

Supplementary material

Supporting Information

Appendix 1. Description of multi-state model assumptions and assessment of model accuracy.

Statement of model assumptions

Multistate models assume that states are accurately classified (Kendall, Hines, & Nichols 2003). Because female sage-grouse do not incubate during egg laying, detection of nests is lower until the onset of incubation (Blomberg et al. 2015). Therefore it is likely we temporarily misclassified some females as non-nesting by failing to detect them on nests during egg-laying. In contrast, once initiation begins females spend ~ 23 hours per day on nests (Coates & Delahanty 2008), making state misclassification far less likely. Although recent developments in multistate robust design models in Program MARK allow for misclassification of a state, these models require that a subset of detections for each state are correctly classified, with the remainder assigned to an uncertain state. In our case, we could not be certain that a female found off a nest was actually not nesting, and so could not apply those more complex analyses.

The effect of temporary misclassification of breeding individuals as non-breeders was explored by Kendall, Hines, and Nichols (2003), who found it introduced a non-trivial bias into estimates of breeding propensity, as well as other modeled parameters. Kendall et al.'s (2003) approach to correct for misclassification bias was to incorporate repeated observations of individuals (secondary occasions) per breeding season (primary occasion) to estimate the probability of detecting the offspring with its mother, which was used to account for the misclassification of breeders as non-breeders due to imperfect detection of offspring. We assumed our estimates of nesting propensity would be biased low due to misclassifications of females whose nests failed before detection during the egg-laying phase, and used simulations to quantify the magnitude of this bias.

Model assessment

To evaluate the accuracy of our multi-state approach and to assess the consequences of state-misclassification on estimates of nesting propensity, we developed a series of simulated datasets using the Poptools Add-in (www.poptools.org) of Microsoft Excel. Each simulated dataset contained 500 individuals monitored over a period of 30 occasions, and allowed for occasion-specific probabilities of nest initiation ($\psi(Nest)$), nest survival (DNS; conditioned on nest initiation in a prior interval), initiation of a second nest ($\psi(ReNest)$; conditioned on nest failure in a prior interval), and detection (p). Detection and transitions on each occasion were determined by sampling at random from a binomial distribution defined by our estimates of p and ψ . We assessed how variability in nest survival and observer visitation frequency introduced bias into estimates of nest initiation by simulating a series of datasets that allowed true nest survival and visitation rates to vary among datasets, but fixed overall nest initiation rates to be constant among all datasets. We imposed a quadratic relationship on occasion-specific probabilities of daily nest initiation throughout the nesting season, which ranged from 0.03 to 0.16 and was equivalent to an overall nest initiation probability of 0.90 during our simulated 30 occasion period. Among simulated datasets, we allowed probabilities of overall nest survival to vary from 0.10 to 0.50 in increments of 0.10, and probabilities of visitation varied from 0.20 to 1.0 to represent daily variation in nest visitation rates (i.e., females were visited anywhere from daily to once every five days). These visitation rates were designed to resemble variation in monitoring protocols that would be common among radio telemetry studies. For all simulated datasets, we allowed individuals to attempt one nest, as well as one re-nest, and individuals were not allowed to die. If an individual transitioned once between states (e.g., not nesting to nesting) between two detections, the transition was recorded on the later state. We conducted two

alternative simulations, one in which all state-transitions were assumed to be known with perfect accuracy ($p=1.0$), and a second in which we assumed state classification was imperfect ($p<1.0$). In simulated datasets with $p < 1.0$, if an individual transitioned between pre-nesting, nesting and post-nesting states without being discovered, the transition was not documented because it was not ‘observed’, and the individual remained in the pre-nesting state. This would reflect the realistic scenario of a nest being initiated and failing before being correctly classified, thus leading to state misclassification.

We used the multistate module in Program MARK to derive estimates from our simulated data, where we constrained DNS, ϕ , and p to be constant across occasions and states, and applied a quadratic relationship on $\psi(Nest)$ across occasions. This model structure approximated the known structure of our simulated data. Bias associated with resulting parameter estimates was calculated by subtracting the difference in estimated nesting propensity from the known proportion of nesting females in our simulated dataset.

Estimates of overall nesting propensity in scenarios with perfect classification and detection were nearly identical to the specified simulation parameters (Fig. S3), suggesting that our approach to using the multistate model was appropriate for evaluating nesting propensity. However, when nesting state was misclassified due to nests failure prior to discovery, models produced some degree of bias in estimates of nesting propensity. This bias was positively associated with the duration between observations, and negatively associated with nest survival; as females were observed more frequently, or as nests survived for a longer amount of time, bias decreased (Fig. S4A). The magnitude of the bias was more sensitive to visitation rate (i.e., a factor that is under a researcher’s control) than to nest success (a factor that is not controllable). In our study system, with a target field protocol of 3 days between visits and a nest success of

approximately 20%, we predict that nesting propensity estimates would be biased by a value of 0.05. This equates to an approximately 6% bias in primary nesting rate, and an approximately 11% bias in secondary nesting rate. We suggest that this bias affects our absolute estimate of nesting and re-nesting rates (i.e. they are biased low), but our major results and interpretations related to the drivers of primary and secondary nesting should be unaffected so long as state misclassification occurred randomly with respect to the explanatory variables we used in our analysis.

Literature Cited

- Blomberg, E. J., Gibson, D., and Sedinger, J. S. 2015. Biases in nest survival associated with choice of exposure period: a case study in North American upland game birds. – *Condor: Ornithological Advances* 117: 577-588.
- Coates, P.S. and Delehanty, D.J. 2008. Effects of environmental factors on incubation patterns of greater sage-grouse. – *Condor* 110: 627-638.
- Kendall, W.L., Hines, J.E., and Nichols, J.D. 2003. Adjusting Multistate Capture-Recapture Models for Misclassification Bias: Manatee Breeding Proportions.. – *Ecology* 84: 1058-1066.

Appendix 2. Derivation of primary and secondary nesting propensity from modeled transition probabilities.

Deriving parameters

The various ψ parameters can be used to derive demographic rates of interest, such as occasion-specific nest initiation rates, overall primary nest initiation rates, and overall secondary nesting rates. The occasion-specific nest initiation rate (Equation 1) represents an estimate of the probability of nest initiation during a specific interval, after accounting for the probability an individual could have initiated a nest earlier in the season.

Equation 1:

$$\psi_{Occasion_j} = \psi_{Nest_j} \times \prod_{i=1}^{j-1} (1 - \psi_{Nest_i})$$

The overall nest initiation rate represents the probability that an individual initiated a nest once during a nesting season (Equation 2).

Equation 2:

$$\psi_{Nest} = 1 - \prod_{i=1}^n (1 - \psi_{Nest_i})$$

We define the overall secondary nesting rate as the probability that an individual initiated at least one secondary nest, conditioned on failure of a first nesting attempt during the same nesting season.

Equation 3:

$$\psi_{ReNest} = 1 - \prod_{i=1}^n (1 - \psi_{ReNest_i})$$

This probability should not be interpreted as applying to the entire population level (i.e., 50% of the population re-nested), rather it is conditioned on having attempted to nest and failing (i.e., 50% of individuals that attempted a first nest and failed, re-nested).

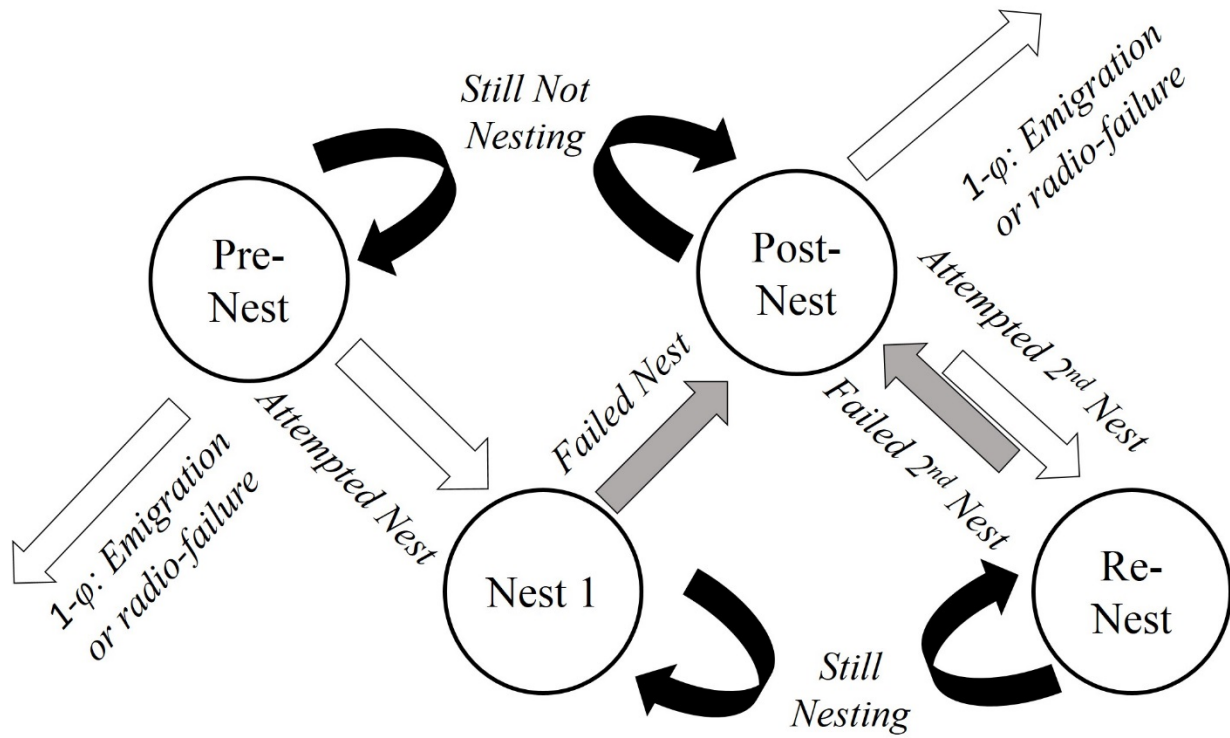


Figure A1. Conceptual model of state transitions from the multi-state model used in Program MARK.

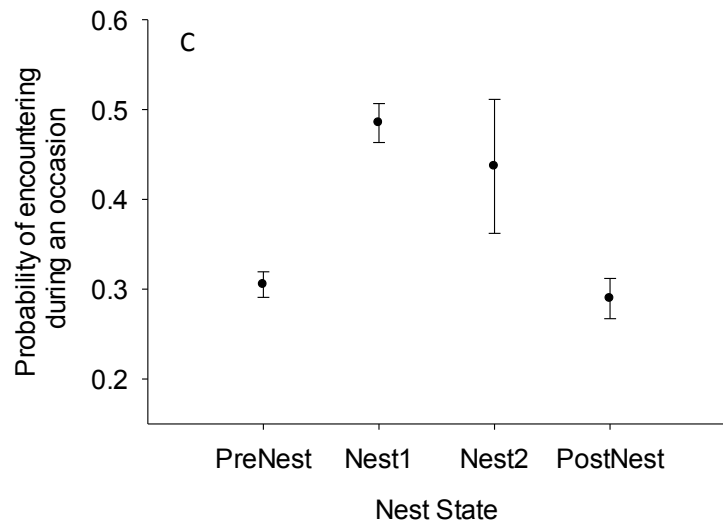
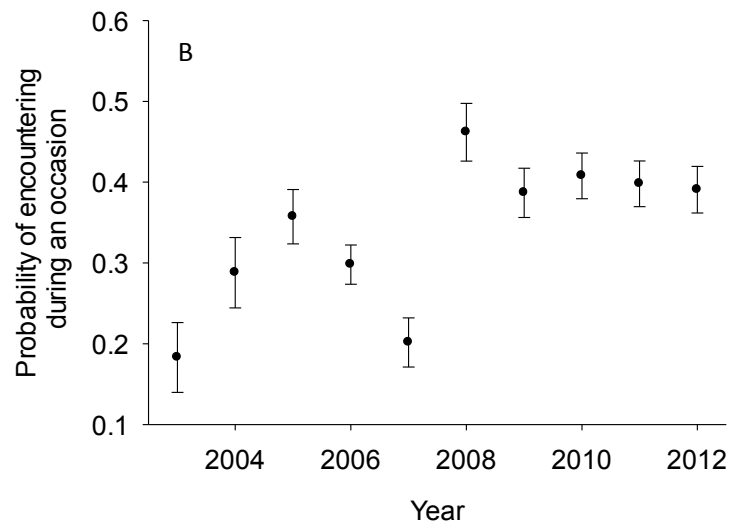
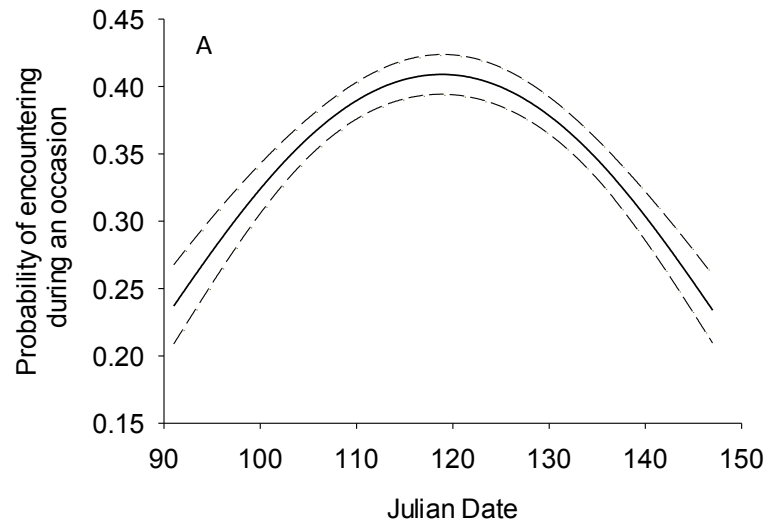


Figure A2. Estimated probabilities that an observer visited a radio-marked female sage-grouse during a two-day interval in Eureka County, NV, U.S.A., (A) within a nesting season (April 1st-May 31st), (B) among nesting seasons (2003-2012), and (C) among nesting states. States are given as female not yet associated with a nest (PreNest), female on a primary nest (Nest1), female on a secondary (Nest2), and female not currently associated with a nest having lost an earlier nest (PostNest). Error bars and dashed lines represent 95% confidence intervals.

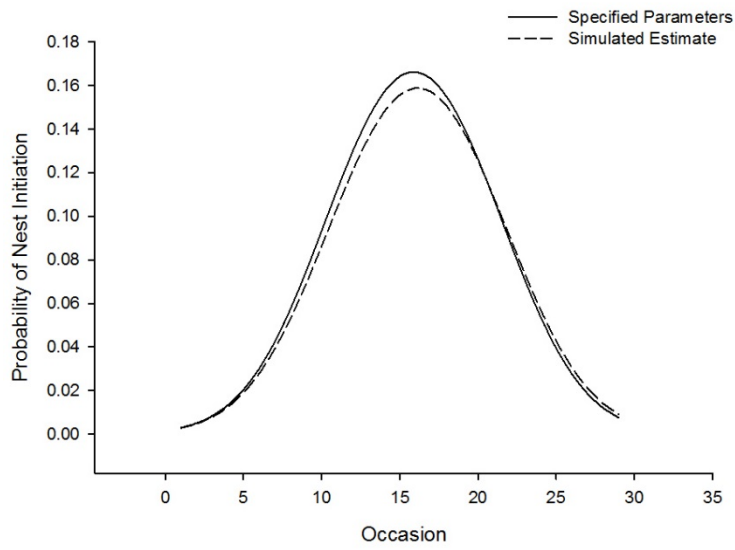


Figure A3. Estimated nesting propensity (dashed lined) from the multi-state models compared to the ‘true’ nesting propensity in a simulated scenario with detection = 1.0 and perfect accuracy in state classifications.

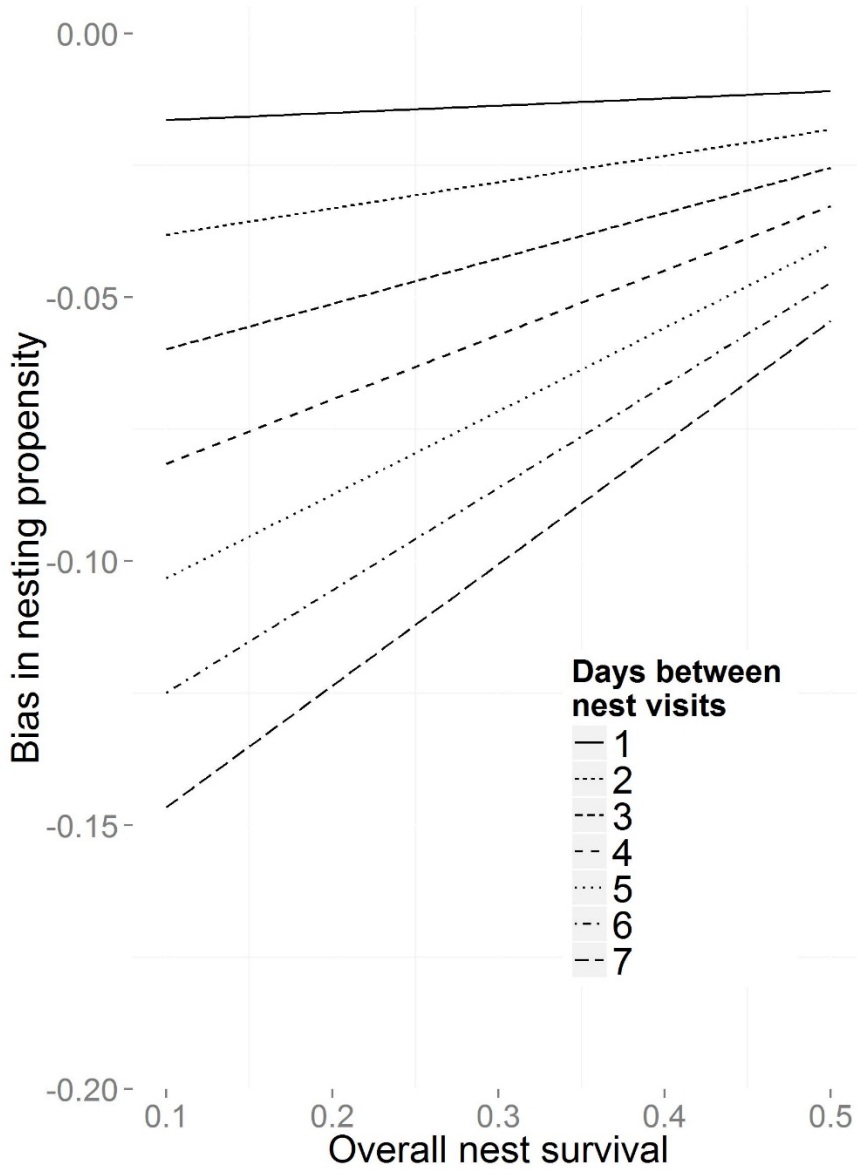


Figure A4. Bias in estimated nesting propensity (difference between the estimate and truth) that could occur as a function of state misclassification during egg-laying. Because the likelihood of state misclassification increased as observation frequency decreased and nest survival decreased, we varied both nest success and female visitation rate.