How 'secondary' sex characters can drive the origin of species

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The ostentatious, sometimes bizarre qualities that improve a creature's chances of finding a mate may also drive the reproductive separation of populations and the evolution of new species, say two Indiana University Bloomington biologists.

In the September 2008 issue of *Evolution* (now online), Armin Moczek and Harald Parzer examine males from four geographically separated populations of the horned beetle species Onthophagus taurus. The beetles have diverged significantly in the size of the male copulatory organ, and natural selection operating on the other end of the animal -- horns atop the beetles' heads -- seems to be driving it.

Shown are males of four of the 10 Onthophagus species examined in the study. From top to bottom: O. watanabei (North Borneo), O. taurus (Mediterranean), O. gazella (South Africa), and O. sagittarius (Indonesia). Credit: Armin Moczek

"Biologists have known that in these beetles there is an investment trade-off between secondary sexual characters and primary sexual characters,"

Moczek said. "As horns get bigger, copulatory organs get smaller, or vice versa. What was not known was how frequently and how fast this can occur in nature, and whether this can drive the evolution of new species."

Structures directly involved in mating are known as primary sexual characters, whereas combat structures like horns -- or seductive attributes like a cardinal's vibrant plumage or a bullfrog's deeply resonant baritone -- are known as secondary sexual characters.

Evolutionary biologists believe changes in copulatory organ size and shape can spur speciation by making individuals from different populations sexually incompatible.

Native to Italy, O. taurus exists in other parts of the world only because of recent human activity. This means, Moczek and Parzer say, that the marked divergences they observed in O. taurus's horn and copulatory organ size must have occurred over an extremely short period of time -- 50 years or less.

Despite what many of us are led to believe, variation in male copulatory organ size within species tends to be very low, humans and beetles included. Yet the four O. taurus populations Moczek and Parzer studied in the U.S. (North Carolina), Italy, and western and eastern Australia, exhibit substantial changes in both horn and genitalia length -- as much as 3.5 times, in terms of an "investment" index the scientists devised that takes body size into account.

The scientists examined 10 other Onthophagus species, and as expected, they found vast differences between the species regarding horn and male copulatory organ size. Moczek says this suggests that trade-offs between primary and secondary sexual traits continue to shape the way species diverge well after speciation has occurred.

The speed and magnitude of divergence within O. taurus presents something of a paradox. How is it that copulatory organ size can be so rigorously maintained within the populations of a single species, yet appear so restless to change?

"In terms of the integrity of a species, it's important for these things not to change too much," Moczek explains. "So there is a lot of evidence suggesting that within species or within the populations of species, natural selection maintains genital characters. But if these primary sex characters are linked to other characters that can change readily, then you've got what we think is a very exciting mechanism that could prime populations for reproductive isolation."

Horn length and shape can change for many reasons, Moczek says. Among densely populated species, fighting (which favors large horns) may not be an effective strategy for winning mates. As combative males fight each other, a diminutive, smaller-horned male could simply employ a sneaking strategy to gain access to unguarded females. Under these circumstances, reduced investment in horns seems to result in larger copulatory organs. Alternately, in lower density populations, most male beetles spend a great deal of time fighting. Longer, bigger horns could serve these males well -- and also lead to smaller genitalia.

"If this is all it takes to change genitalia, it may be easier to make new species than we thought," Moczek said.

The notion that genital size is related to the origin of species is not new. But how they are related has perplexed evolutionary biologists. The individuals of most species do not choose mates according to the size and shape of genitalia. Indeed, genitalia may not be relevant until the latter stages of courtship, if at all.

An early "lock and key" model of reproductive isolation was first

proposed by L. Dufour in 1844 to explain why some pairs of species, outwardly identical in every way, are unable to mate.

Source: Indiana University