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Is evolution predictable?

Simple traits may not have simple, predictable evolutionary paths

By **David Reznick¹** and **Joseph Travis²**

Forty years ago, Anderson (1, 2) and Poole (3, 4) debated the value of predictive models for understanding population dynamics in a temporally varying environment. Poole argued that he could predict the future with high confidence if he had a good record of the past. Anderson (1) expressed doubts. He pointed out that long-term predictions will hold only if past conditions persist into the future. He also argued that although sophisticated statistical models may be able to predict the future, they do not tell us why they succeed or, more pointedly, why they fail. Without deep biological understanding of the system under

study, predictive models are not likely to offer much insight into either the past or future. On page 765 of this issue, Nosil *et al.* (5) apply the same scrutiny to evolution.

Evolution is like population dynamics because evolutionary change over time can be governed by multiple factors, the relative influence of which vary over time. Nosil *et al.* used a series of observational data taken over 25 years on natural populations in combination with experiments to show that in one case, evolution can be predicted very well, but in another, it cannot. More generally, they show that without deep biological knowledge, we cannot understand either past or future, much less predict the future from the past.

The authors worked on the stick insect *Timema cristinae* in the chaparral biome of California. There are three color combinations: uniform green, green with a white stripe, and melanic (dark gray) (see the photos). These insects feed and live on *Adenostoma fasciculatum* (chamise, or greasewood) or *Ceanothus spinosus* (greenbark or redheart). They are small (2 to 3 cm), wingless, and not very mobile, so each shrub or clump of shrubs is a semi-isolated community. The striped morph is most cryptic (camouflaged) and abundant on *Adenostoma*, whereas the green form is most cryptic and abundant on *Ceanothus*, but both morphs can be found on both plants. The melanic morph is found at low frequencies on both types of shrubs but predominantly on the gray trunks of *Adenostoma* (6).

This species has become a model for the study of local adaptation (6, 7). The poor

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A green-striped stick insect rests on chamise, the host plant on which this color morph is most abundant (left). Green, unstriped, and melanic color morphs of the stick insect are shown (right).

mobility of the stick insect, the patchy distribution of host plants, and the visual predators of these insects combine to maintain the associations between morph frequencies and host plant (6). In addition, local populations are under strong selection to adapt to the chemistry of the host plant; this contributes to reduced interbreeding and possibly incipient reproductive isolation between populations adapted to either species of plant, which can be a step to forming new, host-specific species (8).

Nosil *et al.* demonstrate that these stick insects undergo direct selection based on color and pattern (the presence or absence of the stripe). They identified a region of the genome in which variants are associated with the color and pattern morphs. There are three alleles at this “mel-stripe” locus, corresponding to unstriped (u), striped (s), and melanic (m). U is dominant to s, and s is dominant to m. The u/u, u/s, and u/m genotypes are green and unstriped, the s/s and s/m genotypes are green and striped, and the m/m genotype is melanic. In three experimental field studies, they found that the short-term changes in al-

lele frequencies at this locus were significantly faster than those in similarly sized segments of the genome, indicating ongoing selection.

Because they could genotype all individuals, they could estimate the relative fitness of each genotype, not just the fitness of the different morphs. In an experiment on adult survival within a generation, they found that the s/s genotype had the highest fitness, but the s/m genotype had close to the lowest relative fitness among the six genotypes. In an experiment that spanned two generations (2 years) of stick insect, they found that s/s and s/m were nearly equal in fitness and both had higher fitness levels than the other four genotypes. The two genotypes s/s and s/m have the same phenotype (green striped), so the dramatic change in fitness of s/m between experiments indicates that there is more at stake with this portion of the genome, either because the color locus affects more than color or because there is a closely linked locus that in turn has a large effect on fitness.

The authors then investigated whether the past can predict the future. Using an 18-year data set of morph frequencies from one locality, they examined whether temporal patterns early in the series predict the patterns later in the series. When they applied the analysis to color by comparing the abundance of green (both striped and unstriped) versus melanic, they were able to predict the abundance of the color morphs. Although the data were a significant match to the predictions, the match was weak: The past predicted, on average, 14% of the variation occurring years in the future. The predictive power improved slightly when the authors incorporated spring temperatures in the model because warmer, drier springs were associated with an increase in the abundance of the melanic morph.

The past was far more successful in predicting the future in the relative abundance of green striped versus green unstriped morphs. It accounted for 80 to 95% of the variation in future abundances. The trajectory had a distinctive, sawtooth pattern, with the frequency of the striped morph consistently

rising then falling on alternate years. This pattern suggests negative frequency-dependent selection (NFDS), or selection in favor of a phenotype when it is rare but against the phenotype when it is common. This type of selection on color pattern has been described in earlier studies of other animals, such as the snail *Cepaea nemoralis* or guppies (*Poecilia reticulata*) (9, 10). It happens because some predators preferentially feed on the most common morph, which gives rare color morphs an advantage, but only for as long as they are rare (11, 12).

Nosil *et al.* tested the NFDS hypothesis by introducing striped and unstriped morphs on to *Adenostoma* in either 1:4 or 4:1 ratios. Striped morphs had much higher survival when rare, but the two morphs did not differ in survival probability when striped was more common, fulfilling half of the conditions for NFDS. The authors suggest that perhaps the ratios needed to be more extreme for striped morphs to lose their advantage when common.

Questionable predictability is not specific to stick insects. Nosil *et al.* analyzed data sets for other long-term studies of evolution in various species, including Galapagos finches and the peppered moth, and show that they also offer low temporal predictability. In these cases, the likely cause is also multiple forms of selection the strength of which varies over time.

These results show that an iconic example of a simple trait subjected to a single agent of strong selection is actually much more complicated. Similar lessons have been taught by other seemingly simple phenomena. For example, the complex ways in which known agents of selection on the color polymorphism of *Cepaea* snails meant that “each population is subject to a unique explanation” (10). This is in stark contrast to studies of microbial, viral, and immune system selection, for which evolution seems to be highly predictable (13). Why this is the case, when it is not so in organisms such as stick insects and others, is a new challenge for evolutionary biologists. ■

REFERENCES

- O. D. Anderson, *Theor. Popul. Biol.* **14**, 68 (1978).
- O. D. Anderson, *Theor. Popul. Biol.* **13**, 179 (1978).
- R. W. Poole, *Theor. Popul. Biol.* **9**, 25 (1976).
- R. W. Poole, *Theor. Popul. Biol.* **13**, 190 (1978).
- P. Nosil *et al.*, *Science* **359**, 765 (2018).
- C. P. Sandoval, *Evolution* **48**, 1866 (1994).
- C. P. Sandoval, *Biol. J. Linn. Soc.* **52**, 341 (1994).
- P. Nosil, B. J. Crespi, C. P. Sandoval, *Nature* **417**, 440 (2002).
- B. A. Fraser *et al.*, *J. Evol. Biol.* **26**, 2597 (2013).
- J. S. Jones *et al.*, *Annu. Rev. Ecol. Syst.* **8**, 109 (1977).
- J. A. Allen, *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* **319**, 485 (1988).
- S. A. Langley *et al.*, *Oecologia* **150**, 172 (2006).
- M. Lässig *et al.*, *Nat. Ecol. Evol.* **10.1038/s41559-017-0077** (2017).

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