



# Rate of molecular evolution and life history traits of social insects

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Biology students traditionally learn that in animals, life history traits such as lifespan, body size, and lifetime reproductive output are correlated. Frequently, they also learn that life history traits have interesting and predictable relations with such physiological parameters as metabolic rate and somatic cell size and number. The old saying, “Live fast, die young”, encapsulates the idea that life history traits tend to correlate in predictable ways; for instance, small vertebrates have high metabolism, short lifespans, and breed quickly, whereas large ones have lower metabolism, long lifespans, and breed slowly. As more and more animal genomes are sequenced, it is interesting to think about which aspects of their molecular biology might also correlate with life history and physiology. One molecular trait that may correlate is a lineage’s rate of molecular evolution.

Rate of molecular evolution (RME) can be measured by the number of base changes occurring in a defined DNA sequence over a particular period of time. Identifying and counting substitutions is conceptually simple: homologous sequences are aligned and differences are tallied. By assuming that differences in DNA sequences between species arose since they last shared a common ancestor, we can estimate how many bases in these sequences changed since their last common ancestor. However, base substitution rate is not as straightforward a measure as it may appear. Mutations begin with a DNA lesion or other type of error, followed by faulty DNA repair. When errors are not repaired to the original DNA sequence, daughter cells inherit a mutation. Germline mutations that are preserved, especially those that spread to fixation, are recognized as substitutions in comparisons between ancestral and derived DNA sequences. The longer the time since two lineages diverged from their common ancestor, the more germline cell divisions have taken place, and the more opportunities there have been for mutations to be preserved as substitutions. Therefore, life history traits

that influence the number of germline cell divisions, such as generation time or lifetime reproductive effort, seem especially likely to influence rates of molecular evolution.

In social insects, generation time and brood productivity are linked closely to social behaviour. Solitary species and species with simple sociality tend to have annual life cycles and produce small numbers of offspring during a reproductive lifespan that lasts only a few weeks or months. Hypersocial species (Batra 1977) provide a dramatic contrast—these often live in huge colonies with queens that may produce thousands or even millions of eggs over lifespans measured in years or decades. Their long reproductive lifespans lead to longer generation times and fewer cell divisions per unit time, than in solitary or simple social insects. This generates the prediction that RME should be negatively correlated with colony size. On the other hand, since hypersocial queens do produce huge numbers of eggs, the number of cell divisions per unit time might be considerably higher than predicted by generation time. If so, then RME might be uncorrelated or even positively correlated with colony size. Of course, generation time is not the only factor influencing whether mutations are preserved as substitutions—natural selection and drift influence the fate of mutations that result in changes to the amino acid sequences. Selection removes non-synonymous mutations with negative consequences and preserves those with positive consequences, but how efficiently this happens depends on effective population size ( $N_e$ ). Non-synonymous changes are removed more efficiently at large  $N_e$  than small  $N_e$ , so another way that social traits could influence RME is via their influence on  $N_e$ .

In this issue, Ben Rubin (2022) presents a comprehensive study providing some of the best evidence so far that rate of molecular evolution is influenced by life history and social traits. Rubin examined the relationship between colony size and RME with whole genome comparisons of 26 species representing three independent clades of social insects: the ant genus *Pseudomyrmex*, fungus-growing ants, and bees. The data set represents all levels of hymenopteran sociality, from solitary, annual bees in which mothers produce few offspring (often less than 10), to hypersocial ants and

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honeybees, with perennial colonies and queens that may lay thousands or millions of eggs. These life history differences correlate with both generation time and number of cell divisions. Using whole genome and individual gene alignments, Rubin measured RME using three different measures of the substitution rate, namely  $dS$  (the rate of synonymous substitutions),  $dN$  (non-synonymous substitutions), and  $dN/dS$  (the ratio of synonymous to non-synonymous substitutions), all standard measures in molecular evolutionary studies. He then mapped both colony size and evolutionary rate on phylogenies which enabled correlations to be calculated using phylogenetically independent contrasts. In all three clades examined, colony size was correlated positively with  $dS$ , uncorrelated with  $dN$ , and negatively correlated with  $dN/dS$ .

The consistency of these correlations across ants and bees, is quite remarkable, given that these clades represent independent origins of eusociality and independent transitions to hypersociality. This suggests a common underlying explanation for the correlations with colony size. One thing that complex ant and bee hypersociality have in common are that queens produce enormous numbers of eggs, more or less continuously for years. This entails many cell divisions

per generation, which in general should lead to higher substitution rates. Another shared trait is extreme reproductive skew, which, at least in less populous species, might depress  $N_e$ , which also should lead to higher substitution rates. We cannot yet distinguish among these alternative possibilities, because there are few empirical data on generation time, numbers of cell divisions per generation, or  $N_e$ . Nevertheless, Rubin's study provides strong evidence for correlations between life history, sociality, and molecular traits, pointing to new connections among different levels of organismal organisation, from DNA sequences to behaviour.

## References

- Batra SWT (1977) Bees of India (Apoidea), their behaviour, management and a key to the genera. *Orient Insects* 11:289–324. <https://doi.org/10.1080/00305316.1977.10433811>
- Rubin BER (2022) Social insect colony size is correlated with rates of molecular evolution. *Insect Soc.* <https://doi.org/10.1007/s00040-022-00859-3>