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Modeling temporal phenomena in variable environments with parametric models: An application to migrating salmon

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ABSTRACT

Timing phenomena are integral to many ecological processes but are difficult to analyze due to the unique nature of timing data and because environmental conditions and behavior can vary during the observation period. We demonstrated methods, based on parametric hazard-rate modeling, to analyze "time-to-event" data under time-varying conditions. We developed routines in R to apply parametric models, based on the exponential, Weibull, and modified Weibull distributions, to time-to-event data. We applied the models to data on the time for migrating adult salmonids to successfully pass a hydroelectric dam. The model captured pronounced diel behavior and the effects of time-varying covariates river flow, spill, and water temperature on passage times. The methods we demonstrated have potential application to a broad range of ecological questions.

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1. Introduction

The timing and duration of events plays a key role in countless ecological processes. Examples of event times are time to insect visitation at a flower (Muenchow, 1986), duration of tarantula fighting times (Moya-Larano and Wise, 2000), time to establishment for an introduced population (Sahlin et al., 2010), and survival (Anderson, 2000). Typically, event times vary within a population, with the distribution determined by genetic, phenotypic, and environmental variability, and ecological interactions. Further, behavior can vary during the observation period due to varying endogenous and exogenous factors, and this can influence the timing of events. Understanding the mechanisms underlying timing phenomena is paramount to understanding the ecology of timing. However, basic linear regression methods are not well suited for analyzing "time-to-event" data (Hosmer and Lemeshow, 1999), because they typically reduce response and predictor variables to means or medians, thus potentially losing valuable information. In addition, these data are often skewed and can contain "censored" individuals that were not observed to complete the event, which can further complicate analyses.

Time-to-event data are directly analogous to survival time data, however, and epidemiologists have developed powerful methods to analyze this type of data (Cox, 1972; Hosmer and Lemeshow, 1999; Kalbfleish and Prentice, 1980). Survival analysis examines the entire distribution of event times and incorporates censored individuals into the analysis, which eliminates a potential source of bias. Several ecologists have applied survival or "time-to-event" analysis to a range of event types, considering how event times vary in relation to factors such as sex or initial environmental conditions (e.g., Moya-Larano and Wise, 2000; Muenchow, 1986; Sahlin et al., 2010). However, these applications assumed that explanatory covariates, and consequently behavior, remained constant throughout the observation period. In natural populations, conditions vary over time, and this variability can influence the timing of events. Thus another powerful feature of time-to-event analysis is the capability to incorporate time-varying covariates.

In epidemiological studies, the Cox Proportional Hazards (CPH) model has received vast majority applications in survival studies (Carroll, 2003). CPH models are considered "semi-parametric" because the baseline survivorship function is not specified, but the effects of covariates are fully parameterized. The goal of most of these studies is to demonstrate that a particular factor has a proportionate effect on survival, with this effect expressed as an odds ratio. This type of information is important for survival studies, but we contend that ecologists are often more interested in how covariates affect the duration of events, and predicting this response is potentially more precise with a parametric model such as the Weibull model. A further advantage of parametric models is that by comparing alternative forms of the baseline survivorship function in a model comparison analysis, we can get a better understanding of fundamental process that underlie the temporal process of interest.

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