## Special Feature: Linking capture-recapture and movement

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+---Author Manuscrip Many ecological systems are organized hierarchically, and a full understanding of ecological systems is contingent on our understanding of linkages across levels in these hierarchies. Consider the hierarchy whereby individual organisms are organized into populations. The dynamics of animal populations are influenced by individual-level processes such as establishment of home ranges and selection of habitat. These individual-level processes have important effects on demography, including reproduction, survival, emigration, and immigration, which collectively determine population dynamics. In turn, population dynamics influence how individual-level processes unfold; individual organisms are shaped by the populations they are a part of through forces such as resource competition and social interactions.

Our ability to investigate both population- and individual-level processes has seen substantial growth in recent decades. Since the early 2000s, the study of animal population dynamics has been transformed due in part to the growing field of spatial capture-recapture modeling. Capture-recapture (also referred to as "capture-mark-recapture", "mark-recapture", and related terms) is a large set of statistical methods commonly used by ecologists to estimate abundance and related demographic parameters when it is difficult or impossible to observe (or "detect") all individuals in a population. Spatial capture-recapture is an important extension in which both demographic processes and our (imperfect) observation of these processes are modeled as spatially explicit. Spatial capture-recapture models have expanded our capacity for studying populations and have provided new insights into how populations function in space. Similarly, the study of individual movement has advanced in recent decades, owing largely to the rapid development of animal tracking technology and the simultaneous development of advanced statistical models of animal movement for tracking data. Increasingly realistic models of animal movement have provided exciting new insights about individual behavior, habitat selection, and space use. However, despite the potential for integration of these two frameworks to revolutionize our ability to understand linkages between population- and individual-level processes, there has been relatively little integration to date.

In August 2019, we helped to organize a workshop at the University of Washington, with the express goal of advancing the integration of spatial capture–recapture and movement models. The papers in this Special Feature are an outgrowth of that workshop, are strongly influenced by it, or are based on independent work developed with similar goals. This collection of papers represents the state of the art in the integration of spatial capture–recapture and movement models. The papers demonstrate both the practical challenges of integrating these frameworks, as well as the benefits, from improved demographic estimates for populations with complex movement dynamics to novel ecological insights into how environmental and social forces shape populations through space use. The papers in this Special Feature range from conceptual to applied, and each includes practical insights into how to fit these relatively complex integrated models. In their review and synthesis, McClintock et al. (2021) highlight the advantages of linking individual- and population-level process models to facilitate new and exciting inferences at the intersection of movement, population, and landscape ecology. They establish a common notation

for the Special Feature and outline a general conceptual framework for the integration of spatial capture-recapture and animal movement models. They also identify potential challenges that lie ahead.

Gardner et al. (*in press*) implement complex movement processes — such as simple random walks, correlated random walks, and habitat-driven Langevin diffusion — within spatial capture-recapture models using data augmentation in a Bayesian analysis framework. Using simulation, they demonstrate that these models can perform well with spatial capture-recapture data alone, but that as movement model complexity increases, there will be a need for more intensive location data. Thus, they also show how to integrate auxiliary data from animal-borne sensors to improve parameter estimation over models fit with only spatial capture-recapture data. Theng et al. (2022) explore the consequences of realistic animal movement for inferences arising from standard spatial capture–recapture models of closed population abundance and density. By simulating individual-level responses to internal (e.g., memory, territoriality) and external (e.g., resource dynamics) drivers as animals move through the landscape, they demonstrate that spatial capture–recapture estimators of abundance can be robust to violations of assumptions induced by complex animal movement patterns as long as the resulting individual heterogeneity in detection is low. However, inferences about animal space use and home range size from standard spatial capture–recapture models can be problematic, and integrated spatial capture–recapture and animal movement models offer a potential solution.

Much of the focus of the Special Feature is on animals that move independently of one another. However, in group-living species (e.g., many canids and ungulates), animal movement is statistically dependent, violating assumptions of traditional spatial capture-recapture models. In order to generate unbiased estimates of abundance and group size with properly estimated precision, Emmet et al. (2021) develop a group-living spatial capture-recapture model based on a clustered point process. They test their model using simulation and then apply it to camera trapping data on African wild dogs. Although their model currently requires a few restrictive assumptions (e.g., that group membership is known), we share their optimism that such requirements can be relaxed in future applications and we anticipate that their contribution will lay the groundwork for many future studies of group-living species.

Focusing on landscape connectivity, Dupont et al. (2021) extend spatial capture–recapture models to accommodate a movement kernel based on "ecological distance" instead of Euclidean distance. Unlike other integrated approaches in the Special Feature (i.e., McClintock et al. (2021), Gardner et al. (*in press*), Hostetter et al. (*in press*), and Chandler et al. (2021)), Dupont et al. (2021) use a step-selection model and discrete-space approximation for movement that can be fitted using maximum likelihood methods. Though it incorporates some restrictive

assumptions, the model reduces computational burdens by avoiding the need to integrate over the latent movement paths during model fitting. This approach provides a straightforward modeling framework for including global positioning system (GPS) telemetry data to improve estimates of habitat-related cost functions.

Hostetter et al. (*in press*) were motivated by the practical need to estimate the density of animals that move over large spatial areas. Polar bears (*Ursus maritimus*) can travel hundreds of kilometers over the course of mere days, exhibiting movement dynamics that clearly violate the standard spatial capture–recapture assumption of a bivariate normal home range, and over areas that cannot be adequately sampled by available platforms. Using a combination of physical captures, resights, and telemetry data, they fit a series of integrated spatial capture–recapture movement models that specify more realistic movement processes, including simple and correlated random walks, and model the detection process over space and time conditional on movements. With this model, they provide robust estimates of movement and abundance for polar bears in the remote Chukchi Sea, as well as a framework for monitoring populations of highly mobile vertebrates in heterogeneous landscapes.

Inspired by a white-tailed deer (*Odocoileus virginianus*) study where GPS telemetry and camera trapping were employed in the same study area, Chandler et al. (2021) develop a hierarchical model that integrates both datasets into a single analysis. By conditioning both datasets on a common movement model, the authors are able to estimate abundance and movement parameters simultaneously. Importantly, they are able to account for heterogeneous space use by different animals in a way that is typically not possible with spatial capture–recapture data alone. We suspect that their approach will be especially useful for those wishing to study the synergy between demography and animal behavior, and to scale up inference about movement processes from individuals to populations.

As the articles in this Special Feature illustrate, there is tremendous potential for

modeling more realistic movement processes that integrate the social and environmental features of landscapes to which animals are responding, while using the insights that emerge from these processes to understand demography. Our hope is that the Special Feature inspires continued advances in integrated spatial capture–recapture movement models.

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