

Press Report

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Flora Borne

Life-History Evolution and the Genetics of Fitness Components in *Drosophila melanogaster*

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ABSTRACT Life-history traits or “fitness components”—such as age and size at maturity, fecundity and fertility, age-specific rates of survival, and life span—are the major phenotypic determinants of Darwinian fitness. Analyzing the evolution and genetics of these phenotypic targets of selection is central to our understanding of adaptation. Due to its simple and rapid life cycle, cosmopolitan distribution, ease of maintenance in the laboratory, well-understood evolutionary genetics, and its versatile genetic toolbox, the “vinegar fly” *Drosophila melanogaster* is one of the most powerful, experimentally tractable model systems for studying “life-history evolution.” Here, I review what has been learned about the evolution and genetics of life-history variation in *D. melanogaster* by drawing on numerous sources spanning population and quantitative genetics, genomics, experimental evolution, evolutionary ecology, and physiology. This body of work has contributed greatly to our knowledge of several fundamental problems in evolutionary biology, including the amount and maintenance of genetic variation, the evolution of body size, clines and climate adaptation, the evolution of senescence, phenotypic plasticity, the nature of life-history trade-offs, and so forth. While major progress has been made, important facets of these and other questions remain open, and the *D. melanogaster* system will undoubtedly continue to deliver key insights into central issues of life-history evolution and the genetics of adaptation.

KEYWORDS FlyBook; life-history evolution; fitness components; fitness; variation; selection; adaptation; trade-offs; plasticity

Evolution of Reproductive Behavior

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ABSTRACT Behaviors associated with reproduction are major contributors to the evolutionary success of organisms and are subject to many evolutionary forces, including natural and sexual selection, and sexual conflict. Successful reproduction involves a range of behaviors, from finding an appropriate mate, courting, and copulation, to the successful production and (in oviparous animals) deposition of eggs following mating. As a consequence, behaviors and genes associated with reproduction are often under strong selection and evolve rapidly. Courtship rituals in flies follow a multimodal pattern, mediated through visual, chemical, tactile, and auditory signals. Premating behaviors allow males and females to assess the species identity, reproductive state, and condition of their partners. Conflicts between the “interests” of individual males, and/or between the reproductive strategies of males and females, often drive the evolution of reproductive behaviors. For example, seminal proteins transmitted by males often show evidence of rapid evolution, mediated by positive selection. Postmating behaviors, including the selection of oviposition sites, are highly variable and *Drosophila* species span the spectrum from generalists to obligate specialists. Chemical recognition features prominently in adaptation to host plants for feeding and oviposition. Selection acting on variation in pre-, peri-, and postmating behaviors can lead to reproductive isolation and incipient speciation. Response to selection at the genetic level can include the expansion of gene families, such as those for detecting pheromonal cues for mating, or changes in the expression of genes leading to visual cues such as wing spots that are assessed during mating. Here, we consider the evolution of reproductive behavior in *Drosophila* at two distinct, yet complementary, scales. Some studies take a microevolutionary approach, identifying genes and networks involved in reproduction, and then dissecting the genetics underlying complex behaviors in *D. melanogaster*. Other studies take a macroevolutionary approach, comparing reproductive behaviors across the genus *Drosophila* and how these might correlate with environmental cues. A full synthesis of this field will require unification across these levels.

KEYWORDS *Drosophila*; adaptation; genetics; chemoreception; multigene family; gene–environment interaction; natural variation; selection; mating; courtship; song; postmating behaviors; fitness; pheromones; wing spots; seminal proteins; FlyBook

Rapid and Predictable Evolution of Admixed Populations Between Two *Drosophila* Species Pairs

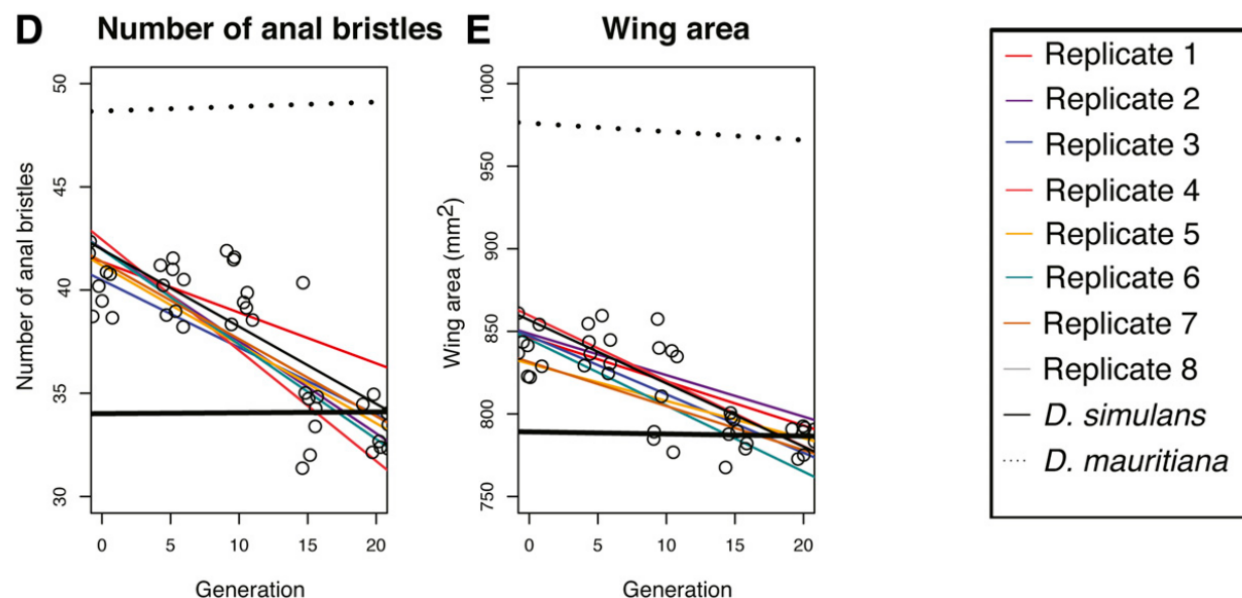
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ABSTRACT The consequences of hybridization are varied, ranging from the origin of new lineages, introgression of some genes between species, to the extinction of one of the hybridizing species. We generated replicate admixed populations between two pairs of sister species of *Drosophila*: *D. simulans* and *D. mauritiana*; and *D. yakuba* and *D. santomea*. Each pair consisted of a continental species and an island endemic. The admixed populations were maintained by random mating in discrete generations for over 20 generations. We assessed morphological, behavioral, and fitness-related traits from each replicate population periodically, and sequenced genomic DNA from the populations at generation 20. For both pairs of species, species-specific traits and their genomes regressed to those of the continental species. A few alleles from the island species persisted, but they tended to be proportionally rare among all sites in the genome and were rarely fixed within the populations. This paucity of alleles from the island species was particularly pronounced on the X-chromosome. These results indicate that nearly all foreign genes were quickly eliminated after hybridization and that selection against the minor species genome might be similar across experimental replicates.



A shared genetic basis of mimicry across swallowtail butterflies points to ancestral co-option of *doublesex*

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Uncovering whether convergent adaptations share a genetic basis is consequential for understanding the evolution of phenotypic diversity. This information can help us understand the extent to which shared ancestry or independent evolution shape adaptive phenotypes. In this study, we first ask whether the same genes underlie polymorphic mimicry in *Papilio* swallowtail butterflies. By comparing signatures of genetic variation between polymorphic and monomorphic species, we then investigate how ancestral variation, hybridization, and independent evolution contributed to wing pattern diversity in this group. We report that a single gene, *doublesex* (*dsx*), controls mimicry across multiple taxa, but with species-specific patterns of genetic differentiation and linkage disequilibrium. In contrast to widespread examples of phenotypic evolution driven by introgression, our analyses reveal distinct mimicry alleles. We conclude that mimicry evolution in this group was likely facilitated by ancestral polymorphism resulting from early co-option of *dsx* as a mimicry locus, and that evolutionary turnover of *dsx* alleles may underlie the wing pattern diversity of extant polymorphic and monomorphic lineages.



P. polytes

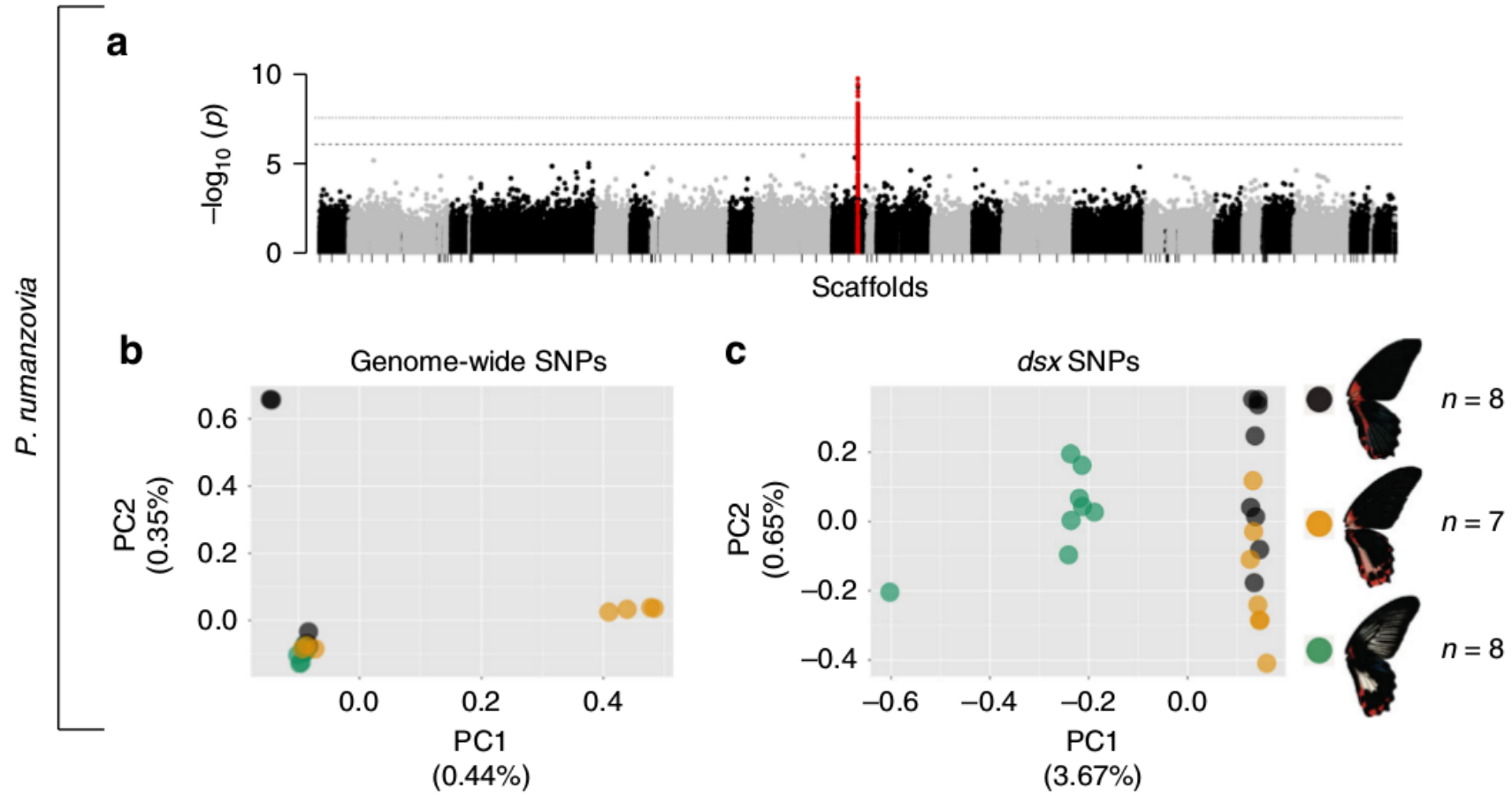


P. memnon



P. rumanzovia

doublesex is associated with polymorphic wing patterning in the four species



How to explain pattern diversity between species?

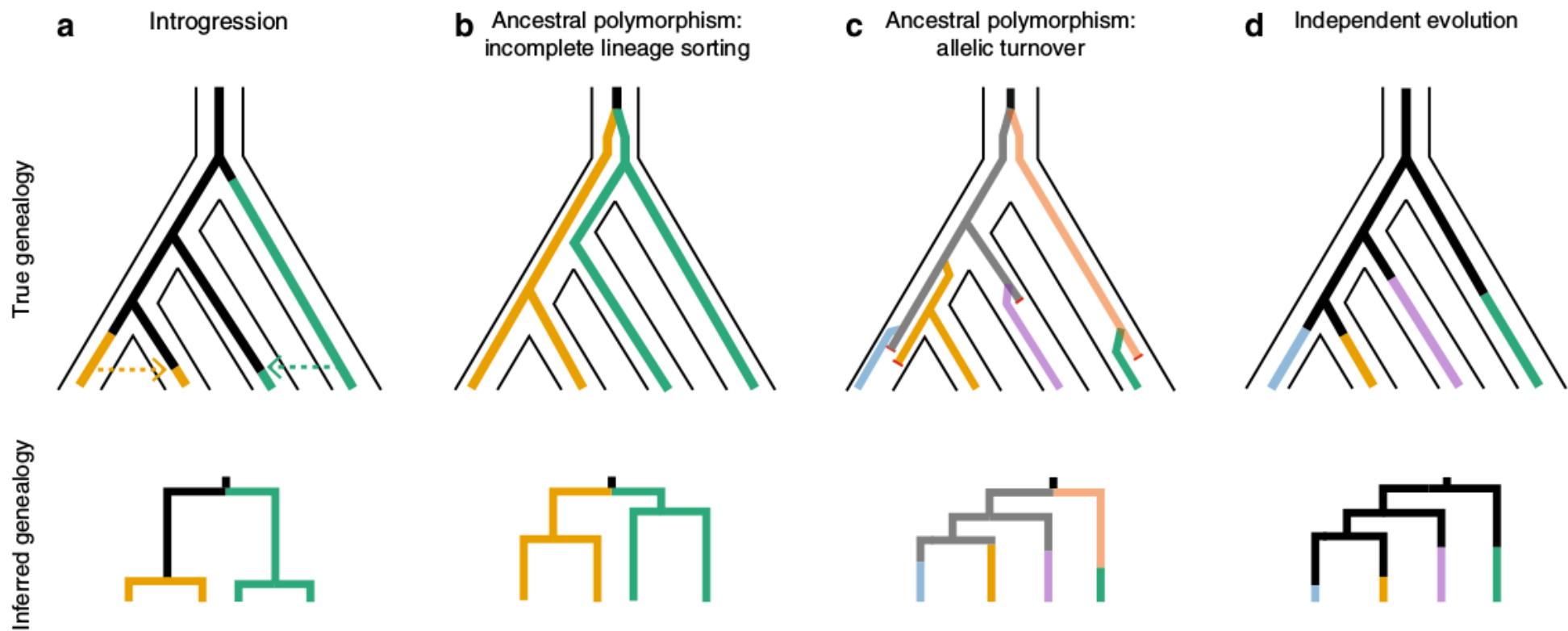
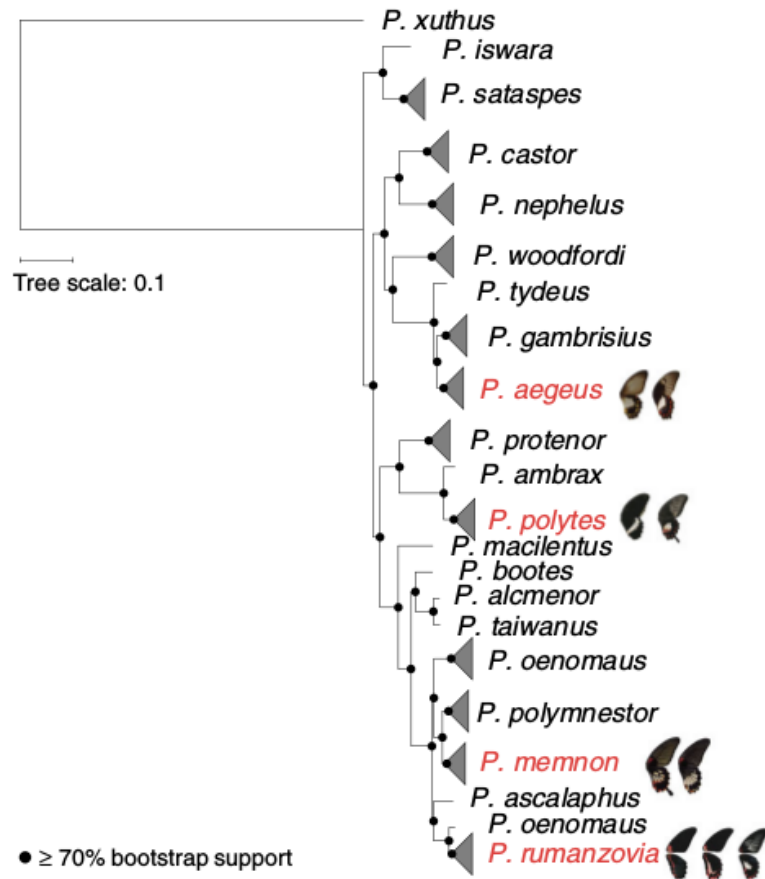


Fig. 1 True (top row) and inferred (bottom row) genealogies under four mimicry evolution hypotheses. Colors represent distinct mimicry alleles/phenotypes. **a** Mimicry alleles are shared because of introgressive hybridization. **b** Mimicry evolves ancestrally, and descendant lineages inherit and maintain the ancestral alleles. **c** Mimicry evolves ancestrally, and alleles are gained and lost so that the extant alleles are distinct from the ancestral alleles. **d** Unique mimicry alleles arise by the independent evolution of mimicry. Under introgression and incomplete lineage sorting (ILS), the inferred genealogies will show alleles grouping by phenotype rather than species (**a**, **b**), but the branch lengths will be relatively shorter for introgression than for ILS. Under allelic turnover and independent evolution, the inferred genealogies will result in alleles grouping by species (**c**, **d**), but the branch lengths are expected to be longer for allelic turnover because of underlying balancing selection. A history of allelic turnover will also leave behind population genetic signatures of balancing selection, such as elevated Tajima's D in the region of interest. Under allelic turnover, the amount of shared ancestral variation should track phylogenetic relatedness, because recombination and gene conversion will erase the evidence of ancestral variants as a lineage ages. Because shared ancestral variation is more likely to be retained at younger timescales, allelic genealogies may show alleles of one species nested within another species for younger lineages. In contrast, independent evolution need not involve balancing selection, and if variants are shared among lineages, these should not be correlated with the lineages' phylogenetic proximity.

a Genome-wide SNPs



b Phased *dsx* SNPs

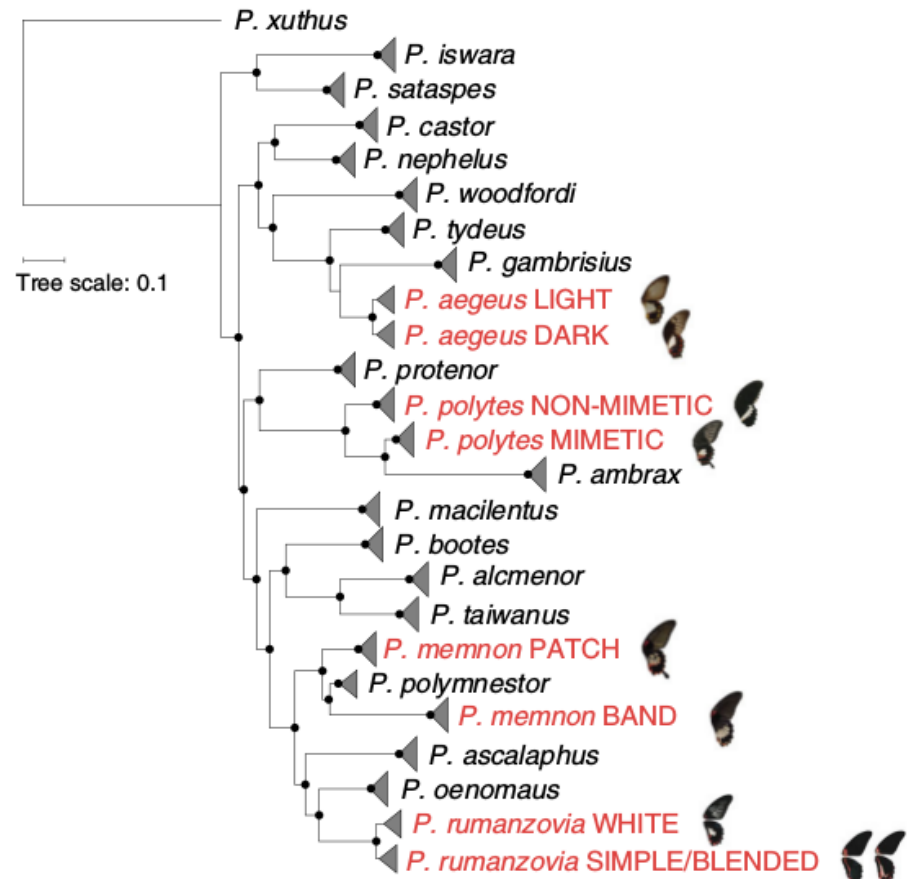


Fig. 5 Phylogenetic relationships and evolution of mimicry in *Papilio*. Maximum-likelihood phylogenies for polymorphic (red) and monomorphic (black) *Papilio* butterflies based on genome-wide SNPs (a) and phased *dsx* SNPs (b).

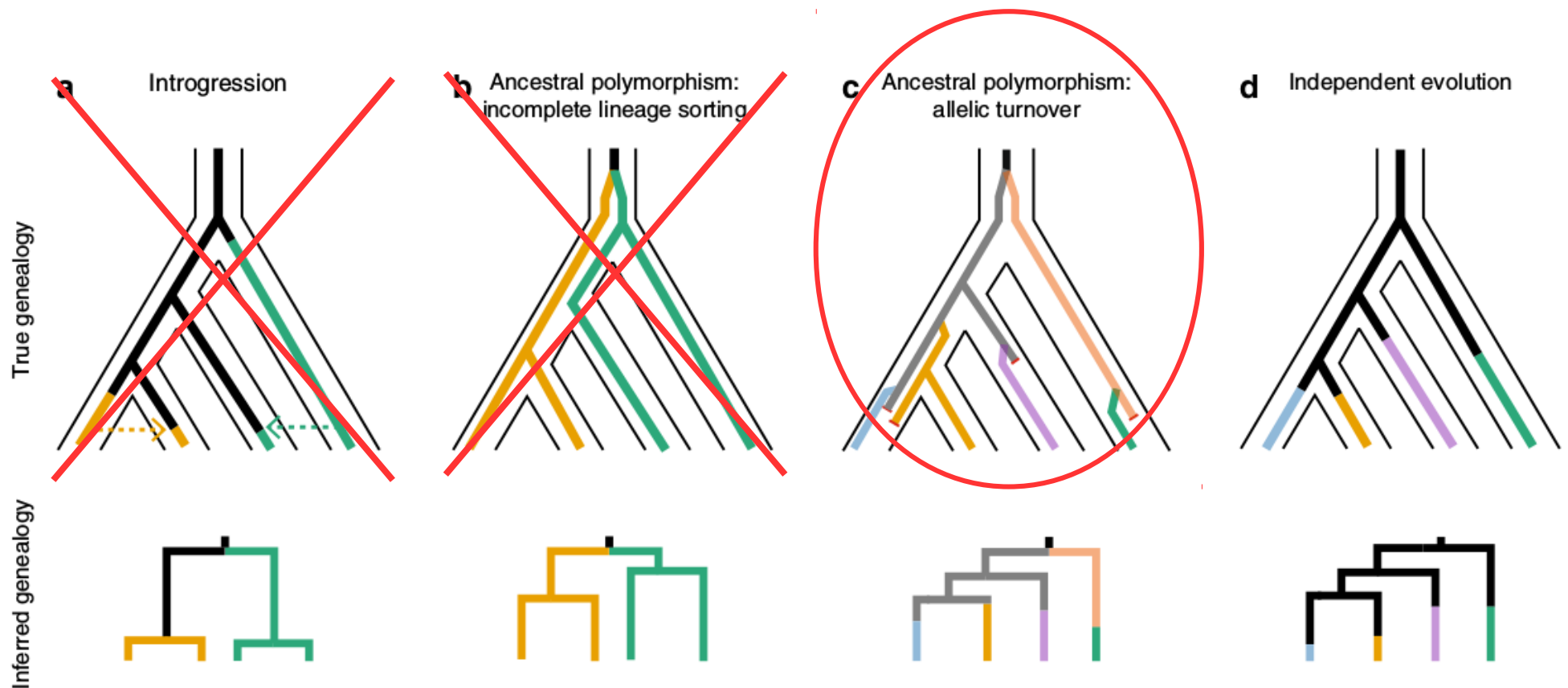


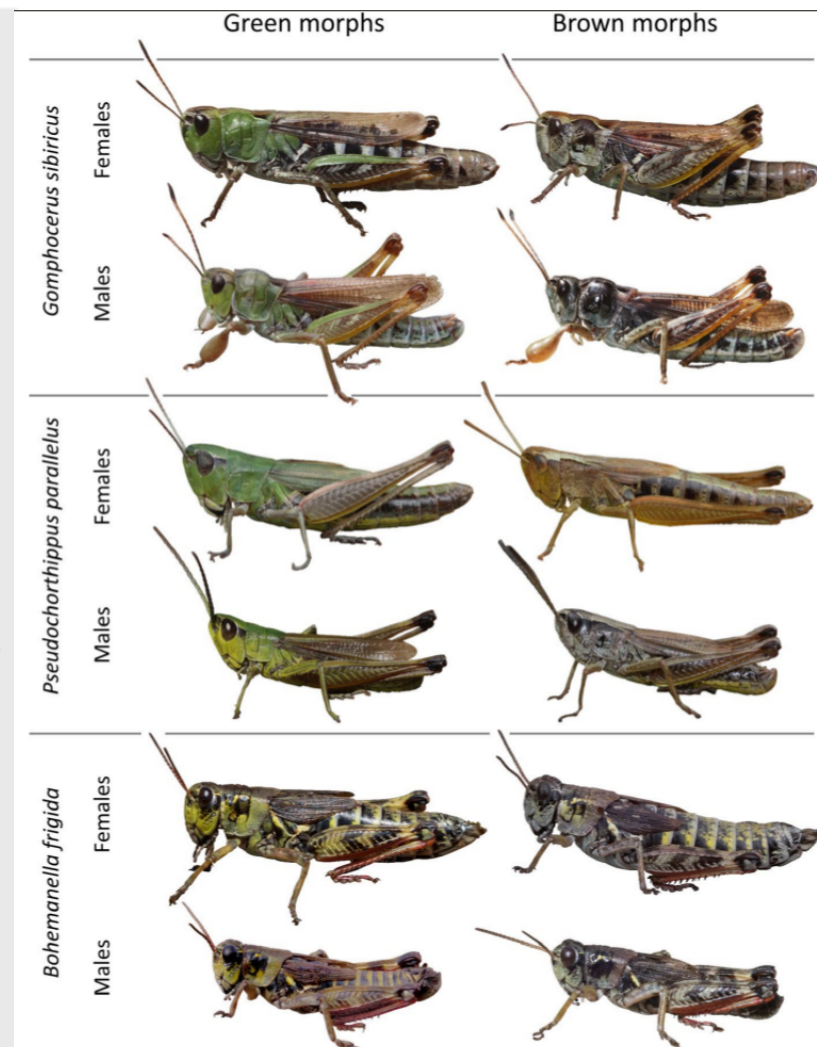
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Green-brown polymorphism in alpine grasshoppers affects body temperature

Günter Köhler | Holger Schielzeth 

Abstract

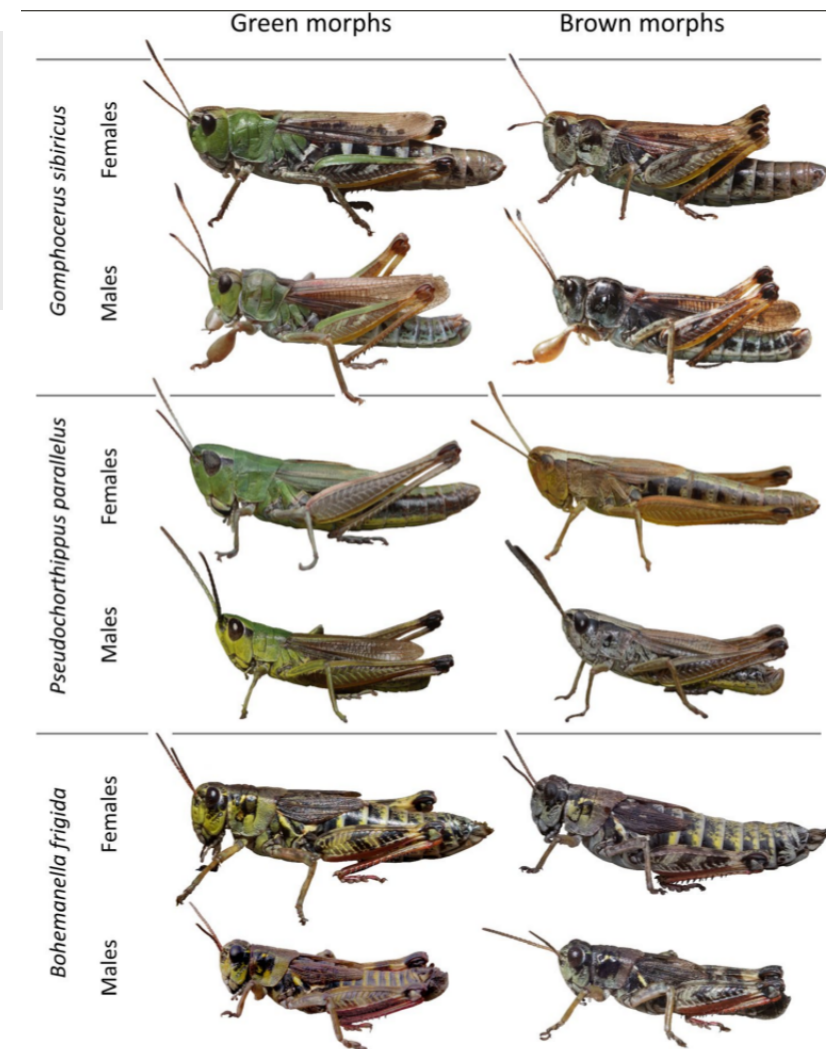
1. Ectothermic animals depend on external heat sources for pursuing their daily activities. However, reaching sufficiently high temperature can be limiting at high altitudes, where nights are cold and seasons short. We focus on the role of a green-brown color polymorphism in grasshoppers from alpine habitats. The green-brown polymorphism is phylogenetically and spatially widespread among Orthopterans and the eco-evolutionary processes that contribute to its maintenance have not yet been identified.
2. We here test whether green and brown individuals heat up to different temperatures under field conditions. If they do, this would suggest that thermoregulatory capacity might contribute to the maintenance of the green-brown polymorphism.
3. We recorded thorax temperatures of individuals sampled and measured under field conditions. Overall, thorax temperatures ranged 1.7–42.1°C. Heat up during morning hours was particularly rapid, and temperatures stabilized between 31 and 36°C during the warm parts of the day. Female body temperatures were significantly higher than body temperatures of males by an average of 2.4°C. We also found that brown morphs were warmer by 1.5°C on average, a pattern that was particularly supported in the polymorphic club-legged grasshopper *Gomphocerus sibiricus* and the meadow grasshopper *Pseudochorthippus parallelus*.



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4. The difference in body temperature between morphs might lead to fitness differences that can contribute to the maintenance of the color polymorphism in combination with other components, such as crypsis, that functionally trade-off with the ability to heat up. The data may be of more general relevance to the maintenance of a high prevalence polymorphism in Orthopteran insects.





THE NATURAL HISTORY OF MODEL ORGANISMS

The Norway rat, from an obnoxious pest to a laboratory pet

Abstract The laboratory rat was the first mammal domesticated for research purposes. It is descended from wild Norway rats, *Rattus norvegicus*, which despite their name likely originated in Asia. Exceptionally adaptable, these rodents now inhabit almost all environments on Earth, especially near human settlements where they are often seen as pests. The laboratory rat thrives in captivity, and its domestication has produced many inbred and outbred lines that are used for different purposes, including medical trials and behavioral studies. Differences between wild Norway rats and their laboratory counterparts were first noted in the early 20th century and led some researchers to later question its value as a model organism. While these views are probably unjustified, the advanced domestication of the laboratory rat does suggest that resuming studies of wild rats could benefit the wider research community.

KLAUDIA MODLINSKA* AND WOJCIECH PISULA

Attacks on genetic privacy via uploads to genealogical databases

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Abstract Direct-to-consumer (DTC) genetics services are increasingly popular, with tens of millions of customers. Several DTC genealogy services allow users to upload genetic data to search for relatives, identified as people with genomes that share identical by state (IBS) regions. Here, we describe methods by which an adversary can learn database genotypes by uploading multiple datasets. For example, an adversary who uploads approximately 900 genomes could recover at least one allele at SNP sites across up to 82% of the genome of a median person of European ancestries. In databases that detect IBS segments using unphased genotypes, approximately 100 falsified uploads can reveal enough genetic information to allow genome-wide genetic imputation. We provide a proof-of-concept demonstration in the GEDmatch database, and we suggest countermeasures that will prevent the exploits we describe.

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"Strong and weak cross-sex correlations govern the quantitative-genetic architecture of social group choice in *Drosophila melanogaster*." *Evolution* 74.1 (2020): 145-155.

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