaster* sister species originated in the Afrotropical region, only *Drosophila melanogaster* and *Drosophila simulans* have spread around the world as a result of human activity. The other seven species have remained restricted to their tropical home range. The ability to colonize depends largely on the broadness of the ecological niche a species occupies. Only species tolerating a wide range of temperatures and using different food sources have the ability to become cosmopolitan. Of the two efficient colonizers in the subgroup, *Drosophila simulans* seems to lag behind its sister species *Drosophila melanogaster*. In 1920, when *Drosophila melanogaster* was already very common throughout northern America, *Drosophila simulans* was found in the eastern part of the United States, but was not contained in rather extensive collections from the Pacific Coast [16]. The colonization of Japan by *Drosophila simulans* dates to around 1972, a time when *Drosophila melanogaster* was already well-established there [17].

Drosophila simulans may lag behind *Drosophila melanogaster* in its speed of dispersal because it is less 'domestic' than *Drosophila melanogaster* — for example, less likely to enter houses [17]. The stronger association with humans of *Drosophila melanogaster* makes it more likely for individuals of this species to be introduced into a new area by human activity. Once a species is introduced to a new location, the number of individuals sometimes increases rapidly. At the ideal temperature and population density, it takes only 10 days for a *Drosophila melanogaster* egg to develop into a sexually mature fly [18]. Because of its short life cycle and the fact that *Drosophila* can disperse several kilometers

in a single day [19], *Drosophila melanogaster* — although it relies on humans to be transported across oceans — can spread efficiently once it is introduced into a new area.

The introduction and subsequent rapid dispersal of *Drosophila melanogaster* has been observed directly by entomologists in the United States and on numerous islands. The first entomologist to describe *Drosophila melanogaster* was the German government employee Johann Wilhelm Meigen [20] (Figure 1A). In 1830, Meigen reported finding *Drosophila melanogaster* in the two German port cities of Kiel and Hamburg, and in Austria. The occurrence in port cities suggests that these specimens may have been introduced by ships and may have been from temporary populations. Meigen's description of the species is brief, six words in the Latin and 14 in the German version. Because of the lack of detail in the description, *Drosophila melanogaster* has been frequently redescribed and was therefore known under many synonyms, including *Drosophila nigriventris*, *Drosophila ampelophila* and *Drosophila uvarum.*

There are too few reports to decide if *Drosophila melanogaster* was rare or absent in middle Europe before 1830. It is quite likely that the species just went unnoticed until then and was actually introduced to parts of Europe and Asia in prehistoric times [21]. In other parts of the world, however, the introduction of *Drosophila melanogaster* has been witnessed by entomologists. *Drosophila melanogaster*'s colonization of North America in the second half of the 19th century has been observed directly [11,22]. The species was first reported in the State of New York in 1875, where the New York State entomologist Joseph Albert Lintner (Figure 1B) reported that it had been "bred from a jar of pickled plums" [23]. The dipteran fauna of the State of New York had been studied before in great detail without any mention of *Drosophila melanogaster* by Asa Fitch, the entomologist of the New York State Agricultural Society. It seems improbable that Fitch, the first professional entomologist in the United States "who described so many minute diptera" [22] would have overlooked *Drosophila melanogaster*. Therefore, the species was most likely introduced into the northeastern United States of America shortly before 1875.

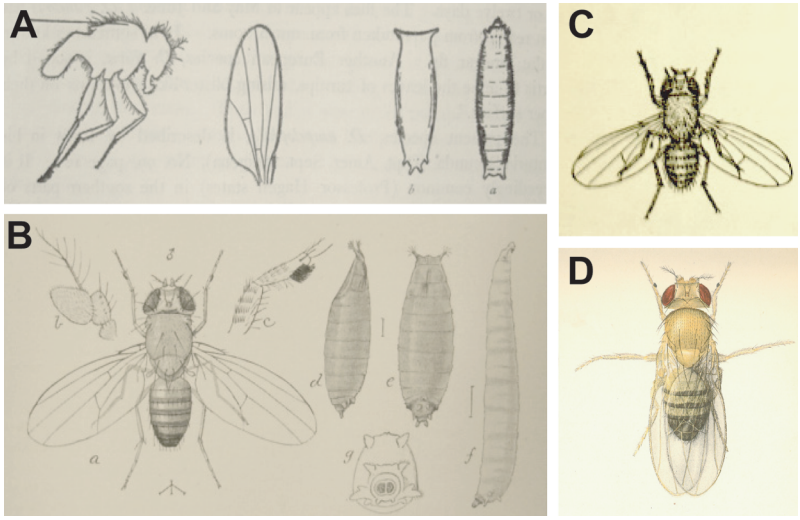

Figure 2. Early historical drawings of *Drosophila melanogaster.*

(A) To my knowledge, the earliest published drawing of *Drosophila melanogaster*, which appeared in *The Canadian Entomologist* in 1882 [34]. It shows the outline of an adult fly and a wing ("magnified 10 diameters") and a pupa and a larva ("magnified 7 diameters"). A much more detailed drawing by Howard appeared in *The Principal Household Insects in the United States* in 1896 [35]. (B) The same drawing was reproduced in 1900 [13]. Here an adult male fly, its antenna and front leg are shown. The puparium is shown from the side and in the dorsal view. The larva and its anal segment are also shown. (C) In 1901 another drawing of a *Drosophila melanogaster* specimen from the Bermuda Islands was published in the *Transactions of the Connecticut Academy of Arts and Sciences* [36]. (D) A detailed color drawing of a male *Drosophila melanogaster*, drawn by E.M. Wallace , appeared in A.H. Sturtevant's *The North American Species of Drosophila* in 1921 [11].

In subsequent years *Drosophila melanogaster* was reported in different parts of the continent, in monographs that included the first depictions of *Drosophila melanogaster* specimens (Figure 2). In 1900, only 25 years after its first report on American soil, *Drosophila melanogaster* was "the commonest species all over the United States" [13] (Figure 3). To my knowledge, however, it was reported from the West Coast only in 1915, when it was found on dried fruits in California [24]. By 1921, *Drosophila melanogaster*'s geographical range in northern America was from Nova Scotia to Washington in the north and from Florida to California in the south [11].

In other geographical regions, *Drosophila melanogaster* was introduced even more recently. In the early 1980s, it was reported for the first time from the Mahé island in the Seychelles archipelago [25]. On Hokkaido, the second largest island of Japan, *Drosophila melanogaster* was not found in an extensive survey of the Drosophilidae in 1961, but later was introduced [26]. The sudden appearance and rapid spread of *Drosophila melanogaster* around Honolulu in the early 1940s has been attributed to escapes from culture bottles at the University of Hawaii [27], and on the Galapagos Islands, *Drosophila melanogaster* was not found in 1966 [28], but later an expedition to the Islands with the specific purpose of investigating Drosophilidae found it in the fruit room of the restaurant at the Charles Darwin Biological Station, suggesting that it was introduced directly to the islands through the human food supply [29].

A population that, like the one in the Charles Darwin Biological Station, is restricted to a single

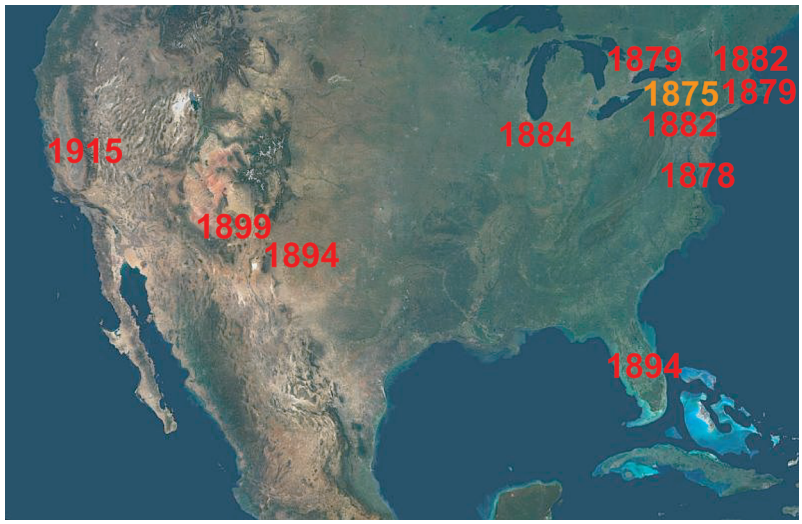

Figure 3. The dispersal of *Drosophila melanogaster* in the United States after 1875.

In the ten years after is was first reported in New York State in 1875 (orange), *Drosophila melanogaster* was reported in the District of Columbia (1878) [37], Montreal (1879) [34], New Haven, Connecticut (1879) [38], Massachusetts and Pennsylvania (1882) [38], and Moline, Illinois (1884) (cited in [35]). It continued its spread to the south and west and was found in St. Augustine, Florida, in Mesilla Valley, New Mexico in 1894 [39], and in Phoenix, Arizona in 1899. It was reported in California in 1915 [24].

source of food, is generally unstable and may eventually disappear. This happened in Okinawa, an island belonging to Japan, where *Drosophila melanogaster* was reported in the 1930s [30]. Thirty years later two independent surveys of the Drosophilidae were carried out and failed to find *Drosophila melanogaster*, despite the large scale of the efforts [31,32]. This example shows that, while *Drosophila melanogaster* is a very efficient colonizer and its spread around the world is still ongoing, its populations outside its home range are very vulnerable and highly dependent on human activity. Some researchers have even suggested that, outside the tropical regions, some populations die out during the winter and new populations are established in the spring from individuals reintroduced from warmer regions [11].

It may be surprising that an animal that is now encountered so frequently in laboratories and kitchens all over the world used to be a forest-dwelling species restricted to a small part of equatorial Africa. The success of *Drosophila melanogaster* as a commensal and its popularity as a laboratory animal has the same reasons. The flies have a short generation span and the capacity to produce lots of offspring and they can utilize a wide variety of food sources and are not afraid to enter human settlements. *Drosophila melanogaster* shares these characteristics with another popular laboratory animal that started as a human commensal and was spread all over the world by human activity, the common house mouse (*Mus musculus*) [33].

Acknowledgments

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Increased outbreeding in yeast in response to dispersal by an insect vector

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Genetic diversity can be maintained in a heterogeneous environment if different alleles are favoured at different sites [1]. Under these circumstances, organisms that remain local are selected to inbreed in order to conserve locally adapted combinations of alleles [2], but those individuals that disperse should outbreed in order to increase the genetic variance among their progeny [3] and to make it more likely that some inherit combinations of alleles highly adapted to their new site. Here we report experimental results from the budding yeast *Saccharomyces cerevisiae* that fit with this theoretical prediction. We found that rates of outbreeding increased more than ten-fold when yeast spores were digested by an insect dispersal vector, the fruitfly *Drosophila melanogaster*. Outbreeding is modulated by the tetrad, a physical structure linking the four spores produced by meiosis of a diploid cell. Tetrads cause low rates of outbreeding by default, but their dissolution in the insect gut results in the liberation of spores, which is necessary for increased outbreeding rates. These findings provide new insights into the little known population biology and life history of one of the prime model organisms.

In yeasts of the genus *Saccharomyces*, sexual reproduction is triggered by adverse environmental conditions. A starved diploid cell enters meiosis and produces a tetrad of four resistant haploid spores. When conditions improve, spores germinate and mate to restore the diploid state. Mating can occur immediately after germination, or after haploid mitotic division. This form of sexual reproduction, however, usually results in selfing between the four spores of a same mother cell, probably because the spores of a tetrad are enclosed within an envelope, the ascus, and joined by inter-spore bridges [4], maintaining them in close proximity. Outbreeding requires that the tetrad breaks up, which frees the spores and allows them to mate with spores generated from other tetrads. In the laboratory, yeast geneticists routinely use enzymes to digest the physical structures that hold spores in the tetrad in order to allow crosses between different yeast strains [5].

Yeasts have long been known to be dispersed by insects [6], in particular fruitflies, which feed on yeast [7]. This raises the intriguing possibility that the digestion of tetrads in the insect gut is the natural equivalent of the geneticist's enzyme, breaking up the tetrads and allowing increased rates of outbreeding in dispersing yeast. We have tested this idea experimentally using two well-known laboratory model species, the yeast *S. cerevisiae,* and the fruitfly *D. melanogaster*. We first performed experiments which confirmed that yeast spores, and not vegetative cells, are the primary dispersal stage for these fungal species. These experiments demonstrated that, as expected, viable spores can be recovered from fly faeces long after ingestion, while vegetative cells cannot be recovered from fly faeces (see Figure S1 in the Supplemental data available on-line with this issue). Microscopic examination also showed that spores were abundant in faeces and were separated into individual spores, in striking contrast to undigested tetrads.

We then investigated whether dissolution of the tetrad in the fly gut facilitates outbreeding in *S. cerevisiae*. To this end, we