

# Speciation: Don't Fly and Diversify?

Loss of flight in Japanese carrion beetles is correlated with greater population subdivision and higher speciation rate. This reveals the complex relationship of trait evolution with dispersal power, range size and diversification.

Alfried P. Vogler\*  
and Martijn J.T.N. Timmermans

Beetles (Coleoptera) are a hugely diverse group of insects that include about one quarter of all described animal species. Why are there so many beetles? It is clear that beetles have adopted to virtually any conceivable habitat, resource and feeding style, and have done so multiple times independently in their evolution [1]. This ecological plasticity presumably permits an expansion into unoccupied niche space and leads to speciation. The Coleoptera also apparently have avoided extinction of most lineages during periods of geological upheavals, hence over time they have accumulated great species richness [2]. Perhaps the most widely held explanation for their taxonomic diversity is their co-evolution with the equally diverse flowering plants [3]. However, support for these hypotheses remains surprisingly elusive, and no single one of them would be satisfactory for every kind of beetle. Now, Ikeda *et al.* [4] weigh in on this discussion, by proposing that in a particular group of carrion beetles (Silphinae) the diversification rate is increased by the loss of flight. It makes intuitive sense that flight loss and the reduced dispersal following from it would promote the separation of populations and ultimately speciation. Because up to a quarter of all beetle species fully or partially lost their flight ability, this may have greatly contributed to their enormous species richness.

Ikeda *et al.* [4] survey the population structure of eight species of carrion beetle across Japan using an impressive genetic data set of mitochondrial and nuclear gene markers. They find a significantly greater degree of geographic subdivision and deeper genetic branching in the two flightless species included in their analysis compared to species in which all or some populations are able to fly (Figure 1). In addition, a phylogenetic analysis places these species into a larger

flightless clade that contains roughly twice as many species compared to its flying sister group. These data suggest that both population subdivision and speciation are promoted by the lack of flight and the resulting decrease in aerial dispersal. Ikeda *et al.* [4] then go on to conduct a literature survey of genetic studies across the Coleoptera showing that flightless species exhibit generally smaller ranges and more pronounced population structure than flighted groups, confirming the findings from Japanese silphids.

The question about the causes of flightlessness has intrigued evolutionary biologists since Charles Darwin used this phenomenon as a prime example of natural selection. At that time, it had been recognized that flightless beetles were over-represented in isolated, exposed habitats, e.g. on islands, mountaintops or desert oases, where they are threatened to be dislocated by high winds with minimal chances of reaching another suitable habitat patch. This situation would select against flight [5]. In addition, the loss of an energetically expensive flight apparatus permits greater resource allocation to reproduction, a widely recognized trade-off [6–8]. However, a more recent survey of beetle communities on islands did not confirm a statistically higher proportion of flightless species, contrary to Darwin's assumption [9]. This result was corroborated by a study of carabid communities on mountaintops in Scandinavia, which equally confirmed a high proportion of long-winged (macropterous) species [10]. Remote areas have to be reached by flight, and depending on the time frame of the colonization event, the processes leading to the loss of flight may not be complete.

The notion that flight is lost *in situ* and gradually over time led to the hypothesis that flightlessness is promoted by habitat stability. Southwood [11] first proposed that habitats differ in their degree of permanence, and accordingly the persistence of populations requires

different degrees of dispersal. Rather than a selection for wing loss by adverse conditions, as proposed by Darwin, under this hypothesis wing loss is a general evolutionary trend in these insects, which in the case of stable habitats is then not counteracted by a need for dispersal. Ikeda *et al.* [4] test this hypothesis by climatic reconstructions of potential species distributions of Japanese silphid beetles since the last ice ages, but find no difference in the predicted range shifts between flighted and flightless species.

Their approach is novel in that they undertook an explicit analysis of stability over much longer times than commonly considered. However, the resulting conclusion that loss of flight, and not habitat stability, is the cause of the greater allopatric population divergence (and speciation) is not entirely convincing. The flightless clade also has undergone an important ecological shift — from carrion feeding in the ancestral flighted lineages to predation on soil invertebrates. Association with ephemeral resources such as carrion and dung is intuitively linked to a need for movement, and was already identified as one of the 'unstable' habitats by Southwood [11], unlike feeding on soil arthropods that are more uniformly distributed and hence constitute a 'stable' resource that would be accessible without a need for aerial dispersal.

This distinction between 'habitats' defined by the specific resource as opposed to climatic parameters is vital for understanding what is cause and effect in population differentiation. Liebherr [12] was the first to discover that the ability to fly was not directly correlated with the degree of genetic differentiation. Instead, the degree of population differentiation results from a combination of relative dispersal ability and the continuity of the habitat. Taking into account the two feeding sources in silphids, carrion and soil-dwelling prey, the association with soil invertebrates requires less movement, removing the requirement for dispersal, and hence is sufficient to cause the differences in genetic differentiation. The loss of flight may be a secondary event, as an indirect response to different habitat conditions, and therefore may not be causal to the greater degree of population differentiation.

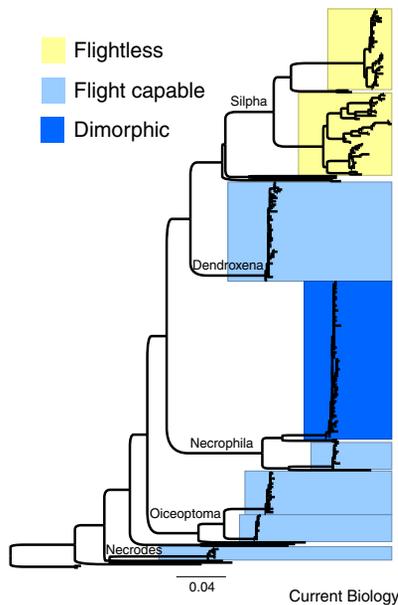


Figure 1. The phylogeny of Japanese carrion beetles.

The tree was recreated from Ikeda *et al.*'s [4] study of the *COII* gene, showing the greater depth of variation within the flightless lineage. 'Dimorphic' refers to species where some populations are able to fly and others aren't.

This hypothesis is supported by a related case in the genus *Eutagenia*, a species complex of darkling beetles (Tenebrionidae) in the Aegean islands [13]. This group is entirely flightless, but populations differ in their habitats. They either live on sandy dunes and beaches that are subject to frequent disturbance, or on stable hard-top soils of the island interiors. The genetic make-up differs greatly between populations, with low divergence and uniform distribution in sandy habitats and deep separation of local groups in the hard soil populations [13], analogous to the flighted-flightless differences seen in silphids. As all *Eutagenia* species are flightless, flightlessness cannot explain the difference. However, movement is a prerequisite for population persistence in the ephemeral sandy habitats, possibly achieved passively by wind and water. In other cases, the loss of flight is compensated for by morphological or behavioral traits, e.g. the greatly increased length of legs and change in body shape in fast-running species within an otherwise flighted clade of tiger beetles in the Australian deserts [14].

These and other studies show that cause and effect may be reversed, i.e. that lineages can persist without dispersal and show genetic differentiation, which is associated with a tendency to lose flight, instead of flightlessness being the primary cause of the genetic differentiation. This notion is also supported by the analysis of beetle species in which populations are polymorphic for the possession of wings, i.e. some populations do and others do not have the ability to fly, such as *Necrophila japonica* that was included in the study of Ikeda *et al.* [4]. Flight-incapable populations in these species are constrained in their dispersal capability just as permanently flightless species are. However, at least in the case of *N. japonica*, their genetic population structure did not differ from fully flighted species (Figure 1) [15]. Flight polymorphism provides a more flexible strategy to respond to environmental changes, as long-term survival of lineages may benefit from occasional long-distance dispersal while generally avoiding the associated risk of displacement when habitat conditions are stable [16]. Flight loss in polymorphic species may result either from the loss of wings or of wing muscles, and is frequently controlled by a single Mendelian locus, with flightlessness as the dominant allele. This means that the trait of flight loss is exposed to selection and likely 're-evolves' each time after founding a new population from long-distance dispersal [16]. Flight-polymorphic species, therefore, are an interesting system to study the direct effect of flight loss on genetic differentiation, but from the data available the evolutionary outcome is very different from the long-term, permanent loss of flight in a lineage. Only in the latter case are deep population divergence and species diversification observed, and flight loss may be only secondary to other factors that limit dispersal.

Another interesting result of Ikeda *et al.* [4] is that in permanently flightless lineages, the strong spatial population structuring also coincides with deeper branches in the phylogenetic tree within a species. The depth of these branches is such that a coalescence-based method for species delimitation reveals separate genetic units that each may be considered separate species given the theory underlying this procedure.

In addition, eyeballing the tree (Figure 1), it is clear that branches in the flightless lineage are much longer than in its sister taxon, even though both lineages are derived from the same common ancestor, i.e. they are of exactly the same age. Hence, the lack of dispersal may not only result in deeper genetic subdivision, but also in a speed-up of molecular rate of change, a finding that is also mirrored by the rate differences in sand vs. soil populations in *Eutagenia* [13]. These comparisons of dispersive and non-dispersive lineages will be of great importance for understanding the processes that determine the rate of species diversification and their effect on molecular evolution. However, this test requires explicit analyses of sister lineages that differ in dispersal propensity, which can be found within genera or tribes of many groups of beetles. Although dispersal is not strictly correlated with the ability to fly, flighted and flightless sister lineages are a good starting point for this analysis. Focusing on this trait, Ikeda *et al.* [4] have shown a fruitful avenue for investigating the correlation of dispersal and lineage diversification at the population and clade levels.

#### References

1. Crowson, R.A. (1981). *The Biology of Coleoptera* (London: Academic Press).
2. Hunt, T., Bergsten, J., Levkanicova, Z., Papadopoulou, A., John, O.S., Wild, R., Hammond, P.M., Ahrens, D., Balke, M., Caterino, M.S., *et al.* (2007). A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. *Science* 318, 1913-1916.
3. Farrell, B.D. (1998). "Inordinate fondness" explained: why are there so many beetles? *Science* 281, 555-559.
4. Ikeda, H., Nishikawa, M., and Sota, T. (2012). Loss of flight promotes beetle diversification. *Nat. Comm.* 3, 648.
5. Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (London: John Murray).
6. Darlington, P.J. (1943). Carabidae of mountains and islands: data on the evolution of isolated faunas and on atrophy of wings. *Ecol. Monogr.* 13, 37-61.
7. Den Boer, P.J., Huizen, T.H.P.V., Boer-Daanje, W.D., Aukema, B., and Biemen, C.F.M.D. (1980). Wing polymorphism and dimorphism in ground beetles as stages in an evolutionary process. *Entomol. Gener.* 6, 107-134.
8. Roff, D.A., and Fairbairn, D.J. (1991). Wing dimorphisms and the evolution of migratory polymorphisms among the Insecta. *Am. Zool.* 31, 243-251.
9. Roff, D.A. (1990). The evolution of flightlessness in insects. *Ecol. Monogr.* 60, 389-421.
10. Nilsson, A.N., Petterson, R.G., and Lemdahl, G. (1993). Macroptery in altitudinal specialists versus brachyptery in generalists - a paradox of alpine Scandinavian carabid beetles (Coleoptera: Carabidae). *J. Biogeogr.* 20, 227-234.

11. Southwood, T.R.E. (1962). Migration of terrestrial arthropods in relation to habitat. *Biol. Rev.* *37*, 171–214.
12. Liebherr, J.K. (1988). Gene flow in ground beetles (Coleoptera: Carabidae) of different habitat preference and flightwing development. *Evolution* *42*, 129–137.
13. Papadopoulou, A., Anastasiou, I., Keskin, B., and Vogler, A.P. (2009). Comparative phylogeography of tenebrionid beetles in the Aegean archipelago: the effect of dispersal ability and habitat preference. *Mol. Ecol.* *18*, 2503–2517.
14. Kamoun, S., and Hogenhout, S.A. (1996). Flightlessness and rapid terrestrial locomotion in tiger beetles of *Cicindela* L. subgenus *Rivacindela* van Nidek from saline habitats of Australia. *Coleopterists Bull.* *50*, 221–230.
15. Ikeda, H., and Sota, T. (2011). Macroscale evolutionary patterns of flight muscle dimorphism in the carrion beetle *Necrophila japonica*. *Ecol. Evol.* *1*, 97–105.
16. Roff, D.A., and Fairbairn, D.J. (2007). The evolution and genetics of migration in insects. *BioScience* *57*, 155–164.

Department of Entomology,  
Natural History Museum, Cromwell Road,  
London SW7 5BD, UK, and Division of  
Biology, Imperial College London,  
Silwood Park Campus,  
Ascot SL5 7PY, UK.  
\*E-mail: [A.Vogler@nhm.ac.uk](mailto:A.Vogler@nhm.ac.uk)

DOI: 10.1016/j.cub.2012.03.015