PHARYNGULA

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ON EXTRAVAGANT PROPORTIONS

Scarab beetles show the influence of genes on the predictability of proportion, even in the face of disruptive environmental influences.

There is a classic Three Stooges film in which they play bumbling plumbers trying to repair some leaky pipes, and, of course, everything goes wrong. Patching a leak in one place sends water spraying out elsewhere; tugging on a pipe sends the faucet in another room flying out of the wall. It's classic slapstick. It wasn't intended to be deep (and I didn't watch it for a lesson in science!), but it does hold a message that applies to biology: In complex systems, everything is interconnected, and sometimes in surprising ways. Changes to one genetic module can cause effects to ripple throughout the entire organism.

This shouldn't be surprising. In a relationship called allometry, one expected feature of developing embryos is coordinated growth, with different subsystems communicating with one another constantly, negotiating with one another to establish their proper relative proportions. The allometric rules for an animal define how large a particular organ should be, given a particular body size, and they specify how body parts should scale relative to one another. These rules define your proportions: how long your arms should be for a given height, for instance, and for that same height, how long your legs should be. What's required for this to work is that there be interconnected regulators of growth that affect many tissues.

While it means that growth is coupled across the organism, it also implies that there may be tradeoffs. An embryo does not have an infinite amount of energy or growth factors, and changes in the allometric rules therefore should have consequences. One might imagine that trying to change the scaling of a human being to have longer legs for a given height, for instance, might mean legs consume more energy during growth, at the expense of the other set of limbs, the arms. As with the Stooges, trying to pull one pipe forward might mean another gets sucked back into the wall.

Since we can't do that kind of experiment on people, though, we have to look for an alternative, and a beautiful one presents itself: scarab beetles of the genus Onthophagus.

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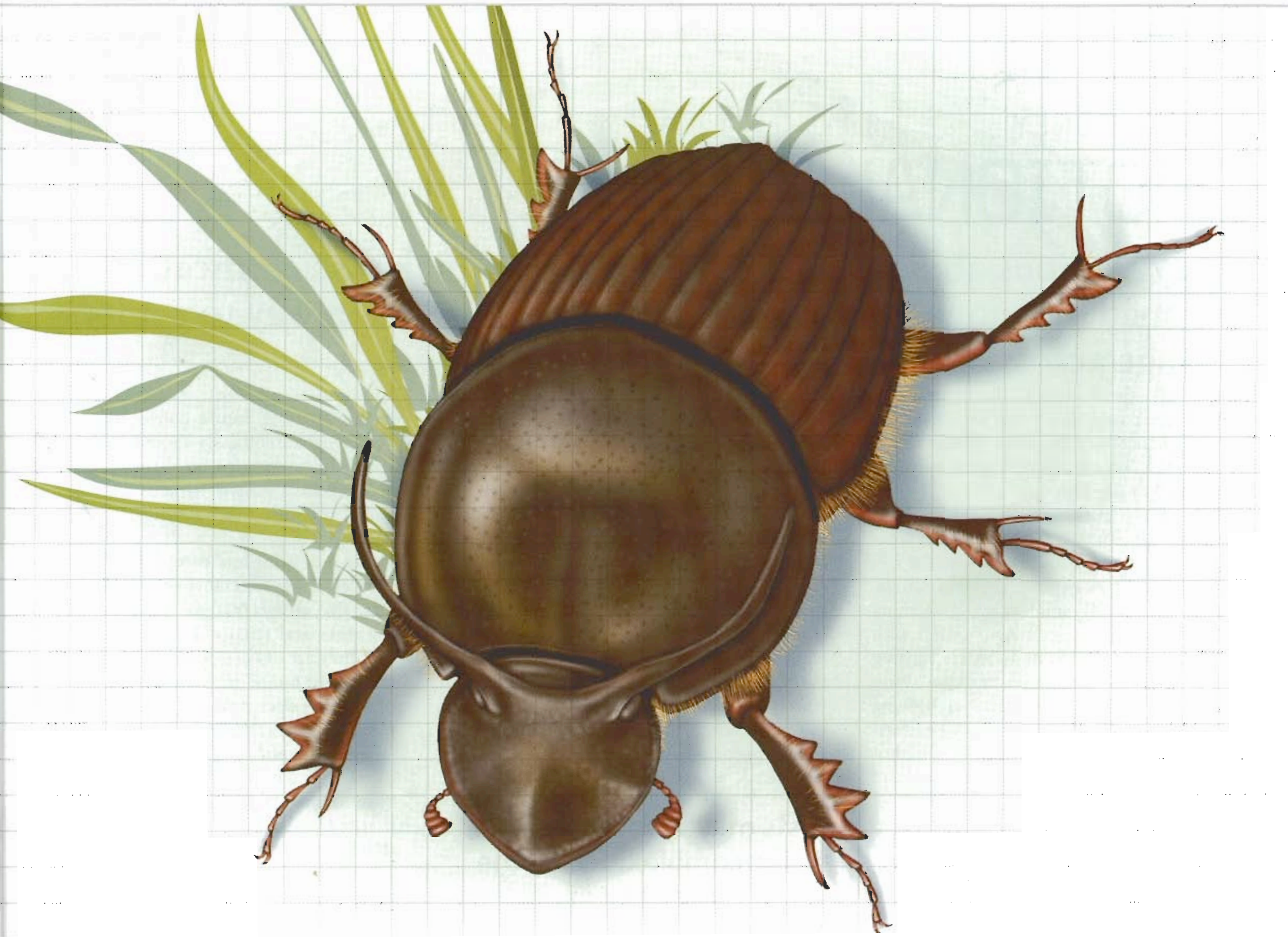
These animals have intense mating competitions in which the males guard their mates to prevent them from breeding with competitors, and they have evolved extravagant weapons for use in battles between males. They have long horns that they use for blocking tunnels to underground dens and for wrestling with competitors, and different species have followed different strategies. Some have a horn at the front of the head and look rhinoceros-like; others sprout a pair of horns, like those of a triceratops, at the back of the head; still others have a long protuberance from their thorax that can make up as much of 40 percent of their body length. These prominent pieces of body armor represent a substantial investment in development. Are there any costs incurred for building them?

Yes, there are. In onthophagine species with horns on the anterior part of the head, horn size is negatively correlated with the size of the antennae, as if the investment in growth of a cuticular horn deprived nearby structures of resources. Similarly, large horns at the back of the head were associated with reduced eye sizes, and thoracic horns were made at the expense of the wings. As a consequence of the interconnectedness of development, shifts in the proportions of one structure are going to have an effect on other structures.

These tradeoffs have been tested experimentally, too. *Onthophagus nigriventris* is a species with a prominent thoracic horn. Simmons and Emlen took larvae, at a stage termed "late instar," and cauterized the patch of cells that would generate the horn, thereby producing hornless beetles. Losing that horn meant the cauterized beetles actually grew *larger* on average than control beetles, by about 25 percent.

In addition, the animals' testes grew disproportionately larger—that is, by significantly more than the 25 percent that one would expect if they were scaling linearly with body size. Conversely, removing the larval genital capsules enhanced horn growth. Horns and testes have an inverse size relationship.

This, then, raises some interesting questions in mating strategy. The horns are used to guard mates and ensure exclusivity of fertilization, but if large horns lead to tiny testes, the animals face a problem of diminishing returns. What's the point of a male's quaran-



tining a mate for exclusive reproductive goals if he is compromising his fertility? The arms race can be counterproductive. Some of the species have "discovered" this contradiction and have males that don't make horns at all but, instead, have larger testes. They are called sneaker males and rely on quick matings that give their sperm an opportunity to compete with the sperm of the large-horned males. Having larger testes and more sperm gives them an opportunity to outnumber the big-horned males where the horn doesn't matter—in the female reproductive tract.

There is a clear-cut developmental linkage between horn size and testes size, but, intriguingly, the evolutionary link is different and more complicated. After noting that within-species variation in the size of horns and testes was inversely correlated, researchers surveyed 25 species of *Onthophagus*, which vary in horn size from species to species, to see if the inverse correlation still held in between-species comparisons—that is, if a beetle species exhibits particularly large horns, are its testes relatively small for its body size, and vice versa? The interesting result is that no, the correlation does not hold up. Suddenly, the robust linkage we see within a species disappears when we look at species that have had many generations to adapt.

The explanation is that there is another, subtle kind of tradeoff going on, between *plasticity* and *canalization*. Developmental phenomena that are plastic are highly responsive to genetic and environmental conditions, or to chance—they can vary more under differing situations. Canalized processes are more tightly locked in by genetic mechanisms and are relatively inflexible; they will show much less variation.

In the large-horned species of beetles, one way to get around the problem of the progressively shrinking testis is to incorporate more mechanisms that regulate the growth of the testis and compensate for the fact that the horn is monopolizing nutrients and growth factors. The addition of these genetic regulators would make the growth of the testis more canalized, which would mean that one would also expect that large-horned beetle species would also show less within-species variation in testis size. Simmons and Emlen also examined the degree of canalization of the testis and discovered that the evolutionary prediction is fulfilled: Beetles had evolved tighter regulation of the growth of the gonad as they invested more energy in the growth of secondary sexual characteristics like horns.

The competition between developing weapons and testes is the most obvious aspect of the evolution of these beetles, but the quieter underlying competition between reliability/canalization and flexibility/plasticity may well be the more significant force in evolution: It constrains the range of morphology that is possible in development. ∞