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Predator-prey dynamics: the role of olfaction, by Michael R. Conover.

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Book Review

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Predator-prey Dynamics: The Role of Olfaction. Michael R. Conover. 2007. CRC Press, Taylor and Francis, New York, NY, USA. 264pp. $89.95 [ISBN-13: 978-0849392702] (hardcover).

Many who study, pursue, work with, or live with mammals (particularly canids and ungulates) fantasize about being able to "see" the world as they do: primarily through the nose. Human olfaction is pathetic compared to the capabilities of many other animals. So, it is not surprising that our speech includes idioms like "hiding in plain sight" and "creeping silently past" but nothing akin to "scentless straight upwind." In "Predator-prey Dynamics: The Role of Olfaction," Michael Conover offers a glimpse into the olfactory universe inhabited by terrestrial animals (mainly mammals). Outlining the properties of this universe, Conover challenges the reader to consider that many wildlife activity patterns and habitat associations commonly explained in terms of resources, thermoregulation, or visual concealment could instead represent adaptations to avoid detection and location by olfactory predators (or, for olfactory predators, adaptations to detect and locate prey). Specifically, Conover hypothesizes that terrestrial prey threatened mainly by olfactory predators should match their locations and activities to places and times when atmospheric conditions are least conducive to olfaction, whereas olfactory predators should do the opposite.

The first half of the book mainly reviews the physical and chemical processes involved in olfaction, differentiates between finding prey via odor trails and plumes, and details the physical laws of fluid dynamics relevant to air flowing around objects and over surfaces. The level of detail in many places is probably excessive for most readers, and equations are often presented without being directly used to derive or highlight insights about how air and scent behave. Much of this material could have been profitably distilled to fundamental concepts and findings,

referring the truly keen reader to more detailed sources. Nonetheless, the reader is eventually shown how varying wind velocity, updrafts, and turbulence can be generated by spatial differences in surface temperature (as between south- and north-facing slopes, or between waterbodies and surrounding uplands) as well as wind blowing over hills and other topographic obstacles, shelterbelts, contiguous vegetation, and even isolated features like boulders or shrubs. Fortunately, each technical chapter ends by relating the micrometeorological concepts to testable, *a priori* predictions about the habits of olfactory predators and their prey.

Consider a staple of wildlife biology: the edge effect. Many animals spend a disproportionate amount of time near edges between different landcover types, and this pattern is typically explained in the context of access to multiple types of resources (e.g., food and cover). However, air flowing over a field is driven upward at the upwind edge of a forest patch and downward at the downwind edge, with turbulence enhanced at both edges (Chapter 7). Also, ground-level temperatures are higher in the field than under the forest canopy, producing convection that draws air out of the forest and carries it aloft. The scent of a prey animal at an edge may therefore be carried over a downwind predator's nose even at close range. In interior forest, however, the temperature difference between sunlit canopy and shaded floor produces an atmospheric inversion that holds scent close to the ground and accessible to predators (Chapter 8), like inversions over Los Angeles that concentrate smog near ground level. So, we must now consider the alternative hypothesis that olfactory conditions, instead of or in addition to resources, are why many prey animals prefer edges over forest interiors.

The reader may ask, are small-scale atmospheric disruptions really effective at impairing or befuddling olfactory predators? To support this assertion, Conover presents some inventive field experiments. In one, he used small electric fans to generate updrafts or cross-breezes at the

sites of bird carcasses and compared the ability of bird dogs downwind to find these versus control carcasses. In another he compared depredation by wild carnivores on artificial nests placed alone (control), next to a vertical garbage can (creating horizontal turbulence), or next to a garbage can laid on its side (creating vertical turbulence). In both experiments, sample sizes were small, but observed detection or depredation rates in turbulence treatments were 50% or more lower than in controls.

The second half of the book relates the physical and chemical principles back to predator-prey interactions and lists specific predictions that arise from the olfactory concealment theory. Conover acknowledges that animals are likely to confront tradeoffs between olfactory concealment and competing needs, as well as the fact that conditions favorable for olfactory concealment may enhance prey fitness by other mechanisms. He then reviews published field studies relevant to these predictions, finding some supported, others contradicted or with weak support, and still others entirely untested. In some cases, olfactory concealment provides a plausible explanation, but so do alternative hypotheses like thermoregulation or visual concealment. This section provides unbroken ground for other researchers to plow with clever empirical studies, particularly if attention is given to disentangling alternative explanations. Conover wraps up by redefining many common terms, such as habitat, edge, patch, etc., in terms of the physics of olfaction. This provides the potential to objectively define concepts that are sometimes used more subjectively, but some of the definitions will likely be a stretch for many wildlifers.

Despite the useful perspective this book conveys, the quality of writing and editing are inconsistent. Repetitive and redundant passages are common, and the structure across chapters is sometimes loose. Some terms (e.g., inclusive fitness) are misused and others (e.g., surface layer

and boundary layer) used inconsistently. A glossary would be a welcome addition. Sure to frustrate the quantitatively minded reader, Conover does not always define variables or give them units, and the notation is confusingly inconsistent in places (e.g., U is a velocity, but $U_{maximum}$ is a distance). Most of the diagrams and graphs (nearly 90 in all) are clear and useful, but some drawings are crude or difficult to decipher, and some concepts are illustrated in multiple graphs where one would do. Many of the more than 83 black-and-white photographs (of greatly varying quality) lack obvious connection to the text. For example, the statement "When given three footprints, the dogs guessed the wrong direction half the time (Figure 2.3)" directs the reader to a half-page photograph of a German shepherd, not the expected graph of direction-finding success.

Perhaps most disappointing was the number of speculative hypotheses presented as fact, such as unsupported olfaction-based explanations for human urges to gasp when frightened or to urinate in water. These explanations are at least plausible, but some of the hypotheses that Conover presents are much more far-fetched. For example, he contends without evidence (logical or empirical) that animals could determine distance to a scent source by detecting differential scent arrival times in the two nostrils or by moving their heads up and down, in olfactory analogies to stereoscopic vision and optical parallax. Such careless speculation detracts from the valuable contributions of this book.

Overall, this book seems to serve two functions. On one hand, it presents a synthetic view of how hunting and hiding in the olfactory universe shape animal behavior and habitat selection, with specific *a priori* hypotheses primed for empirical test. On the other, it serves as a repository for Conover's personal foray into the literature of fluid dynamics and micrometeorology. When scientists catch fire with ideas that lead them outside their original

expertise, there is often a strong temptation to document the entire journey. This book suffers from this temptation, with unnecessarily elaborate quantitative detail. However, I suspect that most readers will simply skim the gory details to glean the general patterns and novel viewpoints, and there lies the book's true value. It will be an important contribution to wildlife biology if readers are stimulated to conduct rigorous field studies to challenge long-held explanations for animal behavior patterns and habitat selection with an eye, or a nose, to the unseen world of scent.

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