### Eva Conquet, Maria Paniw, Natalia Borrego, Chloé R. Nater, Craig Packer, Arpat Ozgul. 2024. Seasonality mediates vital-rate responses to socially- and spatially-explicit density in an African lion population. *Journal.*

### Data and R scripts to reproduce the analysis of the effect of density at the group and home-range levels on survival and between-stage transition rates of African lions *Panthera leo* in the Serengeti.

### Author(s)

Eva Conquet  
Department of Evolutionary Biology and Environmental Studies, University of Zurich   
eva.conquet@uzh.ch

Maria Paniw

Department of Evolutionary Biology and Environmental Studies, University of Zurich

Department of Conservation and Global Change, Doñana Biological Station (EBD-CSIC)

Natalia Borrego

Department of Ecology, Evolution, and Behavior, University of Minnesota

Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior

Department of Biology, University of Konstanz

Chloé R. Nater

The Norwegian Institute for Nature Research (NINA)

Craig Packer

Department of Ecology, Evolution, and Behavior, University of Minnesota

Arpat Ozgul   
Department of Evolutionary Biology and Environmental Studies, University of Zurich

### File list

01\_LionsCaptureHistories.csv

021\_Covariate\_Year.csv

022\_Covariate\_Season.csv

023\_Covariate\_Habitat.csv

024\_Covariate\_NbAFPride.csv

025\_Covariate\_Age.csv

026\_Covariate\_CoalSize.csv

027\_Covariate\_NbNMCoalHR.csv

03\_LionsGroups.csv

041\_Covariate\_PopulationSize.csv

042\_Covariate\_SeasonalPrecipitation.csv

00\_dDHMM\_lionKF.R

01\_MultistateModel.R

02\_MultistateModel\_Continue.R

03\_ModelProcessing.R

04\_SimulatingDatasets.R

05\_PosteriorPredictiveChecks.R

06\_EpsilonRainfallPopulationSize\_Correlations.R

**Description**

01\_LionsCaptureHistories.csv – This dataset contains the capture histories pooled seasonally from data on individual African lions *Panthera leo* monitored between 1984 and 2014 in the Serengeti National Park, Tanzania. The data is stored in a matrix where rows correspond to individuals and columns to seasonal capture occasions. Each number in the matrix corresponds to a life-history stage: 1 = Young subadult (1–1.5 years); 2 = Female old subadult (1.5–2 years); 3 = Male old subadult (1.5–2 years); 4 = Adult female (>2 years); 5 = Young male 1 (2–2.5 years); 6 = Young male 2 (2.5–3); 7 = Young male 3 (3–3.5); 8 = Young male 4 (3.5–4); 9 = Nomadic male (>4 years and not in a pride); 10 = Resident male (>4 years and in a pride); 11 = Found dead; and 13 = Unobserved. These capture histories are used to estimate survival and between-stage transition rates in the lion population and assess the effect of density at the group and home-range level.

021\_Covariate\_Year.csv – This dataset contains a 1-column table with the year in each seasonal capture occasion. Years start in 1985 and end in 2014, and each year occurs twice (one occurrence for the dry season and one for the wet season).

022\_Covariate\_Season.csv – This dataset contains a 1-column table with the season in each seasonal capture occasion. Seasons are expressed in integers: 1 = wet season and 2 = dry season.

023\_Covariate\_Habitat.csv – This dataset contains a matrix with information on the habitat in which each individual (rows) was in each capture occasion (columns) where it was observed. Habitats are expressed as 0 = plains and 1 = woodland. These need to be converted into 1s and 2s for the NIMBLE model to run.

024\_Covariate\_NbAFPride.csv – This dataset contains a matrix with information on the number of adult females in each pride observed throughout the study (rows) at each capture occasion (columns) where it was observed.

025\_Covariate\_Age.csv – This dataset contains a matrix with the age (in years) of each individual (rows) at each capture occasion (columns). The age of individuals in capture occasions where they were not observed is inferred from the length of each season (5 months for the dry season and 7 months for the wet season).

026\_Covariate\_CoalSize.csv – This dataset contains a matrix with information on the number of males in each resident or nomadic coalition observed throughout the study (rows) at each capture occasion (columns) where it was observed.

027\_Covariate\_NbNMCoalHR.csv – This dataset contains a matrix with information on the number of nomadic coalitions in the home range of each pride or resident coalition observed throughout the study (rows) at each capture occasion (columns) where it was observed.

03\_LionsGroups.csv – This dataset contains a matrix with information on the name of the group (i.e. pride or male coalition) to which a given individual (rows) belonged at each capture occasion (columns). When not observed, individuals were assumed to remain in the same group as they were part of in the previous capture occasion.

041\_Covariate\_PopulationSize.csv – This dataset contains a 1-column table with information on the number of individuals in the population at each capture occasion. Population size includes all individuals, including those removed from the capture histories (e.g., lions that could not be clearly identified or nomadic females).

042\_Covariate\_SeasonalPrecipitation.csv – This dataset contains a 1-column table with information on the cumulative amount of rainfall (in mm) in each season throughout the study.

00\_dDHMM\_lionKF.R – This script contains the NIMBLE custom distribution defined using the *nimbleFunction* function from the *nimble* R package. This distribution is built to model probabilities of survival, between-stage transition, and detection of lions in different stages, while integrating over latent states to avoid estimating the stage in which each individual is at each timestep. The latent (i.e. true) stages lions can take correspond to the 10 life-history stages considered in the study (1 = young subadult, 2 = female old subadult, 3 = male old subadult, 4 = adult female, 5 = young male 1, 6 = young male 2, 7 = young male 3, 8 = young male 4, 9 = nomadic male, and 10 = resident male), the “newly dead” stage (11) corresponding to a lion found dead, and the “permanently dead” stage (12) corresponding to a stage in which the lion stays until the send of the study after being found dead. The 12 observed stages correspond to the true stages except for the “permanently dead stage”, which cannot be observed, and with an added “not observed” stage (13). At each time step *t*, the vector of observed state probabilities **Zpi**is updated depending on the possible true, latent states and the detection probabilities (*dp* for pride members, nomadic males, and dead individuals). Similarly, the vector of latent state probabilities **pi** is updated depending on the preceding observations and the survival and transition rates (*surv*, *emigYM*, *transYMNM*, *takeover*, and *eviction*). The log-likelihood *logL* is updated at each timestep *t* by the sum of the vector of observed state probabilities **Zpi**.

01\_MultistateModel.R – This script uses the custom distribution 00\_dDHMM\_lionKF.R, the lion capture histories 01\_LionsCaptureHistories.csv and the density, age, and habitat covariates (standardized at the beginning of the script) to fit a multistate capture-recapture model. The script contains code to setup the data, constants, initial values, and NIMBLE code to model survival and between-stage transition rates as functions of various season-specific density measures at the group and home-range level, age, and habitat. Detection probabilities (except for dead individuals) are also modelled as a function of habitat, and we use a year random effect in all models. In addition, we included a section of code to sample missing covariate values based on observed covariate distributions. We monitor parameters such as beta coefficients, sigmas, and epsilons. To avoid computational overload, we only run 5000 iterations and run each chain of the model in parallel using the *snowfall* R package. We store the model output as an .RData file with a suffix containing information on the date and time at which the file was saved.

02\_MultistateModel\_Continue.R – This script uses the last sample of the output of a previous model run as initial value for each parameter and continues running the model for 5000 iterations in parallel. The output is saved as an .RData file with a suffix containing information on the date and time at which the file was saved. The script should run multiple times until the right amount of MCMC iterations is reached.

03\_ModelProcessing.R – This script uses the processed MCMC output without the burn-in phase to process and plot the results of the multistate model: The season-specific prior-posterior overlap, the size effects, and the predicted vital rates (median and 90% credible intervals) as a function of a given covariate. The script also allows to plot the season-specific median and credible intervals of epsilon samples. All plots are created using the *ggplot2* R package and stored as .png or .pdf files.

04\_SimulatingDatasets.R – This script uses 500 sampled values from the multistate model MCMC posterior samples of each parameter to simulate 10 capture histories per sampled set of parameter values. The simulated capture histories are built from the first capture occasion of each lion and use the observed covariate values and the sampled parameters to assign a stage to each lion in each capture occasion. The resulting 5000 simulated capture histories are stored in a list as an .RData file.

05\_PosteriorPredictiveChecks.R – This script uses the original and simulated capture histories to calculate a set of metrics on each dataset and compare the distribution of metric values calculated on the simulated capture histories to the true value calculated on the true capture histories. This allows to pinpoint issues in the parameter estimates and thus potentially in the model structure. In this script, we also calculate the Bayesian p-values for each metric, that is, the proportion of values obtained from the simulated capture histories that are larger than the true metric value. We then plot the distributions and p-values using the ggplot2 package and save these plots as .png files.

06\_EpsilonRainfallPopulationSize\_Correlations.R – This script uses the multistate model season- and year-specific posterior samples of the epsilon values as well as the rainfall and population size covariates to calculate a correlation coefficient between each sampled time series of epsilons and the covariates. We then obtain a distribution of correlation coefficients that we plot against a 0.5 threshold to gain insight on whether there might be an effect of rainfall and population size on lion survival, between-stage transition rates, and detection probabilities. We store the plots created using the ggplot2 R package as .png files.