Why Female Water Buffalo Have Horns but Impala Do Not?

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(PhysOrg.com) -- The reason some female hoofed animals have horns while others do not has long puzzled evolutionary biologists, even the great Charles Darwin. But now a survey of 117 bovid species led by Ted Stankowich, professor at the University of Massachusetts Amherst, suggests an answer: Females that can't readily hide in protective cover and those who must defend a feeding territory are more likely to have horns than those who live in protective habitat or don't defend a territory.

The idea that horns and antlers evolved in male animals for fighting over mates and territories is well established, but until now no study has been able to come close to explaining every case of female horns in antelope, gazelles and similar species, says Stankowich, a former Darwin Postdoctoral Fellow. But that is just what he and co-author Tim Caro of the University of California Davis have done.

By developing the conspicuousness measure—the product of openness of habitat and shoulder height—as well as female territoriality for this analysis, Stankowich and Caro say they can explain "nearly every instance of horns in female bovids (80 of 82 species)." Their article appears in the current issue of the Proceedings of the Royal Society B. Results suggest that the evolution of horns in these females is driven by natural selection to enhance their ability to defend themselves and their young against predators. The two researchers are the first to specifically test female territoriality as a possible factor, Stankowich notes.

Other variables to explain female weaponry such as body size and group size had been tested before, but Stankowich and Caro pitted all the hypotheses against each other in a statistical analysis and found conspicuousness was the best predictor of the pattern.

In developing the conspicuousness measure, the researchers hypothesized that taller species living in the open are more visible from longer distances and more likely to benefit from horns to defend themselves against predators. “We show that female bovids that are conspicuous to predators because they are large or live in open habitats are far more likely to bear horns than inconspicuous species that can simply rely on being cryptic or hidden in their environment. However, females of some small species like duikers in which females fight over territories also bear horns,” says Stankowich.

Past hypotheses about horns evolving for defense in females predicted that only heavy species are able to defend themselves and would benefit from horns. “Our study shows that it is not necessarily the animal’s size but rather its conspicuousness that counts most, and this is a product of the openness of habitat and body height,” Stankowich adds.

Thus, a medium-sized species living in the desert like a gazelle is very conspicuous and could benefit from horns, but a large species living in the dense jungle like a bushbuck can still remain hidden from predators and have no use for horns. “Different selection pressures are responsible for diverse weaponry in ungulates,” Caro and Stankowich summarize.

Specifically, to investigate factors involved in the evolution of weaponry in female bovids, Stankowich and Caro first categorized the females of 117 bovine species as horned or not. They then used a series of statistical steps to test how well the different predictive variables matched the presence or absence of horns in each species.

Their first analysis tested shoulder height and habitat openness separately, but they also designed a composite measure that accounted for shoulder height while weighting openness more heavily. This exposure metric multiplied a species' shoulder height measurement factor by mean openness of primary habitat. It allowed bongos, a tall species living in dense forests, to score low on the scale, for example, while medium-sized species such as gazelles score in the middle and tall species in open country such as musk oxen score high.

Pitting the different variables against each other in a series of multiple linear regression models, Stankowich and Caro calculated phylogenetic contrasts for each factor and found that conspicuousness had a statistically significant effect on presence of horns in females and the greatest effect among the five variables. The use of phylogenetic contrasts meant the researchers could take species relatedness with one another into account.

Territoriality among females and body weight of the species also had a significant effect on the presence of horns. That is, large size may reduce escape speed and enhance the need for horns. However, shoulder height and group size did not have an effect.

The two exceptions identified by Stankowich and Caro are the female African bongo, large antelope found in dense forests which use their horns to establish dominance within female groups, and the female mountain anoa, a small water buffalo, which we know very little about but the females may indeed be territorial like other members of its genus (Bubalus). "Our goal was to explain EVERY instance and we think we did just that, given what we know about these two exceptions," notes Stankowich.

Overall, the two evolutionary biologists believe their findings may be relevant to other female ruminants, but further study is needed.