

A Bayesian state-space nest survival model that incorporates breeding phenology to address unknown age and unknown fate data

Reproductive output is a key component driving population dynamics, and understanding this demographic rate is fundamental to the conservation and management of wild populations. Nest survival models have traditionally required knowledge of the age and fate of monitored nests, which can be difficult or impossible to obtain in studies of wild populations due to imperfect observation processes, cryptic life history traits, or variable chick fledging ages. We present a novel approach for estimating reproductive output that accounts for uncertainty in nest age, state, and fate that is useful when either the study design or location of nests precludes observing precisely when nests are initiated, eggs hatch, or chicks fledge, but where repeated observations of parental behavior can provide information about the likely true state of the nest (e.g., when an egg or hatchling is present). We demonstrate the ability of this approach to integrate prior information on species-specific breeding phenology and extend open-population modelling approaches to estimate the total number of nests that produced at least one chick or fledgling. A robust simulation analysis indicated that the precision of daily nest state transition probabilities degrades with decreasing data quality and quantity, but the model framework produced unbiased and precise estimates of stage-specific nest survival and abundance, which are often of greatest ecological interest. We use this model to evaluate the effects of environmental indices on trends in reproductive success for the Pigeon Guillemot (*Cepphus columba*) in Puget Sound, Washington, USA. The cryptic nesting behavior of this indicator species precludes traditional nest monitoring techniques and demography therefore remains poorly understood. This work extends nest survival modeling techniques, is applicable to other populations with fully or partially unobservable nests, provides the first estimates of demographic rates for this species in the region, and lends insight into the relationship between population dynamics and environmental variability that will be useful for ongoing monitoring and conservation efforts.