things unknown, and in between are the doors of perception''.

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Behavioral Evolution: Can You Dig It?

Michael J. Sheehan*, Caitlin H. Miller, Caleb C. Vogt, and Russell A. Ligon
Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853, USA
*Correspondence: msheehan@cornell.edu
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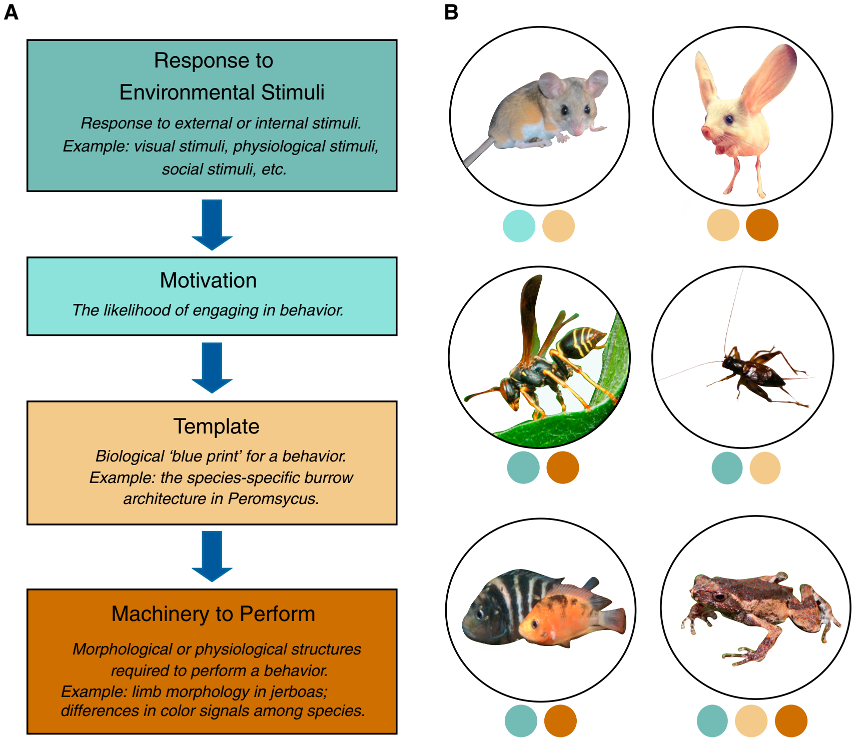
Behaviors are among the most complex phenotypes, making the genetic dissection of behavioral differences extremely challenging. A careful dissection of ontogenetic differences in burrowing behavior between mouse species highlights the importance of integrative approaches to the study of behavioral evolution.

A major goal of researchers studying the evolution of behavior is to link mutations to specific changes in complex behavioral traits [1]. Behavioral evolution may involve changes in sensory systems, in the brain or even anatomical changes in the structures used to carry out a behavior (Figure 1). This complexity often requires significant efforts just to describe behavioral differences between species, let alone to map them genetically. For example, detailed analyses of schooling differences between marine and freshwater sticklebacks revealed multiple distinct behavioral modules that had evolved to reduce schooling in freshwater sticklebacks [2]. Similarly, courtship songs from closely related *Drosophila* species differ in multiple features, controlled by distinct loci [3]. Increasingly, it is clear that careful dissection of the behavioral differences between species is key to linking mutations to changes in specific aspects of behavioral phenotypes. A new study by Hillery Metz, Hopi Hoekstra and colleagues [4] in *Current Biology* details the ontogeny of burrowing in two species of deer mouse and suggests that one locus may influence the motivation to dig burrows. This provides a potential link between the genomic and neuronal architecture of behavioral evolution.

Efforts to uncover the genetic basis of complex behavioral adaptations have been especially fruitful drawing on natural diversity in North American deer mice (*Peromyscus* Spp.). Hopi Hoekstra and colleagues have tackled the genetic differences in burrow architecture [5] between two closely related species of deer mouse, *Peromyscus maniculatus*



Current Biology

Figure 1. Targets of behavioral evolution.

(A) Targets of behavioral evolution span the steps from the detection of stimuli through the production of behaviors. In many cases behavioral evolution will involve selection on multiple steps. (B) Examples highlighting the proposed targets of selection with evidence to suggest selection acting strongly at one or more levels, from top: burrow digging in deer mouse [4,6] (photo: Gregory "Slobirdr" Smith/Flickr by a CC BY-SA 2.0); and escape behavior in jerboas [8] (photo: Soozle Bea/Flickr by a CC BY-SA 2.0); individual recognition in *Polistes* paper wasps [9,10] (photo: Hectonichus/Wikimedia Commons); male chirping and female preferences in crickets [11]; color-based mate choice in cichlids [12] (photo: Ad Konings); and calling in frogs [13] (photo: Mike Pingleton/fieldherping.org). Colored circles indicate potential targets of behavioral evolution.

and *Peromyscus polionotus.* Most *Peromyscus* species tend to dig simple burrows featuring a short entrance tunnel and a modest nest chamber [6]. The architecture of *P. polionotus* burrows differs from its close relatives by a much longer entrance tunnel and the presence of a second escape tunnel. Work in the 1980s demonstrated that differences in burrow architecture had a strong genetic basis [7], but the loci involved were not identified. More recently, mapping of quantitative trait loci (QTL) has demonstrated that complex differences in the size and architecture of burrows between *P. maniculatus* and *P. polionotus* are controlled largely by just four loci [5]. The challenge now is to work out the phenotypic consequences of each QTL.

Broadly, behavior can evolve through changes in four different processes (Figure 1): the sensory perception or processing of stimuli, the threshold or motivation to respond to stimuli, the template for behavioral output or the morphological or physiological effectors of the behavior. The challenge of identifying the mechanisms of behavioral evolution is a general problem for behavioral genomics studies. In the case of deer mice, adults of both species readily dig burrows when given the opportunity, which suggests sensory differences are an unlikely cause. One of the previously identified QTL explains the presence or absence of an escape tunnel, suggesting differences in burrowing behavior are driven, at least in part, by the presence of different 'blue prints' or behavioral templates between the two species. The ontogenetic study of burrowing reported by Metz and colleagues [4] provides further support for genetically encoded alterations to the burrow's architectural 'blue print', as well as changes in the motivation to dig.

The authors report genetic differences in the onset of burrowing behavior between the two species of mice. *P. polionotus* not only build larger and more complex burrows but start burrowing nearly two weeks earlier, despite being the smaller and more slowly maturing of the two species. That only burrowing behavior is accelerated in the otherwise less developed *P. polionotus* juveniles argues against any morphological or physiological adaptations for increased burrowing. Some of the juvenile *P. polionotus* build smaller versions of adult burrows, including escape tunnels. These miniature but architecturally complete burrows persisted even in cross-fostered mice, providing further evidence that the differences in burrow architecture are genetically encoded and not the result of learning.

Through multiple generations of inter-species mating the authors were able to show that adult burrowing behavior that is more like that of *P. polionotus* is genetically correlated with the earlier onset of burrowing. This suggests that either a pleiotropic locus influences both development and adult performance or that the loci influencing each trait are tightly linked. Indeed, one of the four previously published QTL [5] influencing adult burrow construction is significantly associated with the onset of burrowing in juveniles. This connection is interesting and surprising in its own right. Many juvenile *P. polionotus* show robust burrowing behavior at only 17 days, nearly a week before they are weaned. Many behaviors are expressed at a specific life stage (e.g. begging, courtship), and as such there is no reason to expect that the onset of burrowing and the mode of adult burrowing would be genetically correlated. This genetic correlation makes it hard to understand the selective pressures leading to *P. polionotus* burrowing behavior — does selection favor earlier burrowing behavior, more elaborate burrows, or both? However, the link between the age of burrowing onset and adult burrow construction suggests the underlying QTL may influence the motivation to dig.

Ideally, we want to know the nature of genomic changes underlying behavioral evolution: How many loci contribute to behavioral changes and what is the distribution of effects? Do behavioral differences tend to involve coding or regulatory mutations? Do similar behaviors across lineages evolve via convergent mutations in the same genes or pathways? Mutations influencing behavior may act to differently organize neural circuits during development or may alter the function or sensitivity of structurally similar circuits. Determining how mutations lead to behavioral changes will require functional developmental studies. For organisms with even modestly long developmental times such as mice or other interesting cases of behavioral evolution (Figure 1), it is prohibitively time intensive and expensive to sample all of neuronal development. Carefully conducted studies of the development of genetically controlled behaviors such as the one reported by Metz and colleagues [4] have the potential to dig away at the genetic basis of adaptive behavioral evolution by allowing for more targeted functional studies. Importantly, functional genomic studies of developing brains will not only provide evidence of how QTL are influencing neural development, but may also help pinpoint the causative mutations within QTL peaks in conjunction with population and comparative genomic data.

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Bird Migration: Life on the High Seas

Stephen Votier
Environment and Sustainability Institute, and Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Cornwall TR10 9EZ, UK
Correspondence: s.c.votier@exeter.ac.uk
https://doi.org/10.1016/j.cub.2017.11.032

Migratory animals show great diversity of movement within populations, but the causes and consequences of this variability are poorly understood. Tracking a migratory seabird across its range reveals how environmental, latitudinal and demographic conditions shape migratory journeys and fitness.

Migration is one of the greatest spectacles in the natural world. Found across a huge diversity of animals from butterflies to birds and wildebeest to whales it involves the transfer of huge amounts of biomass in space and time [1], often over vast distances [2]. As well as variation among species, there is also great variation within the same species [3]. Understanding the drivers of this variation and how they impact on the demographic process is central to the study of animal migration, but studies shedding light on this are about as common as the proverbial hen's teeth. In a new paper in *Current Biology,* Annette Fayet, Tim Guilford and colleagues [4] study in detail the migration patterns of Atlantic puffins (*Fratercula arctica)* in several populations across this seabird's range.

Tracking individual animals with tags, known as 'bio-logging' [5], has revolutionised our understanding of animal movement [6], and has the potential to address fundamental questions about variation in migratory