New model illuminates why some greater sage grouse males 'strut' better than others

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When it comes to mating displays, a little persistence can go a long way, at least for the greater sage grouse. In "Hidden Markov Models Reveal Tactical Adjustment of Temporally Clustered Courtship Displays in Response to the Behaviors of a Robotic Female," published in The *American Naturalist*, Anna C. Perry and her colleagues at the University of California in Davis (USA), the Max Planck Institute in Leipzig (Germany) and the University of Florida (USA) use a custom-built statistical model to understand an under-explored dimension of greater sage grouse mating display behavior. The authors report that males that show greater display persistence, even in the face of seemingly uninterested females, have a competitive advantage over their peers.

The greater sage grouse, a bird native to North America, has an elaborate courtship ritual. Every year, males congregate at locations known as "leks" to perform competitive mating displays to entice females to copulate. Each mating display, in which the male performs a series of ritualized movements and sounds with his air sacs inflated, is referred to as a "strut." These "struts" are typically performed one after another in quick succession, in what is referred to as a "bout." Mating success is highly skewed, with a percentage of birds never once mating and a privileged few mating dozens of times.

In studies that seek to understand why some individuals are so much more successful than others, researchers have often counted the total number of display events or averaged the lengths of the intervals separating displays within a bout. "These 'bout agnostic' analyses

collapse each animal's multidimensional display effort into a single metric, potentially discarding important information," Perry and her coauthors write.

Perry's custom-built hidden Markov model, on the other hand, offered several advantages over simpler models. For one, it accounted for differences in display persistence—characterized by the number of "struts" that a sage grouse does in a row—as well as the length of time that males rested between struts in a single bout. It also enabled Perry and her coauthors to analyze whether males' display tactics changed depending on the presence and behavior of females.

Strut events were recorded using high definition cameras and on-site observations at three leks in Fremont County, Wyoming. At each location, male display activity was tracked when no female was present, when a robotic female was present and showing either "interested" or "uninterested" behavior, and in the presence of real female sage grouse. "Most males cannot display at their peak levels indefinitely; these males may need to tactically adjust their display bout behavior across different conditions," Perry and her coauthors write.

Perry and her colleagues found that the number of times a male consecutively struts in a bout was a better predictor of male mating success than either the length of time between struts or the average amount the male displayed overall. "In retrospect, this makes sense: within-bout display rates are relatively constrained, with 95% of intervals are between 5 and 9 seconds," Perry writes. "Bout length, on the other hand, varies widely, from 2 struts to more than 20."

Perry and her colleagues also found that sage grouse females seem to prefer males that show greater display persistence, specifically when a female is in close proximity, regardless of whether or not her behavior indicates she's interested in copulation. Males with lower mating success

tended to have a higher "baseline" display activity level when females were absent. When females were present, they tended to focus their display efforts on the ones who were already signaling their interest.

One possible explanation for this observation is that younger or lower quality males may need to allocate more display effort toward defending their territory and thus have less energy to expend on courtship. Another possible explanation is that males that mate more are able to do so because they are more skillful at tactically adjusting their display effort to invest more when females are present and in close proximity. Further studies are required to test these and other hypotheses.

Perry predicts her model will be useful for studying other species with complex mating displays. "Our hidden Markov model could prove especially enlightening for studying trade-offs in multiple, dynamic components of display effort," she writes.

More information: Anna C. Perry et al, Hidden Markov Models Reveal Tactical Adjustment of Temporally Clustered Courtship Displays in Response to the Behaviors of a Robotic Female, *The American Naturalist* (2019). DOI: 10.1086/703518

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