Multifaceted density dependence: Social structure and seasonality effects on Serengeti lion demography

A manuscript for consideration as a Research article for publication in Journal of Animal Ecology

Eva Conquet[1*], Maria Paniw[1,2], Natalia Borrego[3,4,5], Chloé R. Nater[6], Craig Packer[3], Arpat Ozgul[1]

1. Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich 8057, Switzerland

2. Department of Conservation and Global Change, Doñana Biological Station (EBD-CSIC), Seville 41092, Spain

3. Department of Ecology, Evolution, and Behavior, University of Minnesota, Saint Paul MN 55108, USA

4. Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, Konstanz 78467, Germany

5. Department of Biology, University of Konstanz, Konstanz 78457, Germany

6. The Norwegian Institute for Nature Research (NINA), Trondheim 7485, Norway

Corresponding author: Eva Conquet, Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich 8057, Switzerland, eva.conquet@gmail.com

Author’s ORCID IDs:
Eva Conquet: 0000-0002-8047-2635
Maria Paniw: 0000-0002-1949-4448
Natalia Borrego: 0000-0002-8859-571X
Chloé R. Nater: 0000-0002-7975-0108
Craig Packer: 0000-0002-3939-8162
Arpat Ozgul: 0000-0001-7477-2642

Word count (title page through references): 11,135
Number of citations: 83
Number of tables in main document: 1
Number of figures in main document: 4

Acknowledgments

We are grateful to all the volunteers and researchers who have helped collect data on lions in the Serengeti throughout the years. We thank Gabriele Cozzi for his insights on lion movement and reproduction, and for his feedback on several parts of this manuscript. We also thank Daniel Turek for clarifying for us the details of the NIMBLE custom distribution code. Finally, we are grateful to Jean-Michel Gaillard, the Associate Editor, Rémi Fay, and an anonymous reviewer for their feedback, which largely helped improving the previous version of this manuscript. Data collection was supported by National Science Foundation grants: BE-0308486, DEB-0343960, DEB-0918142, and DEB-1020479 to C.P. Both M.P. and E.C. were supported by a Swiss National Science Foundation Grant (31003A_182286) to A.O.

Conflict of interest statement

The authors declare no conflict of interest.

Author Contributions

Eva Conquet: Conceptualization, Methodology, Software, Validation, Formal analysis, Data curation, Writing – original draft, Writing – review and editing, Visualization.

Maria Paniw: Conceptualization, Writing – review and editing, Supervision, Funding acquisition.

Natalia Borrego: Conceptualization, Investigation, Resources, Data curation, Writing – review and editing.

Chloé R. Nater: Methodology, Validation, Resources, Writing – review and editing.

Craig Packer: Investigation, Resources, Data curation, Writing – review and editing.

Arpat Ozgul: Conceptualization, Resources, Writing – review and editing, Supervision, Project administration, Funding acquisition.

Statement on inclusion

Our study does not include scientists based in the country where the study was carried out. We recognise that it is paramount to include the local scientific community in our research and are planning to address these caveats in future research wherever possible.

Data and Code Availability Statement

The processed data and MCMC samples necessary for reproducing results and graphs presented in the study will be available on Zenodo [link placeholder] [citation placeholder]. Original data can be requested from Craig Packer (packer@umn.edu). Data and code for implementing and running models and analyses, and plotting results is available on GitHub: https://github.com/EvaCnqt/LionsDensity. The version of code used for this study will be archived on Zenodo [link placeholder] [citation placeholder].

Abstract

1. Interactions between density and environmental conditions have important effects on vital rates and consequently on population dynamics and can take complex pathways in species whose demography is strongly influenced by social context, such as the African lion, *Panthera leo*. In populations of such species, the response of vital rates to density can vary depending on the social structure (e.g., effects of group size or composition).
2. However, studies assessing density dependence in populations of lions and other social species have seldom considered the effects of multiple socially-explicit measures of density, and—more particularly for lions—of nomadic males. Additionally, vital-rate responses to interactions between the environment and various measures of density remain largely uninvestigated.
3. To fill these knowledge gaps, we aimed to understand how a socially- and spatially-explicit consideration of density (i.e., at the local scale) and its interaction with environmental seasonality affect vital rates of lions in the Serengeti National Park, Tanzania. We used a Bayesian multistate capture-recapture model and Bayesian GLMMs to estimate lion stage-specific survival and between-stage transition rates, as well as reproduction probability and recruitment, while testing for season-specific effects of density measures at the group and home-range levels.
4. We found evidence for several such effects. For example, resident-male survival increased more strongly with coalition size in the dry season compared to the wet season and adult-female abundance affected subadult survival negatively in the wet season, but positively in the dry season.

Additionally, while our models showed no effect of nomadic males on adult-female survival, they revealed strong effects of nomads on key processes such as reproduction and takeover dynamics.

5. Therefore, our results highlight the importance of accounting for seasonality and social context when assessing the effects of density on vital rates of Serengeti lions and of social species more generally.

Keywords: density dependence, density-environment interactions, sociality, Bayesian models, multistate capture-recapture models, demographic rates

Introduction

Population dynamics are shaped by vital-rate responses to both density-dependent and -independent (e.g., environmental) factors. Interactions between density and environmental variables (hereafter environment-density interactions) occur across many systems, with important consequences on populations dynamics (Coulson et al. 2001; Gamelon et al. 2017). For example, density dependence can mediate the effects of environmental factors through compensatory density feedbacks that can buffer adverse environmental effects (e.g., through an increase in offspring survival due to a lower competition following a decline in recruitment under reduced food availability; Reed et al. 2013). By capping population abundances to a certain upper threshold, density feedbacks can also exacerbate detrimental environmental effects by exposing populations to demographic stochasticity (e.g., Jaatinen et al. 2021), or even dampen positive effects of beneficial environmental conditions by constraining populations to remain under that threshold even when the environment has strong positive effects on vital rates (e.g., Layton-Matthews et al. 2020). In specific cases, such as social species, density feedbacks can affect populations through complex pathways, as vital rates can show strong responses to both intra- (e.g., number of reproducing adults) and extra-group density factors (e.g., home range of a focal group; Packer & Pusey 1983a; Maag et al. 2018; Behr et al. 2020), with contrasting effects of such factors on vital rates of different social statuses (e.g., Paniw et al. 2019). While studies commonly assess the role of environment-density interactions (e.g., Coulson et al. 2001; Gamelon et al. 2017), assessing vital-rate responses to interactions between environmental conditions and several measures of density at different scales could help obtain better insights on the role of density feedbacks in shaping population demography.

Socially structured populations are often more susceptible to multifaceted density effects (e.g., Behr et al. 2020; Ausband et al. 2021). Such complexity in density effects on vital rates is likely to be at play in African lions, for which sociality has strong effects on demography (Bygott et al. 1979; Packer & Pusey 1987; Elliot et al. 2014; Borrego et al. 2018). The African lion is therefore an ideal case study for investigating the response of vital rates to density measures at different scales and their interactions with the environment. Lion sociality is characterized by fission-fusion dynamics with an egalitarian social structure represented by prides (permanent, stable groups of females) and coalitions (permanent, stable groups of males) (Schaller 1972; Packer 2023). Young males in the Serengeti system disperse from their natal pride by four years of age and enter a nomadic phase during which they band together with related or unrelated males to form coalitions of 1–9 individuals with no defined territory that can travel very long distances (Bygott et al. 1979; Packer & Pusey 1982; Hanby & Bygott 1987; Packer & Pusey 1987). Nomadic males play a key role in shaping lion demography (Whitman et al. 2004; Borrego et al. 2018). Male coalitions compete for access to prides; coalitions successfully taking over a pride from a rival coalition gain reproductive benefits by killing the ousted coalition's cubs (infanticide; Packer & Pusey 1983a; 1983b) and subsequently mating with its females. Additionally, the newly resident males oust any subadult males, who are sometimes too young to survive this forced dispersal (Elliot et al. 2014). Once they become resident, male coalitions typically remain with a pride for 2–3 years and often father only a single cohort. Takeover dynamics thus greatly affect young survival (Bertram 1975; Elliot et al. 2014; Borrego et al. 2018) and largely depend on the size of the coalition of resident males—who are the primary defenders of a pride against rival males (Schaller 1972)—and on the size of the challenging nomadic coalition (Bygott et al. 1979; Packer & Pusey 1987). Females also take part in defending a pride against nomadic males, consequently decreasing both young mortality and the probability of a successful takeover of a pride with females living in groups compared to singletons (Grinnell & McComb 1996). Successful takeovers also affect the reproductive status of females, who come into oestrous and subsequently give birth synchronously (Bertram 1975). This synchrony allows them to raise their cubs in crèches (Schaller 1972; Packer et al. 1990), where cubs are better protected and have a higher survival rate (Bertram 1975). These studies show the importance of socially-explicit density dependence in lion populations but often focus on a single density measure (e.g., male coalition size or number of females in a pride). However, we lack a comprehensive analysis of the relative effects of various density measures on lion vital rates. Despite the decline in the overall African lion population (Trinkel & Angelici 2016), the Serengeti population is one of the few to remain apparently stable (Bauer et al. 2015; but see Riggio et al. 2016). A better understanding of the density-dependent drivers of vital-rate variation in the Serengeti population could therefore benefit other lion populations as well as social species beyond the African lion.

The effects of density on vital rates are typically mediated by environmental factors (Courchamp et al. 1999; Paniw et al. 2019) but little is known about the response of lion vital rates to interactions between density and environmental variables, such as seasonal climatic patterns. Serengeti lions experience strong environmental seasonality due to seasonal rainfall patterns driving prey availability (Norton-Griffiths et al. 1975; Sinclair et al. 2013). These seasonal patterns in turn affect vital rates and population dynamics. For instance, in wetter years, the increase in prey availability favours recruitment through higher cub survival, leading to increases in the lion population size (Packer et al. 2005). Additionally, Serengeti lions live in two distinct habitats: the plains and the woodland, which are characterized by differences in seasonal patterns of prey availability (Packer et al. 2005). Lions in the plains experience strong decreases in prey availability during the dry season—when migrating herds leave for the north. In the woodland, prey abundance (but not composition) is relatively constant throughout the year, leading to higher lion density (Hanby & Bygott 1979) and hence less opportunities for plain lions to settle in the woodland. In a context of strong environmental seasonality, and under the predicted important changes in seasonal patterns (IPCC 2014), understanding how season-density interactions affect the vital rates of lions would provide more insights on how density-dependent processes affect lion demography (Conquet et al. 2023) and could ultimately benefit other social species living under strong environmental periodicity.

To understand how different density-dependent variables affect seasonal lion vital rates, we fitted a Bayesian multistate capture-recapture model and Bayesian generalized linear mixed models (GLMMs) to data from a uniquely long monitoring (30 years) of a population of African lions in the Serengeti to estimate season-specific local density effects (as opposed to density at the population scale) by assessing the response of lion survival, between-stage transition, and reproductive rates (i.e., reproduction probability and recruitment) to socially- and spatially-explicit density measures and to the habitat (plains or woodland). We used socially-explicit density measures taken at the group level, more specifically the number of females in a pride and the size of a resident or nomadic male coalition. For the spatially-explicit effect of density, corresponding to density at the home-range level, we tested for the effect of the number of nomadic coalitions in the home range of a pride or resident coalition. Notably, ours is the first analysis to include multiple density measures, including from nomadic males, in a multi-state African lion population model. Considering the strong responses of vital rates of young lions to both season and density, we expected the strongest seasonal effects of socially-explicit density measures on young survival.

Methods

Study species

Demographic data

We used individual-based life-history data of 1347 lions (65 prides and 242 male coalitions ranging size from 1–8 individuals), collected between 1984 and 2014 during a consistent monitoring in a 2000-km^2 area located in the Serengeti National Park (SNP), Tanzania (-2°27' N, 34°48' E) (Packer & Pusey 1987; Appendix S1). Starting in 1984, one or two females per pride were equipped with VHF collars (VanderWaal et al. 2009; Packer 2023). Each pride was then visited at least once every two weeks by locating the collared females (VanderWaal et al. 2009; Borrego et al. 2018). Additionally, lions or groups of lions away from their pride, as well as nomadic males, were observed and recorded opportunistically during the monitoring. Lions were identified by eye based on photographs of features such as scars and individual-specific whisker spots recorded at the first sighting (Pennycuick & Rudnai 1970; Packer & Pusey 1993). The age of individuals not observed as cubs was determined from nose coloration, coat condition, and tooth wear (Whitman et al. 2004). Using these natural markings allowed tracking of each individual from its birth (or entry into the study area) until its death (or permanent emigration from the study area). Additionally, while the death of most individuals could not be observed, we used dead-recovery data available for 105 lions found dead from natural causes—i.e., not killed by humans—opportunistically during the regular pride surveys to provide the model with additional insights on the difference between mortality and lack of observation, thereby better informing the survival process and obtaining more accurate survival estimates.

Life history

We divided the lion life history into 10 stages based on age, sex, and social status (Fig. 1a). Subadults were divided into young subadults (SA_Y; 1–1.5 years), and old subadults (1.5–2 years), separated into females ($SA_{O,F}$) and males ($SA_{O,M}$). Female subadults then become adult females (AF; > 2 years) in their natal pride. We considered females to become adults at 2 years old; although females do not necessarily reproduce at that age, their contribution to the pride is similar as that of older females. In contrast, males could leave their natal pride as early as 2 years of age but could also remain up to 4 years of age; males were considered as adults at their departure from their natal pride. To represent males older than 2 years and still in their natal pride and ensure they automatically left their natal pride after 4 years, we used four young-male stages: YM_1 (2–2.5 years), YM_2 (2.5–3 years), YM_3 (3–3.5 years), and YM_4 (3.5–4 years). Finally, we divided males outside their natal pride between two stages: nomadic male (NM; > 2 years and nomadic), and resident male (RM; > 2 years and resident in a different pride). In the resulting life cycle (Figure 1a), transitions between stages are all conditional on survival (σ). Additionally, transitions from young subadult to female or male old subadult assume a fixed female-to-male sex ratio of 0.55, representing a conservative value of the observed female-biased sex ratio in the population (~ 0.60). Young males in stages YM_1 to YM_3 can leave their natal pride conditional on emigration probability $\varphi_{Em}{}^{YM}$, while young males in YM_4 automatically leave their natal pride to become adult males. An emigrated young-male can transition to either of the two adult-male stages (nomadic or resident) conditional on the probability of becoming nomadic (φ_{YM}). Nomadic and resident males then transition to the other adult male stage when respectively gaining (φ_{T}) or losing tenure of a pride (φ_{Ev}). Adult females recruit cubs conditional on their survival and reproduction probability ($P_{\mathrm{reproduction}}$), and on the per-female number of cubs born in a given season that survived until their first birthday (Recruitment). Therefore, in our analysis, reproduction probability is not a component of recruitment and is estimated separately, with recruitment being conditional on reproducing.

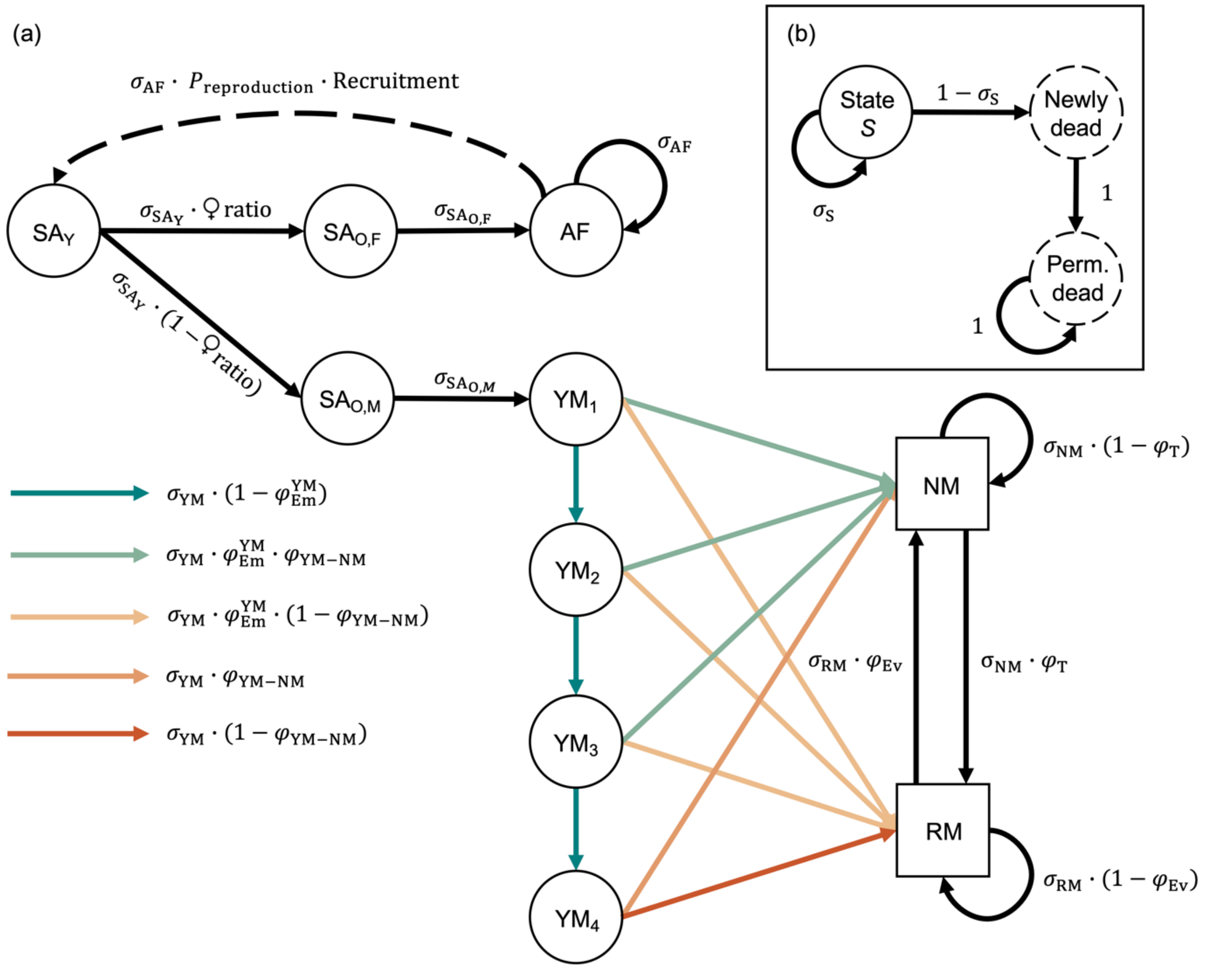


Figure 1 – Lion life cycle. (a) The life cycle represents seasonal transitions between stages (solid arrows) and reproduction (dashed arrow); all transitions are conditional on survival (σ). The first stage, young subadult (SA$_{\mathrm{Y}}$; 12–18 months), is sex-independent. Young subadults transition to female (SA$_{\mathrm{O,F}}$) or male (SA$_{\mathrm{O,M}}$) old

subadults (18–24 months) depending on the sex ratio (0.55). Female old subadults then transition to adult females (AF; >2 years), and male old subadults to the first young-male stage (YM_1; 2–2.5 years in their natal pride). Young males (YM_1, YM_2, YM_3, and YM_4; 2–4 years in their natal pride) transition to nomadic (NM; >2 years nomadic) or resident males (RM; >2 years in another pride) conditional on emigration ($\varphi_{\mathrm{Em}}{}^{YM}$; except for YM_4) and probability of transitioning to nomadic male (φ_{YM}). Nomadic and resident males transition to the other adult male stage conditional respectively on takeover (φ_{T}) and eviction (φ_{Ev}). Cubs are recruited by adult females conditional on adult-female survival and reproduction probability ($P_{\mathrm{reproduction}}$) as well as on recruitment (Recruitment), which corresponds to the number of cubs born in a given season that survived their first year per female. Circles and squares respectively represent stages inside and outside their natal pride (in another pride for resident males and in no pride for nomadic males). (b) To take advantage of the dead-recovery data available for 105 lions, we included two dead stages: Newly and permanently dead. Any alive state can transition to the newly dead state conditional on survival. Newly dead individuals then transition to the absorbing permanently dead state. The solid circle represents any alive state, dashed circles represent dead states.

Estimation of lion vital rates

Survival and transition rates

We estimated stage-specific survival and transitions, as well as detection probabilities of pride individuals and nomadic males for the Serengeti lion population using a Bayesian multistate capture-recapture model (MSCR; Lebreton & Pradel

2002; Schaub et al. 2004). In addition to the life stages described above, we also included two more states, an observable newly dead and unobservable permanently dead state (Gauthier & Lebreton, 2008), which allowed us to take advantage of the dead-recovery data available for 105 individuals (i.e., lions found dead, as opposed to lions with unknown fates) (Fig. 1b). Overall, we estimated the following parameters: state-specific survival (σ_S), young-male emigration and transition to nomadic male ($\varphi_{Em}{}^{YM}$ and φ_{YM}), resident-male eviction (φ_{Ev}), and nomadic-male takeover (φ_T). Lion prides are stable, territorial social groups (Schaller 1972); we can thus expect that all pride members are in a fixed area in the vicinity of the collared female in the pride. Consequently, we assumed all lions belonging to a pride to have the same detection probability (p_{pride}) but estimated a separate parameter for nomadic males (p_{NM}). In addition, we estimated the probability to observe a dead lion (p_{dead}). Details on the multistate capture-recapture model can be found in Appendix S2.

Reproductive rates

We estimated female reproduction probability and recruitment (i.e., number of cubs born in a given season that reached their first birthday per female, conditional on survival and reproduction) using a Bayesian generalized linear mixed model. Following previous studies on the Serengeti lion, we defined recruitment as the number of cubs reaching their first birthday (Packer et al. 2001). Because females raise their cubs in crèches, the true mother of a given cub can be unknown. Therefore, we first used data on cubs with known mothers to assign the total number of cubs with a unique ID–i.e., the initial litter size regardless of whether they survived their first year—to the right females. From the obtained number of identified cubs per female, we created an initial litter-size distribution and used it to assign the cubs left to their true mother among several potential females. We assigned each cub born in a given season to a female among those available in the pride (i.e., with no more than the maximum number of cubs observed; see details in Appendix S3).

We treated reproduction probability as a binary variable (i.e., 1 to females who reproduced, 0 to females who did not). Based on the assignment of mothers to cubs described above, we assigned 1 to females with cubs in the birth season of the cubs (wet or dry) if the cubs were born more than 105 days after the beginning of the season (i.e. the average gestation period; Schaller 1972) , or in the previous season otherwise. We also assigned 1 to females identified as having lost their litter. In addition, we assigned 0 to females without dependent offspring—young < 2 years old—who could reproduce and NA to females with dependent offspring. We modelled reproduction probability with a binomial distribution and recruitment with a Poisson distribution using a generalized linear mixed model (GLMM) fitted in a Bayesian framework (Kéry & Royle 2016).

Effects of density, season, and habitat on vital rates

Density dependence

To understand how socially- and spatially-explicit density measures affect lion vital rates, we investigated vital-rate responses to various density-dependent factors at the group (i.e. pride or male coalition) and home-range level (Table 1). To assess the effect of density at the group level, we used the number of females in a pride and the size of a resident or nomadic male coalition as density measures at the group level. Both measures corresponded to the observed number of individuals in a given group in each season. For the home-range level, we tested for the effect of the number of nomadic coalitions in the home range of a pride or of a resident male coalition using the overlap between that home range and the GPS location points of a nomadic coalition (see Appendix S4 for details on the computation of home ranges and of the number of nomadic coalitions in a home range). As nomadic coalitions do not have assigned home ranges, we only tested for the effect of nomadic coalitions on the vital rates of pride individuals. We only investigated the response of nomad vital rates (i.e. survival and takeover probabilities) to coalition size and habitat.

Table 1 compiles the covariates included in the different vital-rate models and the justification for their inclusion. While we estimated separate intercepts for female and male old-subadult survival (Appendix S5: Fig. S5), we did not test for sex-specific effects of density to avoid increasing model complexity. Due to methodological constraints on the complexity of the model, we focused on assessing lion vital-rate responses to density at the group and home-range level and did not explicitly test for the effects of density at the higher population level. However, we investigated the presence of signals of such effects by evaluating the correlation between time-varying overall population size and season-specific yearly random effects (Appendix S5: Fig. S3). Constraints on model complexity also prevented us from properly testing for senescence in survival and reproduction—for which we only included a quadratic age effect—which could have been done using a threshold model (e.g., Lemaître et al. 2020; Moullec et al. 2023).

Seasonality

Lions in the Serengeti experience strong seasonal patterns in rainfall (Norton-Griffiths et al. 1975; Sinclair et al. 2000; 2013), and variability in such patterns can have important consequences on food availability and thereby on lion demography (Packer et al. 2005; Borrego et al. 2018). To understand whether seasonal environmental patterns lead to seasonal density feedbacks, we estimated season-specific vital rates—i.e., we estimated season-specific coefficients in all vital-rate models described above—, with the wet season starting mid-November and the dry season mid-May. However, due to a lack of data, we could not estimate a season-specific effect of the number of nomadic coalitions on old-subadult survival and thus only estimated the mean effect across seasons. Although we did not include the effect of rainfall in our models, we investigated signals of potential effects of rainfall on vital rates by assessing the correlation between rainfall and coefficients of random effects (Appendix S5: Fig. S3).

Table 1 – Socially- and spatially-explicit density covariates included in the various vital-rate models. We tested for the effect of density measures at the group- (number of adult females in the pride and male coalition size) and home-range level (number of nomadic coalitions in the home range) on lion survival, transition, and reproductive rates. In addition, we tested for the effect of age on adult-female survival and reproduction probability, and of its quadratic term on reproduction probability. Each covariate (Covariate) is associated to the corresponding vital rates (Vital rate) according to previous studies or assumptions that have previously not been investigated (Motivation).

Covariate	Vital rate	Motivation
Number of adult females in the pride	Young subadult survival	Takeovers can be prevented by females protecting their offspring, thus reducing the probability of a successful takeover in groups of females compared to singletons (Grinnell & McComb 1996), and consequently the mortality of young individuals (Packer et al. 1990). However, small and large prides can attract nomadic coalitions more, leading to a higher takeover rate in these prides and thereby a higher mortality of young through infanticide or forced dispersal (Packer & Pusey 1987; Pusey & Packer 1994; Elliot et al. 2014), with potentially severe consequences at the population level (Whitman et al. 2004). Moreover, the survival of adult females can be affected by the size of the pride: Females in small prides have lower survival rates, probably due to encounters with infanticidal males or females of other prides competing for the territory (Pusey & Packer 1994; Packer & Pusey 1997).
	Old subadult survival	
	Young male survival	
	Adult female survival	
	Reproduction probability	
	Recruitment (number of cubs surviving to their first birthday per female, conditional on reproduction)	
Number of adult females in the pride[2]	Reproduction probability	Reproduction is mainly driven by takeover dynamics and interpride competition (Packer 2023), with small prides being unable to defend their cubs against outside males or defend their territories against larger neighbouring prides, and large prides attracting more frequent male takeovers and suffering greater within-pride feeding competition. We thus expect a u-shaped response of reproduction to the number of adult females in the pride (Packer 2023), which can be detected by including a quadratic term.
Coalition size	Nomadic male survival	Successful takeovers are affected by the size of both resident and nomadic coalitions (Bygott et al. 1979; Packer & Pusey 1983a; Borrego et al. 2018).
	Resident male survival	
	Nomadic male takeover	
	Resident male eviction	
	Young subadult survival	

Number of nomadic coalitions in the home range	Old subadult survival	Nomadic coalitions taking over prides can increase the mortality of subadults and older young through infanticide and forced dispersal (Packer & Pusey 1987; Elliot et al. 2014; Packer 2023). Protective encounters by mothers with nomadic coalitions can lead to injuries and lower survival of adult females (Pusey & Packer 1994; Packer & Pusey 1997).
	Young male survival	
	Adult female survival	
	Resident male survival	More nomadic coalitions increase takeover rates (Borrego et al. 2018). Although this has not been explicitly tested, higher numbers of nomadic males could also lead to more encounters with resident males, potentially affecting their survival.
	Resident male eviction	
	Reproduction probability	Higher numbers of nomadic coalitions in the population can lead to more takeovers, increasing cub mortality due to infanticide (Bertram 1975; Pusey & Packer 1994; Whitman et al. 2004; Borrego et al. 2018).
	Recruitment (number of cubs surviving to their first birthday per female, conditional on reproduction)	
Number of adult females in the pride : Number of nomadic coalitions in the home range	Reproduction probability	While it has not yet been explicitly tested, this interaction would enable us to understand whether the effect of nomads on reproduction can be counterbalanced by females in the pride.
	Recruitment (number of cubs surviving to their first birthday per female, conditional on reproduction)	
Age	Adult female survival	Testing for senescence and age-dependent reproduction.
	Reproduction probability	
Age^2	Reproduction probability	Females in our population have been observed to reproduce between 2.5 and 15 years old, but most reproduce between 3 and 10 years old. We should thus observe lower reproduction probabilities for young and old females.

Habitat

Lions in our study population inhabit two different habitats (plains and woodland) where vital rates can display different patterns. Food availability in the plains strongly varies between seasons and is particularly scarce in the dry season (Schaller 1972; Sinclair & Norton-Griffiths 1995; Packer et al. 2005; Sinclair et al. 2013). On the other hand, lions in the woodland benefit from a somewhat continuous food availability throughout the whole year (Hanby & Bygott 1979; VanderWaal et al. 2009; Packer et al. 2005). We thus tested for the season-specific effect of habitat on all lion vital rates except for the probability of young males becoming nomadic (φ_{YM}), due to the lack of data on this transition. As for density, we did not test for sex-specific habitat effects on the survival of old subadults. We accounted for differences in detection probabilities between habitats by including a habitat effect on all stage-specific detection probabilities.

Correlation among covariates and year random effect

We checked for correlations between covariates using the Pearson correlation coefficient for two density-dependent (continuous) variables (using the *cor* function from the *stats* R package; R Core Team 2022), and the biserial correlation coefficient for a density-dependent (continuous) variable and the categorical habitat variable (using the *binomial.cor* function of the *ltm* R package version 1.2-0; Rizopoulos 2007). We considered two variables to be uncorrelated when the absolute value of the correlation coefficient was under 0.5. In addition to density, season, and habitat, we included a yearly season-specific random effect in all models to account for among-year variation unexplained by density or habitat.

Standardization of continuous covariates

We standardized all non-binary covariates using the approach described by Gelman (2008):

$$\mathrm{covariate}_{\mathrm{scaled}} = \frac{(\mathrm{covariate}_{\mathrm{unscaled}} - \mu_{\mathrm{covariate}_{\mathrm{unscaled}}})}{2 \cdot \sigma_{\mathrm{covariate}_{\mathrm{unscaled}}}} \quad \text{(Equation 1)}$$

where *μ* and *σ* are respectively the mean and standard deviation of a given unscaled covariate. In comparison with the common standardization by one standard deviation, this standardization approach enables the comparison of the effect sizes of both categorical (i.e. habitat) and continuous covariates (i.e. density-dependent variables).

Implementation using NIMBLE

We used NIMBLE (version 1.0.1 of the *nimble* package; de Valpine et al. 2017; 2022) to implement both the multistate capture-recapture model and the generalized linear mixed models in a Bayesian framework. For the multistate capture-recapture model, to decrease the runtime and memory requirements of the Markov chain Monte Carlo algorithm (MCMC), we created a custom distribution integrating over latent states, based on Nater et al. (2020; see Appendix S2 for details). We used non-informative priors for all parameters and ran the MCMC for four chains of 60,000 iterations with no thinning and a burn-in phase of 15,000 iterations the multistate model and 10,000 for the GLMM. We tested for parameter extrinsic identifiability using prior-posterior overlap (Gimenez et al. 2009) and assessed model fit using posterior predictive checks (Conn et al. 2018). The detailed methods are available in Appendix S2. All analyses were performed in R 4.2.2 (R Core Team 2022) using RStudio (Posit team 2023). R code for running analyses and plotting results is available on Zenodo [citation placeholder] and on GitHub at [Github link placeholder].

Results

Socially- and spatially-explicit density dependence of vital rates

Most vital rates were influenced by at least one measure of density at the group or home-range level, the only exception being adult-female survival. Moreover, some density effects varied between seasons (Fig. 2, Fig. 3, Fig. 4, and Appendix S5: Fig. S1). Many vital rates also differed between the plains and woodland habitats, but the degree of vital-rate variation due to density dependence was generally higher than that due to habitat (Fig. 2 and Appendix S5: Fig. S1). In Figure 2 and Figure 3, we highlight the lack of response of adult-female survival to the density measures we considered (Fig. 2a). In addition, we show the most compelling examples of how lion vital rates respond to various density measures at the group (reproduction probability, and old-subadult, resident-male, and nomadic-male survival; Figs. 2b-d and Figs. 3a-d) and home-range levels (recruitment; Fig. 3f). We also show notable examples of seasonal differences in density effects on lion vital rates (old-subadult and resident-male survival; Figs. 2c, d). In the following, all results are presented using the median of the posterior distribution for each parameter and the 90% credible interval (more stable than the 95% CRI, following Kruschke 2014) on the probability (for survival and transition rates and reproduction probability) or natural scale (for recruitment).

Among all vital rates for which we tested the effect of density, the survival of adult females was the only one not markedly affected by at least one density measure at the group or home-range level (Fig. 2a and Appendix S5: Fig. S3). Otherwise, many vital rates were largely affected by density variables at the group level (Fig. 2 and Appendix S5: Fig. S1). The number of adult females in the pride negatively affected young subadult survival in the dry season (with a median survival probability of 0.98 [0.95, 0.99] with 2 females in the pride and 0.95 [0.90, 0.99] with 8 females). The number of females in a pride also affected reproduction probability in the wet season, with a quadratic effect indicating a higher reproduction probability in small and large prides compared to prides of average size (0.21 [0.17, 0.28] with 2 females in the pride, 0.15 [0.12, 0.20] with 8 females, and 0.17 [0.13, 0.23] with 12 females; Fig. 2b and Fig. 3a). The effect of the number of females in the pride on old subadult survival strongly differed between seasons (Fig. 2c and Fig. 3b). In larger prides with more adult females, old-subadult survival decreased in the wet season (0.94 [0.89, 0.97] with 2 females in the pride to 0.89 [0.82, 0.94] with 8 females) but increased in the dry season (from 0.92 [0.82, 0.98] to 0.98 [0.94, 1.0]). In contrast, the number of adult females in the pride did not affect young-male survival or recruitment (Appendix S5: Fig. S1).

Adult males were affected by density measures at the group level as well, with resident-male eviction probability decreasing with the size of the resident coalition in the wet (from 0.0034 [0.00019, 0.017] for a coalition of 2 males to 0.00065 [0.000029, 0.0046] with 3 males) and dry season (from 0.035 [0.016, 0.062] to 0.015 [0.0052, 0.032]) (Appendix S5: Fig. S1). Resident-male survival increased with coalition size in both seasons but showed large differences in the seasonal response to coalition size (see Fig. 2d and Fig. 3c), with survival increasing more strongly with larger coalitions in the dry season (from 0.89 [0.85, 0.92] for a coalition of 2 males to 0.95 [0.91, 0.97] with 3 males) than in the wet season (from 0.88 [0.84, 0.91] to 0.89 [0.86, 0.92]). Moreover, while the size of a nomadic coalition did not affect takeover probability in the wet season, larger nomadic coalitions had higher chances to take over a pride in the dry season (from 0.28 [0.20, 0.37] for a coalition of 2 males to 0.40 [0.28, 0.54] with 3 males; Fig. 3d). Nomadic coalition size also increased nomadic-male survival both in the wet (from 0.88 [0.77, 0.95] for a coalition of 2 males to 0.96 [0.85, 0.99] with 3 males) and dry season (from 0.98 [0.93, 1.0] to 1.00 [0.99, 1.0]) (Appendix S5: Fig. S1).

In addition, at the home-range level, the number of nomadic coalitions negatively affected recruitment in the wet season (from 0.54 [0.43, 0.67] cubs surviving their first year per reproducing female with 2 nomadic coalitions in the home range to 0.33 [0.17, 0.61] cubs with 5 coalitions; Fig. 3e). By contrast, nomadic coalitions in the home range positively affected dry-season survival of young subadults (with survival probabilities ranging from 0.93 [0.87, 0.97] with no nomadic coalition in the home range to 0.99 [0.96, 1.0] with 2 coalitions) and young males (from 0.82 [0.71, 0.93] to 1.0 [0.91, 1.0]), with both vital rates showing a particularly strong seasonal response to nomadic coalitions (Appendix S5: Fig. S1). This unexpected positive effect of nomadic males might be attributable to favourable environmental conditions. As described by Borrego et al. (2018), increasing numbers of nomadic coalitions coincide with years where wet-season rainfall is abundant; such conditions could have positive effects on young-subadult and young-male survival rates. More nomadic coalitions in the home range of a pride in the wet season also increased the probability of eviction of resident males (from 0.0022 [0.000081, 0.014] with 1 nomadic coalition in the home range to 0.019 [0.0026, 0.062] with 4 coalitions). While we found no effect of nomadic males on reproduction probability, reproduction was affected by the interaction between the number of nomadic coalitions in the home range and the number of females in the pride in the wet season. That is, increasing numbers of nomadic coalitions had larger effects on reproduction probability in prides with higher numbers of females (with 4 nomadic coalitions in the home range of a pride, reproduction probability was 0.25 [0.16, 0.37] in prides of 4 females and 0.31 [0.19, 0.45] with 10 females; Fig. 2b and Fig. 3f and Appendix S5: Fig. S1). However, we found no effect of nomadic coalitions on the survival of old subadults and resident males (Fig. 2c and Fig. 2d).

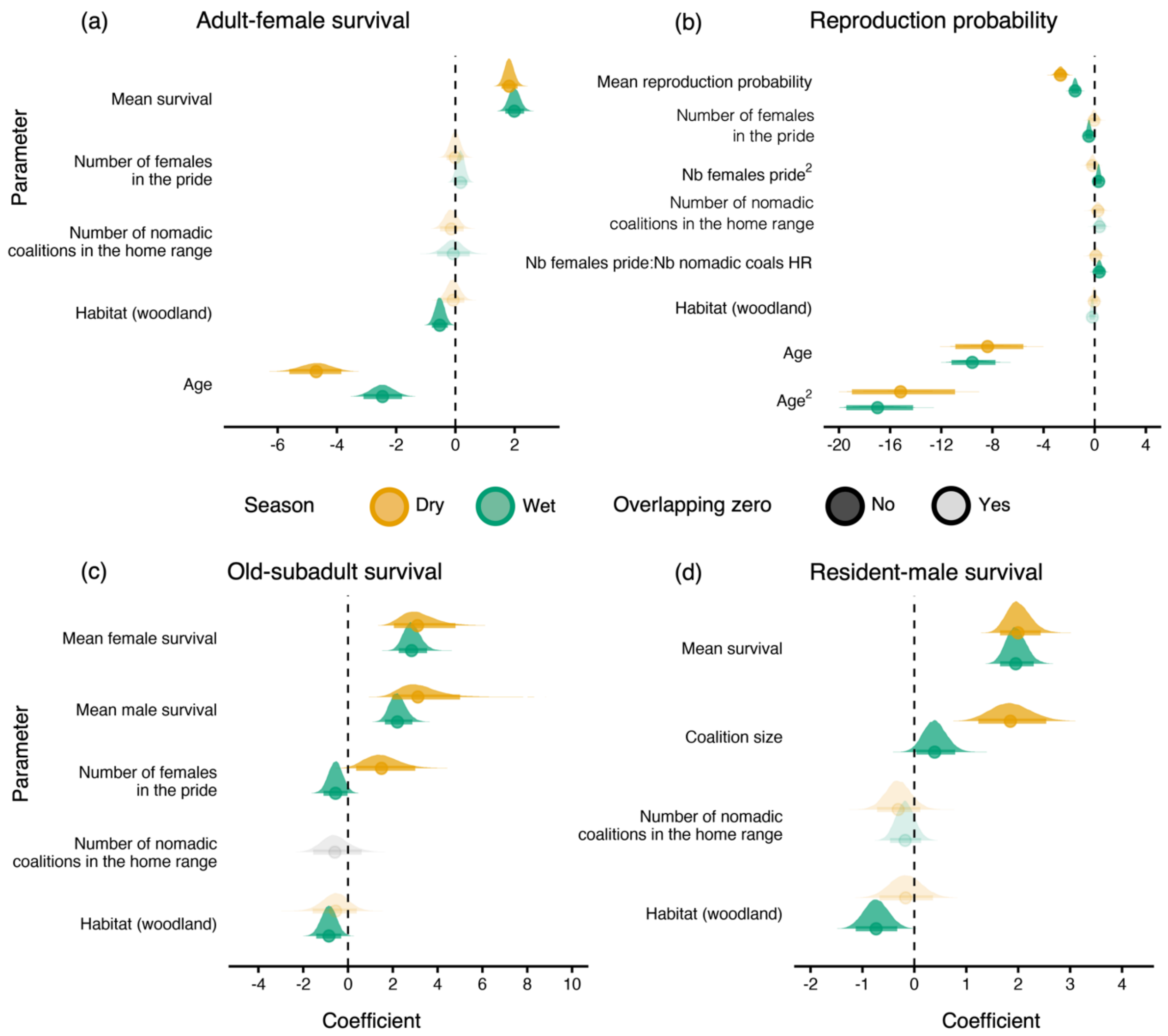


Figure 2 – Seasonal effects of habitat and density variables at the group and home-range level on lion vital rates. Using a Bayesian multistate capture-recapture and Bayesian GLMMs, we investigated the presence of seasonal patterns in the response of lion survival, transition, and reproductive rates to the habitat type (woodland or plains), within-group density (number of adult females and coalition size), and the number of nomadic coalitions in the home range. The figure represents the effect sizes of these covariates on adult-female (a) survival and (b) reproduction probability; and on the survival of (c) old subadults; and (d) resident males. Each plot represents, on the logit scale, the median (dots) and 90% Credible Interval (CRI; lines) of each coefficient obtained from the multistate capture-recapture model and the GLMMs. The density plots above each estimate show the

posterior distribution of each parameter. Shaded dots and CRIs indicate coefficients with 90% CRI overlapping zero.

Habitat effects on vital rates

In addition to density, we found effects of habitat (plains or woodland) on most vital rates, but these effects largely varied depending on the season and life-history stage (Fig. 2). Overall, while we found no differences in survival between the plains and the woodland in the dry season, survival was lower in the woodland in the wet season compared to the plains (e.g., the survival probability of old subadults was 0.83 [0.74, 0.90] in the woodland and 0.92 [0.88, 0.95] in the plains, and resident males had a survival probability of 0.77 [0.70, 0.83] in the woodland and 0.88 [0.84, 0.91] in the plains; see Fig. 2c, and Fig. 2d). Unlike density, the habitat did affect adult-female survival, which decreased from 0.88 [0.85, 0.91] in the plains to 0.82 [0.76, 0.86] in the woodland in the wet season (Fig. 2a). The survival of nomadic males also decreased in the woodland in the dry (0.97 [0.92, 0.99] in the plains and 0.85 [0.68, 0.97] in the woodland) and wet season (0.85 [0.76, 0.93] and 0.74 [0.56, 0.88]), while recruitment increased from 0.60 [0.51, 0.71] in the plains to 0.96 [0.79, 1.2] cubs per female in the woodland in the dry season (Appendix S5: Fig. S1). Additionally, habitat-specific takeover probabilities for nomadic males strongly varied between seasons, with takeover probability increasing from 0.26 [0.18, 0.35] in the plains to 0.47 [0.30, 0.68] in the woodland in the dry season but decreasing from 0.30 [0.21, 0.40] in the plains to 0.15 [0.066, 0.28] in the woodland in the wet season. However, we found no differences in young-male emigration probability and female reproduction probability between habitats.

Finally, older females had a lower probability of survival, especially in the dry season (0.99 [0.98, 0.99] at 3 years old and 0.87 [0.84, 0.90] at 13 years old) compared to the wet season (0.97 [0.96, 0.98] and 0.89 [0.86, 0.91]; see Fig. 2a), with seasonal differences in survival increasing with age. Similarly, age had a quadratic effect on female reproduction probability in both seasons, indicating a lower reproduction probability for young (at 4 years old, 0.26 [0.23, 0.30] in the wet season and 0.091 [0.072, 0.11] in the dry season) and old females (at 12 years old, 0.28 [0.23, 0.32] in the wet season and 0.10 [0.076, 0.14] in the dry season) compared to 8 year-old females (0.46 [0.41, 0.50] in the wet and 0.18 [0.15, 0.22] in the dry season; Fig. 2b).

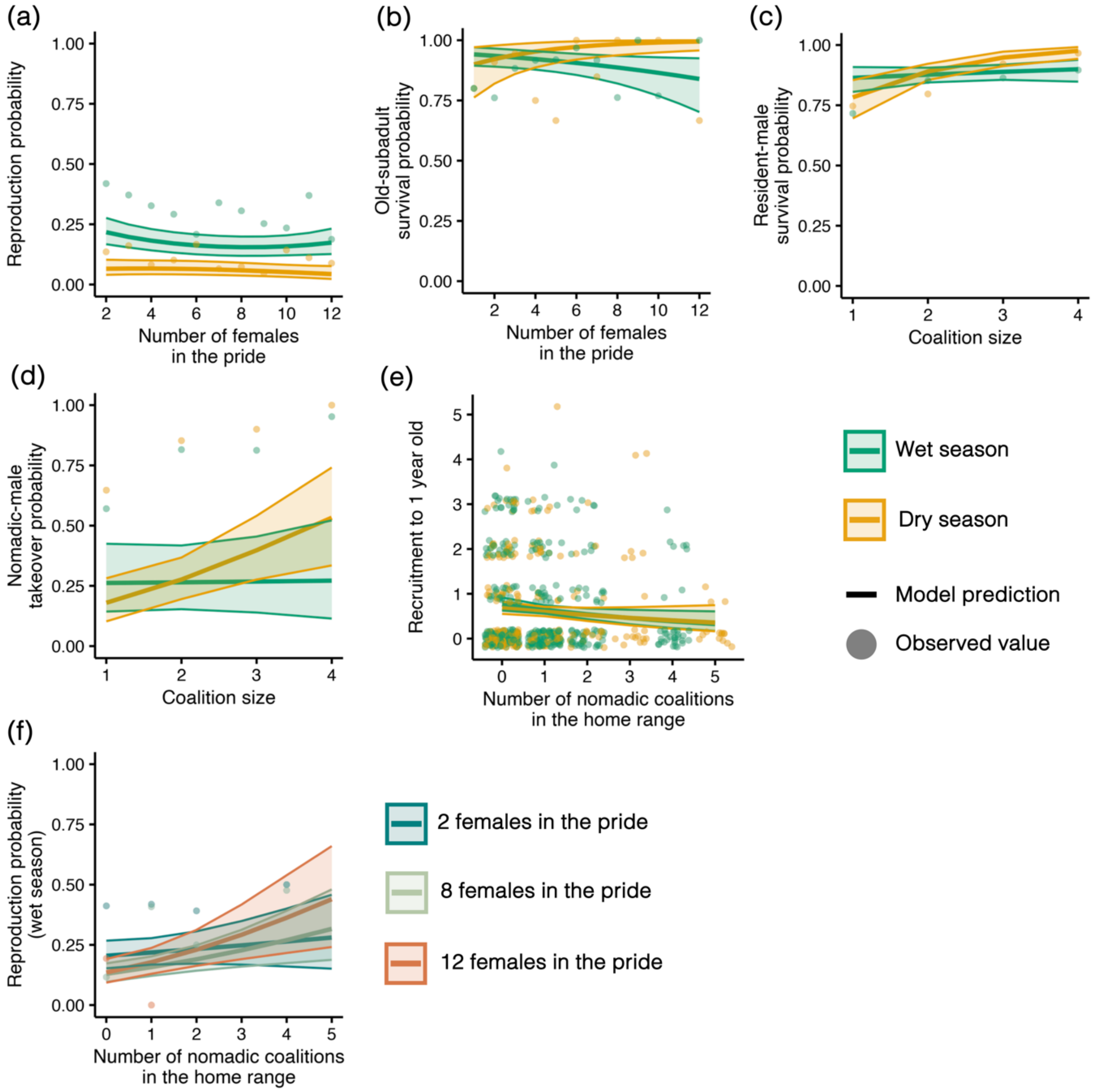
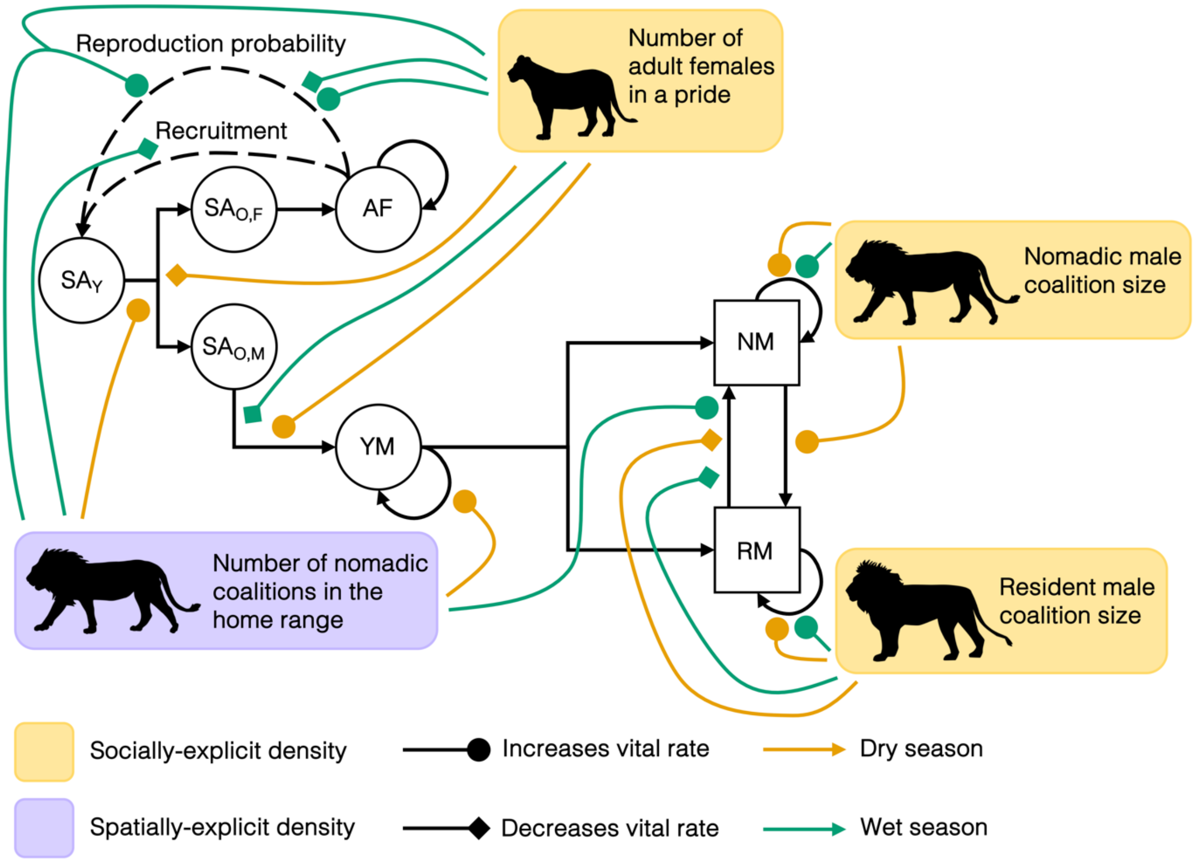


Figure 3 – Seasonal effects of socially- and spatially-explicit density measures on lion vital rates. Using a Bayesian multistate capture-recapture, we investigated the presence of seasonal patterns in the response of lion survival and transition rates to the habitat type (woodland or plains), group density (number of adult females and coalition size), and the number of nomadic coalitions in the home range of a pride. The figure represents the model predictions of the response (a) reproduction probability and (b) old-subadult survival to the effect of the number of females in the pride; (c) resident-male survival and (d) nomadic-male takeover probability to male coalition size; (e) recruitment to 1 year old to the number of

nomadic coalitions in the home range of a pride; and (f) wet-season reproduction probability to the number of nomadic coalitions in the home range of a pride depending on the number of females in the pride. Each plot represents the median estimate (line) and 90% Credible Interval (CRI; lines) of each vital-rate prediction derived from the output of the multistate capture-recapture model and the GLMMs.

Parameter identifiability and model fit

We found no strong evidence of non-identifiability for either the multistate capture-recapture model or the GLMMs (Appendix S5: Fig. S4). Additionally, the posterior predictive checks showed that the GLMMs fitted the data appropriately (Appendix S5). This was also largely the case for the multistate capture recapture model, with the exception of a few metrics (e.g., number of nomadic males becoming residents or number of resident males becoming nomadic). For these, posterior predictive checks suggested some estimation bias, and the results for the corresponding vital rates (e.g., takeover or eviction probabilities) should be interpreted with caution.



Silhouettes available on phylopic.org.
The female and nomadic-male silhouettes were designed by Gabriela Palomo-Munoz and available under the CC BY 4.0 licence (https://creativecommons.org/licenses/by/4.0/).
The resident-male silhouette was designed by Lisa Nicvert.

Figure 4 – Seasonal effects of socially- and spatially-explicit density measures on lion vital rates. Socially- and spatially-explicit density measures (yellow and purple boxes) have positive and negative effects on the different vital rates of Serengeti lions (round and diamond arrowheads; only the effects of covariates for which the coefficient 90% CRIs do not overlap 0 are represented), with differences in these effects between the dry and wet seasons (orange and green arrows). The complexity of vital-rate density dependence emphasizes the need to account for socially- and spatially-explicit considerations of density to assess the role of density feedbacks in shaping vital-rate variation in social species.

Discussion

Our study unveiled strong effects of local measures of density on the vital rates of the Serengeti lion population, with seasonal differences in these effects for some vital rates. Our results show variation both in the magnitude and direction of vital-rate responses to a combination of season-specific socially-, and spatially-explicit density measures at the group and home-range levels (Fig. 4). Importantly, our results show strong effects of nomadic coalitions on key processes such as reproduction and takeover dynamics. In addition, while the effects of season-specific density were overall stronger than that of the habitat, we found lower survival probabilities in the woodland in the wet season, and seasonal differences in the effect of habitat type for various vital rates. Interestingly, our results indicate that habitat and age were the only variables affecting the survival of adult females—a key vital rate in many long-lived species (e.g., Eberhardt and Siniff 1977; Gaillard et al. 1998; Hunter et al. 2010). Unlike the other vital rates, adult-female survival thus appeared buffered against changes in density measures considered in our study. Overall, our findings emphasize the need for studies accounting for socially- and spatially-explicit considerations of density when investigating vital-rate density dependence in social and potentially other species. Moreover, our results highlight the necessity to assess the effects of environment-density interactions, which can play a key role in shaping vital-rate variability in a context of strong environmental seasonality (Gamelon et al. 2017; Conquet et al. 2023).

Socially-explicit density dependence

With vital rates being affected by density measures at multiple scales (e.g., group or population level), density feedbacks can affect social species through complex pathways. For instance, Ausband et al. (2021) showed that both population density and group size affected reproduction of grey wolves (*Canis lupus*), with interacting effects of the two density measures. Additionally, in African wild dogs (*Lycaon pictus*), different measures of density at the intra-group level (e.g., number of pups or number of adults) had very variable effects on dispersal probabilities, with sex-specific responses (Behr et al. 2020). Our results highlight this complexity, revealing that also lion demography is affected by a combination of density measures at the group (pride and male coalition size) and home-range level (number of nomadic coalitions). As expected, the size of a social group (i.e. pride or male coalition) had important, complex effects on many vital rates, corroborating previous findings on density effects on lion vital rates. More specifically, larger male coalitions gave an advantage to males both in survival and in gaining (for nomads) or maintaining the tenure of a pride (for residents) (Bygott et al. 1979; Packer & Pusey 1983a; Borrego et al. 2018). Additionally subadult survival decreased in prides with more females and female reproduction probability was higher in small and large prides than in prides of average size. This may be explained by females struggling to defend smaller prides—where resident coalitions are often absent (Packer et al. 1988; Pusey & Packer 1994)—and a greater competition between coalitions for larger prides resulting in more frequent coalition takeovers (Packer & Pusey 1987), leading to higher young mortality due to infanticide and forced dispersal (Packer 2023), and consequently to more frequent reproduction events (Bertram 1975; Packer et al.

1988). In addition, within-pride competition for food is stronger in large prides, where individuals are consequently thinner than in smaller prides, leading to reduced survival rates (Packer 2023). While we found effects of the number of females on reproduction probabilities, our results showed no such effects on recruitment (i.e., the number of cubs surviving to one year old). This is contrary to previous studies, which found notable effects of pride size on female reproductive output (Packer et al. 1990; Packer 2023). This might be due to our analysis underestimating the number of reproducing solitary females (see Appendix S5 for more details), who often must settle in low-quality habitats, causing high rates of litter loss (Packer 2023). Overall, however, our results might indicate that belonging to a pride of at least two lionesses may be key to raising cubs until their first birthday, but two or ten females does not make any discernible difference. Low recruitment in small prides could also possibly be concealed by a strong effect of other density measures, such as the number of nomadic coalitions in the home range of a pride.

While males are often overlooked in demographic studies, they are an important part of the life history of many species (Rankin & Kokko 2007) and often play a key role in shaping their demography (e.g., Borrego et al. 2018; Penteriani et al. 2011). In species where male infanticide due to nomadic individuals replacing residents is prominent, males may have particularly strong effects on vital rates, with potentially drastic consequences for population dynamics and strong population declines when males are especially targeted by regulation or trophy hunting activities (e.g. Swenson 2003; Whitman et al. 2004). Nonetheless, while the effect of nomadic individuals on population demography has been extensively assessed in birds (Penteriani et al. 2006; 2011), the role of nomadic males in shaping demography is rarely accounted for in mammals. Despite data and modelling limitations (see Appendix S5 for details), we found important effects of nomad abundance on several vital rates, which confirm previous findings. For example, the probability of a female reproducing in the wet season increased with the number of nomadic coalitions in the home range of a pride, especially in prides with more females, which are more attractive to nomads (Packer & Pusey 1987). Additionally, as suggested by Borrego et al. (2018), takeover dynamics leading to infanticide—as indicated by the increased eviction probability—had negative effects on recruitment (i.e., the number of cubs surviving the first year per female, conditional on reproduction). Opposite responses of reproduction probability and recruitment to an increased presence of nomadic males—and higher takeover rates—are expected because females who lose their cubs following a takeover can mate soon after (Bertram 1975; Packer et al. 1988). Overall, our results show that nomads can play a key role in shaping vital rates in mammal populations, emphasizing the need to invest efforts in monitoring nomadic or transient individuals to better understand the demography of populations.

Despite most lion vital rates showing important responses to at least one measure of density, our results suggest that adult-female survival is affected only by the habitat and age, and not by the density measures we considered. Population dynamics of long-lived species are typically sensitive to variation in the survival of adult females (e.g., Eberhardt & Siniff 1977; Gaillard et al. 1998; Hunter et al. 2010; but see Gerber & Heppell 2004); the response of such key vital rates to density could therefore have important consequences on population dynamics. For example, under environmental conditions causing population declines, the absence of compensating density feedbacks acting as a buffer against adverse environmental effects (e.g., Reed et al.

2013; Paniw et al. 2019) could prevent populations from recovering. The absence of buffering density dependence could have dire consequences for many populations facing increasing climate-change and anthropogenic pressures with negative effects on vital rates (e.g., Vinks et al. 2021, Conquet et al. 2023). Conversely, the lack of negative density effects on key vital rates such as adult female survival, could favour populations experiencing strong negative density feedbacks in other vital rates. This could contribute to limiting overcompensatory density dependence in populations experiencing strong negative feedbacks coupled with adverse environmental conditions (Coulson et al. 2001; Fauteux et al. 2021). Overall, however, our results reveal important density effects on the vital rates of Serengeti lions at the group and home-range levels, as well as indications of vital-rate responses to population size (Appendix S5: Fig. S3). These findings thus emphasize the need for a systematic assessment of the effects of a socially- and spatially-explicit consideration of density.

Vital-rate responses to season-density interactions

Context dependence in density effects have been widely described in various species, with age-specific and sex-specific density effects (e.g., Fay et al. 2017), and vital-rate responses to density varying among climatic conditions (e.g., Dierickx et al. 2019). Such environment-density interactions can have critical effects on population persistence (Coulson et al. 2001; Gamelon et al. 2017) and are therefore paramount to account for. Lions in the Serengeti experience strong seasonal rainfall patterns driving prey availability (Norton-Griffiths et al. 1975; Packer et al. 2005; Sinclair et al. 2013) and these environmental patterns lead to seasonality in lion vital rates, similarly to several other systems (Letcher et al. 2015; Payo-Payo et al. 2022;

Conquet et al. 2023). The key role of seasonal environmental patterns in driving variations in vital-rate responses to density (e.g., Barbraud & Weimerskirch 2003, Sandvig et al. 2017) is supported by our results. For example, positive or negative density effects can be intensified in a given season, as exemplified by the stronger increase in resident-male survival with higher coalition size in the dry compared to the wet season. Larger male coalitions might be more successful at hunting more and larger prey, ensuring their survival during times of prey scarcity. Additionally, environmental seasonality can lead to opposite density effects between seasons. For example, in the wet season, old subadults fared worse in large prides compared to prides with less females, but the opposite was true in the dry season. This pattern likely arose because our analysis estimates apparent survival and does not discriminate between survival and permanent emigration. Under favourable environmental conditions such as that occurring in the wet season, subadults approaching adulthood may be more likely to emigrate in response to higher lion densities in large prides, causing the observed season-specific effect of density on apparent survival.

While density feedbacks could be key in allowing populations to persist under the predicted changes in seasonality (Conquet et al. 2023), changes in seasonal patterns could also increase negative density effects, potentially leading to population declines (Gamelon et al. 2017; Paniw et al. 2019). For example, in lions, a shift towards drier seasons could strengthen the negative effect of nomads on recruitment, and of the number of females on young subadult survival. If not counterbalanced, for example by wet-season dynamics, such effects could be detrimental to the recruitment of young in the population, thereby critically hampering population persistence. Understanding how such changes in seasonal patterns will affect populations experiencing strong seasonality and density feedbacks (e.g., Hansen et al. 1999; Lima et al. 2002; Marra et al. 2015) requires investigating the presence of season-density interactions, as such interactions are likely to play a crucial role in populations where key demographic processes (e.g., reproduction or dispersal) are restricted to a specific period of the year (e.g., Lima et al. 2002; Lok et al. 2013; Marra et al. 2015).

Habitat effects in lion vital rates

Similar to seasonality, different habitats can expose populations to very different environmental conditions (e.g., resources availability or temperatures), with consequential effects on vital rates (e.g., Ozgul et al. 2006; Swift et al. 2020). While density had stronger effects on lion vital rates than the habitat, we nonetheless found differences in vital rates between the plain and woodland lion prides, as well as seasonal patterns in habitat effects. The two habitats differ mostly in terms of prey availability, with plain lions experiencing an important decline in food availability in the dry season, when the migrating herds of herbivores continue their migration toward the north of the Serengeti to find food, while lions in the woodland have access to similar amounts of prey most of the whole year (Packer et al. 2005). In the dry season, conditions are thus more favourable in the woodland, leading to higher recruitment rates compared to the plains. However, the survival of most stages was lower in the wet season in the woodland compared to the plains, because of the stronger increase in prey availability in the plains between the dry and wet season compared to the stable abundance of prey in the woodland between seasons (Packer 2023).

Variations in environmental conditions among habitat types can lead to differences in density feedbacks among these habitats (e.g., Pärn et al. 2012; Marra et al. 2015), potentially leading to tradeoffs in inhabiting better-quality habitats with stronger negative density effects. While our models did not assess habitat-density interactions and seasonal variation in such interactions, previous studies on the Serengeti lion indicate that density feedbacks might be stronger in the woodland, where living conditions are supposedly more favourable (Hanby & Bygott 1979). Further investigations on seasonal patterns of habitat-density interactions could thus help better understand how habitat differences shape the demography of species beyond African lions through density feedbacks, and assess the potential consequences of changes in habitat structure under anthropogenic land use or climate change.

Conclusion

Vital-rate density dependence is common across taxa and can be an important driver of vital-rate variations, possibly more so than environmental variables. Density can therefore be a key factor shaping demography, especially in species where sociality is at the heart of life history. In such cases, therefore, assessing the effect of density on vital rates requires investigating the relative effects of different measures of socially- and spatially-explicit density that are relevant to each study system. Moreover, vital rates can show complex responses to environment-density interactions, and accounting for such interactions is therefore paramount to understanding how density affects vital rates, more importantly for populations experiencing environmental periodic patterns (e.g., seasonality). Our work not only contributes to the body of literature emphasizing the importance of density in shaping demography but additionally shows that density feedbacks can affect the demography of social species through complex pathways involving density measures at different scales. Consequently, assessing vital-rate responses to density measures beyond group or population size, and accounting for socially- and spatially-explicit considerations of density and their interactions with the environment when estimating vital rates could provide a valuable insight on how density dependence shapes demography in species where such complex feedbacks are likely to be at play. Although methodological and data limitations did not allow for such complexity in our study, assessing vital-rate responses to interacting density measures would undoubtedly provide further invaluable insights on the role of intraspecific density in shaping population demography (see e.g., Behr et al. 2020). Additionally, accounting for the effects of interspecific density would allow for a more exhaustive understanding of density feedbacks, as interspecific interactions can play a key role in shaping population dynamics (Morrissette et al. 2010; Quéroué et al. 2021). Studies accounting for these factors would enable capturing the full picture of the role of density feedbacks in vital-rate variations, consequently leading to a better assessment of the persistence of species beyond the Serengeti lion.

References

Ausband, D. E., & Mitchell, M. S. (2021). The effect of group size on reproduction in cooperatively breeding gray wolves depends on density. *Animal Conservation, 24(6)*, 994–1000. https://doi.org/10.1111/acv.12701.

Bauer, H., Chapron, G., Nowell, K., Henschel, P., Funston, P., Hunter, L. T. B., Macdonald, D. W., & Packer, C. (2015). Lion (*Panthera leo*) populations are declining rapidly across Africa, except in intensively managed areas. *Proceedings of the National Academy of Sciences, 112(48)*, 14894–99. https://doi.org/10.1073/pnas.1500664112.

Barbraud, C., & Weimerskirch, H. (2003). Climate and density shape population dynamics of a marine top predator. *Proceedings of the Royal Society of London B, 270*, 2111–2116. https://doi.org/10.1098/rspb.2003.2488.

Behr, D. M., McNutt, J. W., Ozgul, A., & Cozzi, G. (2020). When to stay and when to leave? proximate causes of dispersal in an endangered social carnivore. *Journal of Animal Ecology 89(10)*, 2356–66. https://doi.org/10.1111/1365-2656.13300.

Bertram, B. C. R. (1975). The social system of lions. *Scientific American, 232(5)*, 54–65. https://doi.org/10.1038/scientificamerican0575-54.

Borrego, N., Ozgul, A., Slotow, R., & Packer, C. (2018). Lion population dynamics: Do nomadic males matter? *Behavioral Ecology, 29(3)*, 660–66. https://doi.org/10.1093/beheco/ary018.

Bygott, J. D., Bertram, B. C. R., & Hanby, J. P. (1979). Male lions in large coalitions gain reproductive advantages. *Nature, 282(5741)*, 839–41. https://doi.org/10.1038/282839a0.

Conn, P. B., Johnson, D. S., Williams, P. J., Melin, S. R., & Hooten, M. B. (2018). A guide to Bayesian model checking for ecologists. *Ecological Monographs, 88(4)*, 526–42. https://doi.org/10.1002/ecm.1314.

Conquet, E., Ozgul, A., Blumstein, D. T., Armitage, K. B., Oli, M. K., Martin, J. G. A., Clutton-

Brock, T. H., & Paniw, M. (2023). Demographic consequences of changes in environmental periodicity. *Ecology, 104(3)*, e3894. https://doi.org/10.1002/ecy.3894.

Coulson, T., Catchpole, E. A., Albon, S. D., Morgan, B. J. T., Pemberton, J. M., Clutton-Brock, T. H., Crawley, M. J., & Grenfell, B. T. (2001). Age, sex, density, winter weather, and population crashes in Soay sheep. *Science, 292(5521)*, 1528–31. https://doi.org/10.1126/science.292.5521.1528.

Courchamp, F., Grenfell, B., & Clutton-Brock, T. H. (1999). Population dynamics of obligate cooperators. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 266(1419)*, 557–63. https://doi.org/10.1098/rspb.1999.0672.

Dierickx, E. G., Robinson, R. A., & Brooke, M. de L. (2019). Survival of a long-lived single island endemic, the Raso lark *Alauda razae*, in relation to age, fluctuating population and rainfall. *Scientific Reports*, *9*, 19557. https://doi.org/10.1038/s41598-019-55782-8.

Eberhardt, L. L., & Siniff, D. B. (1977). Population dynamics and marine mammal management policies. *Journal of the Fisheries Research Board of Canada, 34(2)*, 183–90. https://doi.org/10.1139/f77-028.

Elliot, N. B., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (2014). Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos, 123(9)*, 1049–56. https://doi.org/10.1111/oik.01266.

Fauteux, D., Stien, A., Yoccoz, N. G., Fuglei, E., & Ims, R. A. (2021). Climate variability and density-dependent population dynamics: Lessons from a simple High Arctic ecosystem. *Proceedings of the National Academy of Sciences, 118(37)*, e2106635118. https://doi.org/10.1073/pnas.2106635118.

Fay, R., Barbraud, C., Delord, K., & Weimerskirch, H. (2017). Contrasting effects of climate and population density over time and life stages in a long-lived seabird. *Functional ecology*, *31(6)*, 1275–1284. https://doi.org/10.1111/1365-2435.12831.

Gaillard, J.-M., Festa-Bianchet, M., & Yoccoz, N. G. (1998). Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology &*

Evolution, 13(2), 58–63. https://doi.org/10.1016/S0169-5347(97)01237-8.

Gamelon, M., Grøtan, V., Nilsson, A. L. K., Engen, S., Hurrell, J. W., Jerstad, K., Phillips, A. S., Røstad, O. W., Slagsvold, T., Walseng, B., Stenseth, N. C., & Sæther, B.-E. (2017). Interactions between demography and environmental effects are important determinants of population dynamics. *Science Advances, 3(2)*, e1602298. https://doi.org/10.1126/sciadv.1602298.

Gauthier, G., & Lebreton, J.-D. (2008). Analysis of band-recovery data in a multistate capture-recapture framework. *Canadian Journal of Statistics, 36(1)*, 59–73. https://doi.org/10.1002/cjs.5550360107x.

Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics in Medicine, 27(15)*, 2865–73. https://doi.org/10.1002/sim.3107.

Gerber, L. R, & Heppell, S. S. (2004). The use of demographic sensitivity analysis in marine species conservation planning. *Biological Conservation, 120(1)*, 121–28. https://doi.org/10.1016/j.biocon.2004.01.029.

Gimenez, O., Morgan, B. J. T., & Brooks, S. P. (2009). Weak identifiability in models for mark-recapture-recovery data. In D. L. Thomson, E. G. Cooch, & M. J. Conroy (Eds.) *Modeling demographic processes in marked populations* (pp. 1055–67). Springer US. https://doi.org/10.1007/978-0-387-78151-8_48.

Grinnell, J., & McComb, K. (1996). Maternal grouping as a defense against Infanticide by males: Evidence from field playback experiments on African lions. *Behavioral Ecology, 7(1)*, 55–59. https://doi.org/10.1093/beheco/7.1.55.

Hanby, J. P., & Bygott, J. D. (1979). Population changes in lions and other predators. In A. R. E. Sinclair, & M. Norton-Griffiths (Eds.) *Serengeti: Dynamics of an ecosystem* (pp. 249–62). University of Chicago Press.

Hanby, J. P., & Bygott, J. D. (1987). Emigration of subadult lions. *Animal Behaviour, 35(1)*, 161–69. https://doi.org/10.1016/S0003-3472(87)80221-X.

Hansen, T. F., Stenseth, N. C., & Henttonen, H. (1999). Multiannual vole cycles and population regulation during long winters: An analysis of seasonal density dependence. *The American Naturalist, 154(2)*, 129–39. https://doi.org/10.1086/303229.

Hunter, C. M., Caswell, H., Runge, M. C., Regehr, E. V., Amstrup, S. C., & Stirling, I. (2010). Climate change threatens polar bear populations: A stochastic demographic analysis. *Ecology, 91(10)*, 2883–97. https://doi.org/10.1890/09-1641.1.

IPCC. (2014). Climate Change 2014: Synthesis Report. Contribution of working groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change. Core Writing Team, R. K. Pachauri, & L. A. Meyer. IPCC.

Jaatinen, K., Westerbom, M., Norkko, A., Mustonen, O., & Koons, D. N. (2021). Detrimental impacts of climate change may be exacerbated by density-dependent population regulation in blue mussels. *Journal of Animal Ecology, 90(3)*, 562–73. https://doi.org/10.1111/1365-2656.13377.

Kéry, M., & Royle, A. J. (2016). Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS. Elsevier. https://doi.org/10.1016/C2015-0-04070-9.

Kruschke, J. (2014). Doing Bayesian data analysis: A tutorial with R, JAGS, and Stan. 2nd edition. Elsevier Science.

Layton-Matthews, K., Hansen, B. B., Grøtan, V., Fuglei, E., & Loonen, M. J. J. E. (2020). Contrasting consequences of climate change for migratory geese: Predation, density dependence and carryover effects offset benefits of High-Arctic warming. *Global Change Biology, 26(2)*, 642–57. https://doi.org/10.1111/gcb.14773.

Lebreton, J.-D., & Pradel, R. (2002). Multistate recapture models: Modelling incomplete individual histories. *Journal of Applied Statistics, 29(1–4)*, 353–69. https://doi.org/10.1080/02664760120108638.

Lemaître, J.-F., Ronget, V., & Gaillard, J.-M. (2020). Female reproductive senescence across mammals: A high diversity of patterns modulated by life history and mating traits. *Mechanisms of Ageing and Development, 192*, 111377. https://doi.org/10.1016/j.mad.2020.111377.

Letcher, B. H., Schueller, P., Bassar, R. D., Nislow, K. H., Coombs, J. A., Sakrejda, K., Morrissey, M., Sigourney, D. B., Whiteley, A. R., O'Donnell, M. J., & Dubreuil, T. L. (2015). Robust estimates of environmental effects on population vital rates: An integrated capture–recapture model of seasonal brook trout growth, survival and movement in a stream network. *Journal of Animal Ecology, 84(2)*, 337–52. https://doi.org/10.1111/1365-2656.12308.

Lima, M., Stenseth, N. C., & Jaksic, F. M. (2002). Population dynamics of a South American rodent: Seasonal structure interacting with climate, density dependence and predator effects. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 269(1509)*, 2579–86. https://doi.org/10.1098/rspb.2002.2142.

Lok, T., Overdijk, O., Tinbergen, J. M., & Piersma, T. (2013). Seasonal variation in density dependence in age-specific survival of a long-distance migrant. *Ecology, 94(10)*, 2358–69. https://doi.org/10.1890/12-1914.1.

Maag, N., Cozzi, G., Clutton-Brock, T. H., & Ozgul, A. (2018). Density-dependent dispersal strategies in a cooperative breeder. *Ecology, 99(9)*, 1932–41. https://doi.org/10.1002/ecy.2433.

Marra, P. P., Studds, C. E., Wilson, S., Sillett, T. S., Sherry, T. W., & Holmes, R. T. (2015). Non-breeding season habitat quality mediates the strength of density-dependence for a migratory bird. *Proceedings of the Royal Society B: Biological Sciences, 282(1811)*, 20150624. https://doi.org/10.1098/rspb.2015.0624.

Morrissette, M., Bêty, J., Gauthier, G., Reed, A., & Lefebvre, J. (2010). Climate, trophic interactions, density dependence and carry-over effects on the population productivity of a migratory arctic herbivorous bird. *Oikos, 119(7)*, 1181–91. https://doi.org/10.1111/j.1600-0706.2009.18079.x.

Moullec, H., Reichert, S., & Bize, P. (2023). Aging trajectories are trait- and sex-specific in the long-lived Alpine swift. *Frontiers in Ecology and Evolution, 11*, 983266. https://doi.org/10.1016/j.mad.2020.111377.

Nater, C. R., Vindenes, Y., Aass, P., Cole, D., Langangen, Ø., Moe, S. J., Rustadbakken, A., Turek, D., Vøllestad, L. A., & Ergon, T. (2020). Size- and stage-dependence in cause-specific mortality of migratory brown trout. *Journal of Animal Ecology, 89(9)*, 2122–33. https://doi.org/10.1111/1365-2656.13269.

Norton-Griffiths, M., Herlocker, D., & Pennycuick, L. (1975). The patterns of rainfall in the Serengeti ecosystem, Tanzania. *African Journal of Ecology, 13(3–4)*, 347–74. https://doi.org/10.1111/j.1365-2028.1975.tb00144.x.

Ozgul, A., Armitage, K. B., Blumstein, D. T., & Oli, M. K. (2006). Spatiotemporal variation in survival rates: Implications for population dynamics of yellow-bellied marmots. *Ecology*, *87(4)*, 1027–1037. https://doi.org/10.1890/0012-9658(2006)87[1027:SVISRI]2.0.CO;2

Packer, C. (2023). The lion: Behavior, ecology, and conservation of an iconic species. Princeton University Press.

Packer, C., Herbst, L., Pusey, A., Bygott, J. D., Hanby, J. P., Cairns, S. J., & Borgerhoff-Mulder, M. (1988). Reproductive success of lions. In T. H. Clutton-Brock (Eds.) *Reproductive Success* (pp. 363–83). University of Chicago Press.

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., & Sinclair, A. R. E. (2005). Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science, 307(5708)*, 390–93. https://doi.org/10.1126/science.1105122.

Packer, C., & Pusey, A. E. (1982). Cooperation and competition within coalitions of male lions: Kin selection or game theory? *Nature, 296(5859)*, 740–42. https://doi.org/10.1038/296740a0.

Packer, C., & Pusey, A. E. (1983a). Adaptations of female lions to infanticide by incoming males. *The American Naturalist, 121(5)*, 716–28. https://doi.org/10.1086/284097.

Packer, C., & Pusey, A. E. (1983b). Male takeovers and female reproductive parameters: A simulation of oestrous synchrony in lions (*Panthera leo*). *Animal Behaviour, 31(2)*, 334–40. https://doi.org/10.1016/S0003-3472(83)80051-7.

Packer, C., & Pusey, A. E. (1987). The evolution of sex-biased dispersal in lions. *Behaviour,* *101(4)*, 275–310. https://doi.org/10.1163/156853987X00026.

Packer, C., & Pusey, A. E. (1993). Should a lion change its spots? *Nature, 362(6421)*, 595–595. https://doi.org/10.1038/362595a0.

Packer, C., & Pusey, A. E. (1997). Divided we fall: Cooperation among lions. *Scientific American, 276(5)*, 52–59. https://doi.org/10.1038/scientificamerican0597-52.

Packer, C., Pusey, A. E., & Eberly, L. E. (2001). Egalitarianism in female African lions. *Science, 293(5530)*, 690–93. https://doi.org/10.1126/science.1062320.

Packer, C., Scheel, D., & Pusey, A. E. (1990). Why lions form groups: Food is not enough. *The American Naturalist, 136(1)*, 1–19. https://doi.org/10.1086/285079.

Paniw, M., Maag, N., Cozzi, G., Clutton-Brock, T. H., & Ozgul, A. (2019). Life history responses of meerkats to seasonal changes in extreme environments. *Science, 363(6427)*, 631–35. https://doi.org/10.1126/science.aau5905.

Pärn, H., Ringsby, T. H., Jensen, H., & Sæther, B.-E. (2012). Spatial heterogeneity in the effects of climate and density-dependence on dispersal in a house sparrow metapopulation. *Proceedings of the Royal Society B: Biological Sciences, 279(1726)*, 144–52. https://doi.org/10.1098/rspb.2011.0673.

Payo-Payo, A., Acker, P., Bocedi, G., Travis, J. M. J., Burthe, S. J., Harris, M. P., Wanless, S., Newell, M., Daunt, F., & Reid, J. M. (2022). Modelling the responses of partially migratory metapopulations to changing seasonal migration rates: From theory to data. *Journal of Animal Ecology, 91(9)*, 1781–96. https://doi.org/10.1111/1365-2656.13748.

Pennycuick, C. J., & Rudnai, J. (1970). A method of identifying individual lions *Panthera leo* with an analysis of the reliability of identification. *Journal of Zoology, 160(4)*, 497–508. https://doi.org/10.1111/j.1469-7998.1970.tb03093.x.

Penteriani, V., Ferrer, M., & Delgado, M. M. (2011). Floater strategies and dynamics in birds, and their importance in conservation biology: Towards an understanding of nonbreeders in avian populations. *Animal Conservation, 14(3)*, 233–41. https://doi.org/10.1111/j.1469-1795.2010.00433.x.

Penteriani, V., Otalora, F., & Ferrer, M. (2006). Floater dynamics can explain positive patterns of density-dependent fecundity in animal populations. *The American Naturalist, 168(5)*, 697–703. https://doi.org/10.1086/507995.

Posit team. (2023). RStudio: Integrated development environment for R. Posit Software, PBC, Boston, MA. http://www.posit.co/.

Pusey, A. E., & Packer, C. (1994). Infanticide in lions: consequences and counterstrategies. In S. Parmigiani, & F. vom Saal (Eds.) *Infanticide and Parental Care* (pp. 277–99). Taylor & Francis.

Quéroué, M., Barbraud, C., Barraquand, F., Turek, D., Delord, K., Pacoureau, N., & Gimenez, O. (2021). Multispecies integrated population model reveals bottom-up dynamics in a seabird predator–prey system. *Ecological Monographs, 91(3)*, e01459. https://doi.org/10.1002/ecm.1459.

R Core Team. (2022). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/.

Rankin, D. J., & Kokko, H. (2007). Do males matter? The role of males in population dynamics. *Oikos*, *116(2)*, 335–348. https://doi.org/10.1111/j.0030-1299.2007.15451.x.

Reed, T. E., Grøtan, V., Jenouvrier, S., Sæther, B.-E., & Visser, M. E. (2013). Population growth in a wild bird is buffered against phenological mismatch. *Science, 340(6131)*, 488–91. https://doi.org/10.1126/science.1232870.

Riggio, J., Caro, T., Dollar, L., Durant, S. M., Jacobson, A. P., Kiffner, C., Pimm, S. L., & van Aarde, R. J. (2016). Lion populations may be declining in Africa but not as Bauer et al. suggest. *Proceedings of the National Academy of Sciences, 113(2)*, E107–8. https://doi.org/10.1073/pnas.1521506113.

Rizopoulos, D. (2007). Ltm: An R package for latent variable modeling and item response analysis. *Journal of Statistical Software, 17*, 1–25. https://doi.org/10.18637/jss.v017.i05.

Sandvig, E. M., Coulson, T., Kikkawa, J., & Clegg, S. M. (2017). The influence of climatic variation and density on the survival of an insular passerine *Zosterops lateralis. PLoS ONE*, *12(4)*, e0176360. https://doi.org/10.1371/journal.pone.0176360.

Schaller, G. B. (1972). The Serengeti lion: A study of predator-prey relations. Wildlife Behavior and Ecology Series. University of Chicago Press.

Schaub, M., Gimenez, O., Schmidt, B. R., & Pradel, R. (2004). Estimating survival and temporary emigration in the multistate capture–recapture framework. *Ecology, 85(8)*, 2107–13. https://doi.org/10.1890/03-3110.

Sinclair, A. R. E., Mduma, S. A. R., & Arcese, P. (2000). What determines phenology and synchrony of ungulate breeding in Serengeti? *Ecology, 81(8)*, 2100–2111. https://doi.org/10.1890/0012-9658(2000)081[2100:WDPASO]2.0.CO;2.

Sinclair, A. R. E., Metzger, K. L., Fryxell, J. M., Packer, C., Byrom, A. E., Craft, M. E., Hampson, K., Lembo, T., Durant, S. M., Forrester, G. J., Bukombe, J., Mchetto, J., Dempewolf, J., Hilborn, R., Cleaveland, S., Nkwabi, A., Mosser, A., & Mduma, S. A. R. (2013). Asynchronous food-web pathways could buffer the response of Serengeti predators to El Niño Southern Oscillation. *Ecology, 94(5)*, 1123–30. https://doi.org/10.1890/12-0428.1.

Sinclair, A. R. E., & Norton-Griffiths, M. (1995). Serengeti: Dynamics of an ecosystem. University of Chicago Press.

Swenson, J. E. (2003). Implications of sexually selected infanticide for the hunting of large carnivores. In M. Festa-Bianchet, & M. Apollonio (Eds.) *Animal behavior and wildlife conservation* (pp. 171–189). Washington: Island Press.

Swift, R. J., Rodewald, A. D., Johnson, J. A., Andres, B. A., & Senner, N. R. (2020). Seasonal survival and reversible state effects in a long-distance migratory shorebird. *Journal of Animal Ecology*, *89(9)*, 2043–2055. https://doi.org/10.1111/1365-2656.13246.

Trinkel, M., & Angelici, F. M. (2016). The decline in the lion population in Africa and possible mitigation measures. In F. M. Angelici (Eds.) *Problematic Wildlife: A Cross-Disciplinary Approach* (pp. 45–68). Cham: Springer International Publishing.

https://doi.org/10.1007/978-3-319-22246-2_3.

de Valpine, P., Paciorek, C. J., Turek, D., Michaud, N., Anderson-Bergman, C., Obermeyer, F., Wehrhahn Cortes, C., Rodríguez, A., Temple Lang, D., Zhang, W., Paganin, S., Hug, J., Babu, J., Ponisio, L., & Sujan P. (2022). NIMBLE: MCMC, particle filtering, and programmable hierarchical modeling. R. 10.5281/zenodo.1211190. https://cran.r-project.org/package=nimble.

de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Temple Lang, D., & Bodik, R. (2017). Programming with models: Writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics, 26(2)*, 403–13. https://doi.org/10.1080/10618600.2016.1172487.

VanderWaal, K. L., Mosser, A., & Packer, C. (2009). Optimal group size, dispersal decisions and postdispersal relationships in female African lions. *Animal Behaviour, 77(4)*, 949–54. https://doi.org/10.1016/j.anbehav.2008.12.028.

Vinks, M. A., Creel, S., Schuette, P., Becker, M. S., Rosenblatt, E., Sanguinetti, C., Banda, K., Goodheart, B., Young-Overton, K., Stevens, X., Chifunte, C., Midlane, N., & Simukonda, C. (2021). Response of lion demography and dynamics to the loss of preferred larger prey. *Ecological Applications, 31(4)*, e02298. https://doi.org/10.1002/eap.2298.

Whitman, K., Starfield, A. M., Quadling, H. S., & Packer, C. (2004). Sustainable trophy hunting of African lions. *Nature, 428(6979)*, 175–78. https://doi.org/10.1038/nature02395.

Appendix S1 – Study area and habitat types

The lion study population was monitored in a 2000-km^2 area in the Serengeti National Park, Tanzania (-2°27' N, 34°48' E) (Packer & Pusey 1987; Fig. S1). The population inhabits two main habitat types: In the plains, food availability is strongly seasonal, with migratory herbivores passing through in the wet season but a scarcer prey availability in the dry seasons (Packer et al. 2005). Conversely, in the woodland, lions have access to resident herbivores the whole year.

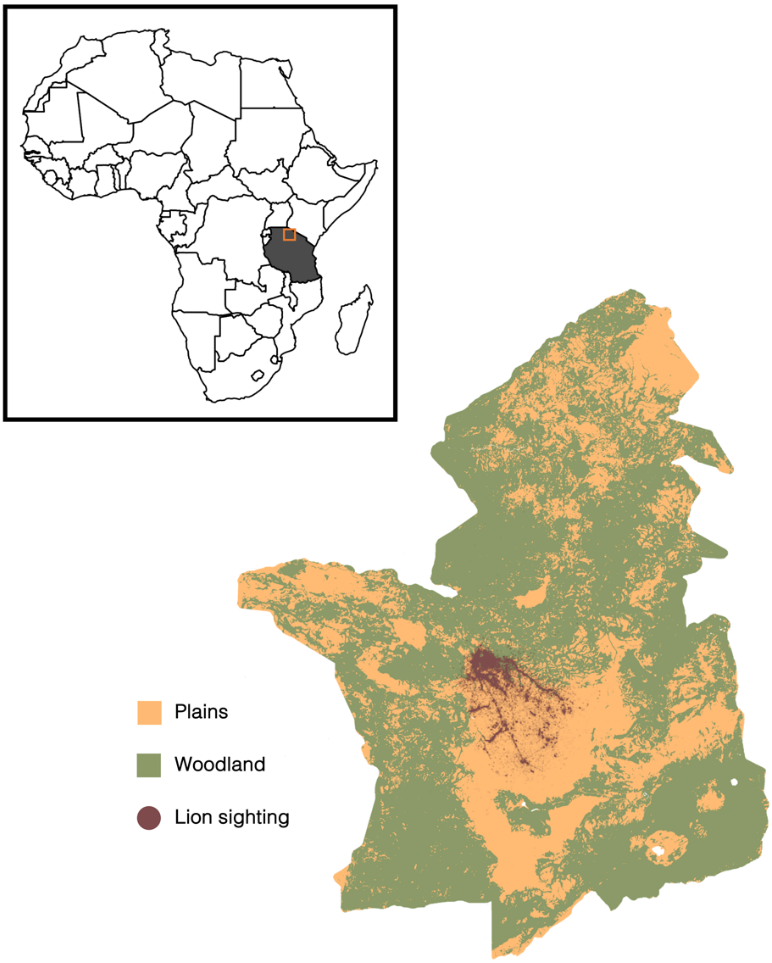


Figure S1 – Study area, habitat types, and lion sightings between 1984 and 2014. The studied population lives in the Serengeti National Park, Tanzania (inset map), and inhabits a region characterized by two main habitats: the plains (light orange areas), where food availability is strongly seasonal, and the woodland (light green areas), where lions have access to prey the whole year. The data on vegetation categories has been obtained by Grant Hopcraft from Reed et al. (2009) and is available at https://serengetidata.weebly.com/. Each transparent maroon dot represents the sighting of a single individual between 1984 and 2014.

References – Appendix S1

Packer, C., Hilborn, R., Mosser, A., Kissui, B., Borner, M., Hopcraft, G., Wilmshurst, J., Mduma, S., & Sinclair, A. R. E. (2005). Ecological change, group territoriality, and population dynamics in Serengeti lions. *Science, 307(5708)*, 390–93. https://doi.org/10.1126/science.1105122.

Packer, C., & Pusey, A. E. (1987). The evolution of sex-biased dispersal in lions. *Behaviour, 101(4)*, 275–310. https://doi.org/10.1163/156853987X00026.

Reed, D. N., Anderson, T. M., Dempewolf, J., Metzger, K., & Serneels, S. (2009). The spatial distribution of vegetation types in the Serengeti ecosystem: the influence of rainfall and topographic relief on vegetation patch characteristics. *Journal of Biogeography*, *36(4)*, 770–782. https://doi.org/10.1111/j.1365-2699.2008.02017.x.

Appendix S2 – Details on the model structure and custom likelihood distribution

Model structure

We used a Bayesian multistate capture-recapture model (Lebreton & Pradel 2002; Schaub et al. 2004) to estimate survival and transition rates as well as detection probabilities of pride individuals and nomadic males for the Serengeti lion population. The true, "latent" state of each individual in a given year, $\mathbf{z}_t$, is among 12 possible states. The first 10 states correspond to the 10 life-history stages we considered: (1) Young subadult ($\mathrm{SA_Y}$; 1–1.5 years) and old subadult (1.5–2 years), separated into (2) females ($\mathrm{SA_{O,F}}$) and (3) males ($\mathrm{SA_{O,M}}$), (4) adult females (AF; > 2 years), young males—(5) $\mathrm{YM_1}$ (2–2.5 years), (6) $\mathrm{YM_2}$ (2.5–3 years), (7) $\mathrm{YM_3}$ (3–3.5 years), and (8) $\mathrm{YM_4}$ (3.5–4 years)—,(9) nomadic male (NM; > 2 years and nomadic), and (10) resident male (RM; > 2 years and resident in a different pride). In addition, to take advantage of the dead-recovery data available for 105 individuals (i.e., lions found dead, as opposed to lions who died or left the study area unwitnessed), we followed Gauthier and Lebreton (2008) and used an additional, observable (11) newly dead state. This approach allows lions in any state to transition to newly dead with a probability of $1 - \mathrm{survival}$. Newly dead lions then transition to an absorbing, unobserved (12) permanently dead state with a probability of 1, and remain permanently dead afterwards.

The state process matrix (Fig. S1a) contains the transition probabilities among all 12 latent states. More specifically, these probabilities are conditional on the sex ratio (♀ ratio, fixed at 0.55; representing the proportion of lionesses and thus the probability of an individual being female), state-specific survival (σ_S), young-male emigration and transition to nomadic male ($\varphi_\mathrm{Em}{}^\mathrm{YM}$ and φ_YM), resident-male eviction (φ_Ev), and nomadic-male takeover (φ_T). The observation process matrix (Fig. S1b) contains the probabilities of observing a lion in its true state (i.e., detection probabilities). Due to the data collection method relying on finding a collared female in each pride, we assumed all lions belonging to a pride to have the same detection probability and therefore only estimated pride and nomad detection probabilities (p_pride and p_NM). In addition, we estimated the probability to observe a dead lion (p_dead).

(a)

$$\mathbf{State}_{t+1}$$

$$\mathbf{State}_{t}\quad \begin{array}{c|cccccccccccc}
 & \mathbf{SA_Y} & \mathbf{SA_{O,F}} & \mathbf{SA_{O,M}} & \mathbf{AF} & \mathbf{YM_1} & \mathbf{YM_2} & \mathbf{YM_3} & \mathbf{YM_4} & \mathbf{NM} & \mathbf{RM} & \mathbf{New.\ dead} & \mathbf{Perm.\ dead} \\
\hline
\mathbf{SA_Y} & 0 & \sigma_{\mathrm{SA_Y}} \cdot \text{♀ratio} & \sigma_{\mathrm{SA_Y}} \cdot (1 - \text{♀ ratio}) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 - \sigma_{\mathrm{SA_Y}} & 0 \\
\mathbf{SA_{O,F}} & 0 & 0 & 0 & \sigma_{\mathrm{SA_{O,F}}} & 0 & 0 & 0 & 0 & 0 & 0 & 1 - \sigma_{\mathrm{SA_{O,F}}} & 0 \\
\mathbf{SA_{O,M}} & 0 & 0 & 0 & 0 & \sigma_{\mathrm{SA_{O,M}}} & 0 & 0 & 0 & 0 & 0 & 1 - \sigma_{\mathrm{SA_{O,M}}} & 0 \\
\mathbf{AF} & 0 & 0 & 0 & \sigma_{\mathrm{AF}} & 0 & 0 & 0 & 0 & 0 & 0 & 1 - \sigma_{\mathrm{AF}} & 0 \\
\mathbf{YM_1} & 0 & 0 & 0 & 0 & 0 & \sigma_{\mathrm{YM}} \cdot (1 - \varphi_{\mathrm{Em}}^{\mathrm{YM}}) & 0 & 0 & \sigma_{\mathrm{YM}} \cdot \varphi_{\mathrm{Em}}^{\mathrm{YM}} \cdot \varphi_{\mathrm{YM}} & \sigma_{\mathrm{YM}} \cdot \varphi_{\mathrm{Em}}^{\mathrm{YM}} \cdot (1 - \varphi_{\mathrm{YM}}) & 1 - \sigma_{\mathrm{YM_1}} & 0 \\
\mathbf{YM_2} & 0 & 0 & 0 & 0 & 0 & 0 & \sigma_{\mathrm{YM}} \cdot (1 - \varphi_{\mathrm{Em}}^{\mathrm{YM}}) & 0 & \sigma_{\mathrm{YM}} \cdot \varphi_{\mathrm{Em}}^{\mathrm{YM}} \cdot \varphi_{\mathrm{YM}} & \sigma_{\mathrm{YM}} \cdot \varphi_{\mathrm{Em}}^{\mathrm{YM}} \cdot (1 - \varphi_{\mathrm{YM}}) & 1 - \sigma_{\mathrm{YM_2}} & 0 \\
\mathbf{YM_3} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \sigma_{\mathrm{YM}} \cdot (1 - \varphi_{\mathrm{Em}}^{\mathrm{YM}}) & \sigma_{\mathrm{YM}} \cdot \varphi_{\mathrm{Em}}^{\mathrm{YM}} \cdot \varphi_{\mathrm{YM}} & \sigma_{\mathrm{YM}} \cdot \varphi_{\mathrm{Em}}^{\mathrm{YM}} \cdot (1 - \varphi_{\mathrm{YM}}) & 1 - \sigma_{\mathrm{YM_3}} & 0 \\
\mathbf{YM_4} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \sigma_{\mathrm{YM}} \cdot \varphi_{\mathrm{YM}} & \sigma_{\mathrm{YM}} \cdot (1 - \varphi_{\mathrm{YM}}) & 1 - \sigma_{\mathrm{YM_4}} & 0 \\
\mathbf{NM} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \sigma_{\mathrm{NM}} \cdot (1 - \varphi_{\mathrm{T}}) & \sigma_{\mathrm{NM}} \cdot \varphi_{\mathrm{T}} & 1 - \sigma_{\mathrm{NM}} & 0 \\
\mathbf{RM} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \sigma_{\mathrm{RM}} \cdot \varphi_{\mathrm{Ev}} & \sigma_{\mathrm{RM}} \cdot (1 - \varphi_{\mathrm{Ev}}) & 1 - \sigma_{\mathrm{RM}} & 0 \\
\mathbf{New.\ dead} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \\
\mathbf{Perm.\ dead} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1
\end{array}$$

(b)

$$\mathbf{Observed}_{t}$$

$$\mathbf{State}_{t}\quad \begin{array}{c|cccccccccccc}
 & \mathbf{SA_Y} & \mathbf{SA_{O,F}} & \mathbf{SA_{O,M}} & \mathbf{AF} & \mathbf{YM_1} & \mathbf{YM_2} & \mathbf{YM_3} & \mathbf{YM_4} & \mathbf{NM} & \mathbf{RM} & \mathbf{Dead} & \mathbf{Unobserved} \\
\hline
\mathbf{SA_Y} & 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\mathbf{SA_{O,F}} & 0 & p_{\mathrm{pride}} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 - p_{\mathrm{pride}} \\
\mathbf{SA_{O,M}} & 0 & 0 & p_{\mathrm{pride}} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 - p_{\mathrm{pride}} \\
\mathbf{AF} & 0 & 0 & 0 & p_{\mathrm{pride}} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 - p_{\mathrm{pride}} \\
\mathbf{YM_1} & 0 & 0 & 0 & 0 & p_{\mathrm{pride}} & 0 & 0 & 0 & 0 & 0 & 0 & 1 - p_{\mathrm{pride}} \\
\mathbf{YM_2} & 0 & 0 & 0 & 0 & 0 & p_{\mathrm{pride}} & 0 & 0 & 0 & 0 & 0 & 1 - p_{\mathrm{pride}} \\
\mathbf{YM_3} & 0 & 0 & 0 & 0 & 0 & 0 & p_{\mathrm{pride}} & 0 & 0 & 0 & 0 & 1 - p_{\mathrm{pride}} \\
\mathbf{YM_4} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p_{\mathrm{pride}} & 0 & 0 & 0 & 1 - p_{\mathrm{pride}} \\
\mathbf{NM} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p_{\mathrm{NM}} & 0 & 0 & 1 - p_{\mathrm{NM}} \\
\mathbf{RM} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p_{\mathrm{pride}} & 0 & 1 - p_{\mathrm{pride}} \\
\mathbf{Dead} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & p_{\mathrm{dead}} & 1 - p_{\mathrm{dead}}
\end{array}$$

Figure S1 – State and observation process matrices. (a) The state process matrix represents the transitions among all twelve true states between time *t* (rows) and *t*+1 (columns), conditional on the sex ratio (♀ ratio) and the survival (*σ*) and transition parameters (*φ*). (b) The observation process matrix represents detection probabilities (*p*), that is, probabilities of observing an individual in a given state (columns) depending on its true state (rows).

Custom likelihood distribution

Given the high number of parameters estimated in our model, we used the opportunity offered by NIMBLE (de Valpine et al. 2017) to create custom distributions and built a custom likelihood distribution allowing us to integrate over latent states (Turek et al. 2016). This avoids the estimation of the true state of each individual at each timestep, consequently greatly reducing the dimension of the MCMC posterior distribution. Additionally, instead of the arrays commonly used in Bayesian multistate models, we rely on vectors (**pi** and **Zpi**), allowing us to use one-dimensional linear algebra instead of matrix algebra to estimate the probabilities and transitions between states. This reduces the memory requirements and running time of the model (by removing latent states corresponding to the true state of an individual at a given time; see Nater et al. 2020 for details). To create this distribution (*dDHMMlionKF*, referring to discrete Hidden Markov Model for lions, including known fate), we used the *nimbleFunction* function of the *nimble* package (version 1.0.1; de Valpine et al. 2017) and provide a description of the various parameters used in the function below. 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*). 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**.

Below, we print the code for the custom distribution. The code can also be found on GitHub at [GitHub link placeholder] and on Zenodo [citation placeholder].

```
# States (S):

# 1 Subadult 1
# 2 Subadult 2 Female
# 3 Subadult 2 Male
# 4 Adult Female
# 5 Young Male 1
# 6 Young Male 2
# 7 Young Male 3
# 8 Young Male 4
# 9 Nomadic Male
# 10 Resident Male
# 11 Newly dead
# 12 Permanently dead


# Observations (O):

# 1 seen as Subadult 1
# 2 seen as Subadult 2 Female
# 3 seen as Subadult 2 Male
# 4 seen as Adult Female
# 5 seen as Young Male 1
# 6 seen as Young Male 2
# 7 seen as Young Male 3
# 8 seen as Young Male 4
# 9 seen as Nomadic Male
# 10 seen as Resident Male
# 11 seen dead
# 13 not seen


dDHMM_lionKF <- nimbleFunction(
  run = function(

      ## Argument type declarations

      x = double(1),          # Vector containing the observed capture history
data
      length = double(),      # Length of the capture history
      init = double(1),       # Initial state probabilities
      survSA1 = double(1),    # State-specific survival
      survSA2F = double(1),
      survSA2M = double(1),
      survAF = double(1),
      survYM = double(1),
      survNM = double(1),
      survRM = double(1),
      transYMNM = double(1),  # Between-state transitions
      emigYM = double(1),
      takeover = double(1),
      eviction = double(1),
      dpPride = double(1),    # Detection probabilities
      dpNM = double(1),
      dpDead = double(1),
      log = double()){        # Logical argument specifying whether the log of
the likelihood should be returned

      logL <- 0               # Initialise log-likelihood
      pi <- init              # Initialise state probabilities
```

```
      for(t in 1:length){     # Iterate over observations

      # x = "recorded as"
      # pi = probability of each latent state, conditioned on preceding
observations
      # Zpi = probability of current observed capture, conditioned on each
possible latent state

      Zpi <- pi # Initialise Zpi with the values of pi to avoid assigning
                # values to Zpi when the observation probability of a given
                # latent state in a given observed state is 1 (e.g. Zpi[12]
                # when x[t] == 13, as permanently dead individuals will
                # always be unobserved).

      # Detection probabilities

      if(x[t] == 1){

      # We do not assign any value to Zpi[1] here because the latent state 1
      # "young subadults" is the first state defined in our model. Therefore,
      # in the capture histories, observations are either (1) an NA if
      # the first capture of an individual took place when it was older than
      # 1.5 years, or (2) a 1 if the first capture happened when
      # it was between 1 and 1.5 years old.

      Zpi[2] <- 0
      Zpi[3] <- 0
      Zpi[4] <- 0
      Zpi[5] <- 0
      Zpi[6] <- 0
      Zpi[7] <- 0
      Zpi[8] <- 0
      Zpi[9] <- 0
      Zpi[10] <- 0
      Zpi[11] <- 0
      Zpi[12] <- 0

      }

      if(x[t] == 2){

      Zpi[1] <- 0
      Zpi[2] <- pi[2] * dpPride[t]
      Zpi[3] <- 0
      Zpi[4] <- 0
      Zpi[5] <- 0
      Zpi[6] <- 0
      Zpi[7] <- 0
      Zpi[8] <- 0
      Zpi[9] <- 0
      Zpi[10] <- 0
      Zpi[11] <- 0
      Zpi[12] <- 0

      }

      if(x[t] == 3){

      Zpi[1] <- 0
```

```
        Zpi[2] <- 0
        Zpi[3] <- pi[3] * dpPride[t]
        Zpi[4] <- 0
        Zpi[5] <- 0
        Zpi[6] <- 0
        Zpi[7] <- 0
        Zpi[8] <- 0
        Zpi[9] <- 0
        Zpi[10] <- 0
        Zpi[11] <- 0
        Zpi[12] <- 0

        }

        if(x[t] == 4){

        Zpi[1] <- 0
        Zpi[2] <- 0
        Zpi[3] <- 0
        Zpi[4] <- pi[4] * dpPride[t]
        Zpi[5] <- 0
        Zpi[6] <- 0
        Zpi[7] <- 0
        Zpi[8] <- 0
        Zpi[9] <- 0
        Zpi[10] <- 0
        Zpi[11] <- 0
        Zpi[12] <- 0

        }

        if(x[t] == 5){

        Zpi[1] <- 0
        Zpi[2] <- 0
        Zpi[3] <- 0
        Zpi[4] <- 0
        Zpi[5] <- pi[5] * dpPride[t]
        Zpi[6] <- 0
        Zpi[7] <- 0
        Zpi[8] <- 0
        Zpi[9] <- 0
        Zpi[10] <- 0
        Zpi[11] <- 0
        Zpi[12] <- 0

        }

        if(x[t] == 6){

        Zpi[1] <- 0
        Zpi[2] <- 0
        Zpi[3] <- 0
        Zpi[4] <- 0
        Zpi[5] <- 0
        Zpi[6] <- pi[6] * dpPride[t]
        Zpi[7] <- 0
        Zpi[8] <- 0
        Zpi[9] <- 0
        Zpi[10] <- 0
```

```
        Zpi[11] <- 0
        Zpi[12] <- 0

        }

        if(x[t] == 7){

        Zpi[1] <- 0
        Zpi[2] <- 0
        Zpi[3] <- 0
        Zpi[4] <- 0
        Zpi[5] <- 0
        Zpi[6] <- 0
        Zpi[7] <- pi[7] * dpPride[t]
        Zpi[8] <- 0
        Zpi[9] <- 0
        Zpi[10] <- 0
        Zpi[11] <- 0
        Zpi[12] <- 0

        }

        if(x[t] == 8){

        Zpi[1] <- 0
        Zpi[2] <- 0
        Zpi[3] <- 0
        Zpi[4] <- 0
        Zpi[5] <- 0
        Zpi[6] <- 0
        Zpi[7] <- 0
        Zpi[8] <- pi[8] * dpPride[t]
        Zpi[9] <- 0
        Zpi[10] <- 0
        Zpi[11] <- 0
        Zpi[12] <- 0

        }

        if(x[t] == 9){

        Zpi[1] <- 0
        Zpi[2] <- 0
        Zpi[3] <- 0
        Zpi[4] <- 0
        Zpi[5] <- 0
        Zpi[6] <- 0
        Zpi[7] <- 0
        Zpi[8] <- 0
        Zpi[9] <- pi[9] * dpNM[t]
        Zpi[10] <- 0
        Zpi[11] <- 0
        Zpi[12] <- 0

        }
```

```
if(x[t] == 10){

Zpi[1] <- 0
Zpi[2] <- 0
Zpi[3] <- 0
Zpi[4] <- 0
Zpi[5] <- 0
Zpi[6] <- 0
Zpi[7] <- 0
Zpi[8] <- 0
Zpi[9] <- 0
Zpi[10] <- pi[10] * dpPride[t]
Zpi[11] <- 0
Zpi[12] <- 0

}

if(x[t] == 11){

Zpi[1] <- 0
Zpi[2] <- 0
Zpi[3] <- 0
Zpi[4] <- 0
Zpi[5] <- 0
Zpi[6] <- 0
Zpi[7] <- 0
Zpi[8] <- 0
Zpi[9] <- 0
Zpi[10] <- 0
Zpi[11] <- pi[11] * dpDead[t]
Zpi[12] <- 0

}

if(x[t] == 13){

Zpi[1] <- 0
Zpi[2] <- pi[2] * (1 - dpPride[t])
Zpi[3] <- pi[3] * (1 - dpPride[t])
Zpi[4] <- pi[4] * (1 - dpPride[t])
Zpi[5] <- pi[5] * (1 - dpPride[t])
Zpi[6] <- pi[6] * (1 - dpPride[t])
Zpi[7] <- pi[7] * (1 - dpPride[t])
Zpi[8] <- pi[8] * (1 - dpPride[t])
Zpi[9] <- pi[9] * (1 - dpNM[t])
Zpi[10] <- pi[10] * (1 - dpPride[t])
Zpi[11] <- pi[11] * (1- dpDead[t])

# We do not assign any value to Zpi[12] here because individuals in
# the latent state 12 "permanently dead" are always unobserved
# (observed state 13). The value of Zpi[12] is therefore the one it has
# been initialised with (pi[12])

}

sumZpi <- sum(Zpi)         # Log-likelihood contribution of given
                           # observed state x
logL <- logL + log(sumZpi) # Overall log likelihood
```

```
      # Transition probabilities

      if(t != length){

      pi[1] <- 0
      pi[2] <- Zpi[1] * survSA1[t] * 0.55
      pi[3] <- Zpi[1] * survSA1[t] * (1 - 0.55)
      pi[4] <- Zpi[2] * survSA2F[t] + Zpi[4] * survAF[t]
      pi[5] <- Zpi[3] * survSA2M[t]
      pi[6] <- Zpi[5] * survYM[t] * (1 - emigYM[t])
      pi[7] <- Zpi[6] * survYM[t] * (1 - emigYM[t])
      pi[8] <- Zpi[7] * survYM[t] * (1 - emigYM[t])
      pi[9] <- Zpi[5] * survYM[t] * emigYM[t] * transYMNM[t] +
               Zpi[6] * survYM[t] * emigYM[t] * transYMNM[t] +
               Zpi[7] * survYM[t] * emigYM[t] * transYMNM[t] +
               Zpi[8] * survYM[t] * transYMNM[t] +
               Zpi[9] * survNM[t] * (1 - takeover[t]) +
               Zpi[10] * survRM[t] * eviction[t]
      pi[10] <- Zpi[5] * survYM[t] * emigYM[t] * (1 - transYMNM[t]) +
                Zpi[6] * survYM[t] * emigYM[t] * (1 - transYMNM[t]) +
                Zpi[7] * survYM[t] * emigYM[t] * (1 - transYMNM[t]) +
                Zpi[8] * survYM[t] * (1 - transYMNM[t]) +
                Zpi[9] * survNM[t] * takeover[t] +
                Zpi[10] * survRM[t] * (1 - eviction[t])
      pi[11] <- Zpi[1] * (1 - survSA1[t]) +
                Zpi[2] * (1 - survSA2F[t]) +
                Zpi[3] * (1 - survSA2M[t]) +
                Zpi[4] * (1 - survAF[t]) +
                Zpi[5] * (1 - survYM[t]) +
                Zpi[6] * (1 - survYM[t]) +
                Zpi[7] * (1 - survYM[t]) +
                Zpi[8] * (1 - survYM[t]) +
                Zpi[9] * (1 - survNM[t]) +
                Zpi[10] * (1 - survRM[t])
      pi[12] <- Zpi[11] + Zpi[12]

      pi <- pi / sumZpi  # Normalise
      }
    }

      returnType(double())

      if(log) return(logL) else return(exp(logL)) # Return log-likelihood
  }
)
```

x	Vector of the observed capture history data
length	Length of the capture history
init	Initial state probabilities
survSA1	Young-subadult survival
survSA2F	Female old-subadult survival
survSA2M	Male old-subadult survival

survAF	Adult-female survival
survYM	Young-male survival
survNM	Nomadic-male survival
survRM	Resident-male survival
transYMNM	Probability of transition between young male and nomadic male
emigYM	Young-male emigration probability
takeover	Nomadic-male takeover probability
eviction	Resident-male eviction probability
dpPride	Pride member detection probability
dpNM	Nomadic-male detection probability
dpDead	Dead detection probability
log	Logical parameter defining whether the log likelihood is returned
logL	Log likelihood of the observed capture history
pi	Latent state probability conditional on observations in previous steps
Zpi	Current observed capture probability conditional on each latent state
sumZpi	Likelihood of a given observation, or marginal probability of current observed capture

References – Appendix S2

Gauthier, G., & Lebreton, J.-D. (2008). Analysis of band-recovery data in a multistate capture-recapture framework. *Canadian Journal of Statistics, 36(1)*, 59–73. https://doi.org/10.1002/cjs.5550360107x.

Lebreton, J.-D., & Pradel, R. (2002). Multistate recapture models: Modelling incomplete individual histories. *Journal of Applied Statistics, 29(1–4)*, 353–69. https://doi.org/10.1080/02664760120108638.

Nater, C. R., Vindenes, Y., Aass, P., Cole, D., Langangen, Ø., Moe, S. J., Rustadbakken, A., Turek, D., Vøllestad, L. A., & Ergon, T. (2020). Size- and stage-dependence in cause-specific mortality of migratory brown trout. *Journal of Animal Ecology, 89(9)*, 2122–33. https://doi.org/10.1111/1365-2656.13269.

Schaub, M., Gimenez, O., Schmidt, B. R., & Pradel, R. (2004). Estimating survival and temporary emigration in the multistate capture–recapture framework. *Ecology, 85(8)*, 2107–13. https://doi.org/10.1890/03-3110.

Turek, D., de Valpine, P., & Paciorek, C. J. (2016). Efficient Markov Chain Monte Carlo sampling for hierarchical Hidden Markov Models. *Environmental and Ecological Statistics, 23(4)*, 549–64. https://doi.org/10.1007/s10651-016-0353-z.

de Valpine, P., Turek, D., Paciorek, C. J., Anderson-Bergman, C., Temple Lang, D., & Bodik, R. (2017). Programming with models: Writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics, 26(2)*, 403–13. https://doi.org/10.1080/10618600.2016.1172487.

Appendix S3 – Female recruitment

In our study, following previous research on the Serengeti lion, we defined recruitment as the number of cubs reaching their first birthday (Packer et al. 2001). Because females raise their cubs in crèches, we could not unequivocally assign a true mother to 42% of the cubs (i.e., at least two females could be the mother or the cub had no potential mother assigned). While in previous studies females could be assigned 0.5 cubs (Packer et al. 2001), we relied on observed data on litter size (i.e., integers only) for females identified as the only known mother of cubs to assign the remaining cubs to females. That is, we first used data on cubs with known mothers to assign the total number of cubs with a unique ID–i.e., regardless of whether they survived their first year—to the right females in each seasonal timestep *t*. From the obtained number of identified cubs per female per timestep *t*, we created an observed litter-size distribution. We used this distribution to assign a litter ID to the cubs left with several potential mothers and born on the same day. For example, for a group of five cubs born on the same day in the same pride and two possible mothers, two different litters of two and three cubs are more likely to be created than a litter of five cubs from a single female (Fig. S1). For each litter, we then chose the potential mothers in order of priority: (1) among the potential mothers assigned to the cub by the observer, or, if all potential mothers already had alive, independent offspring (i.e. young < 2 years old), (2) randomly among the adult females (i.e. > 2 years old) belonging to the natal pride of the cubs in the birth season of the cubs.

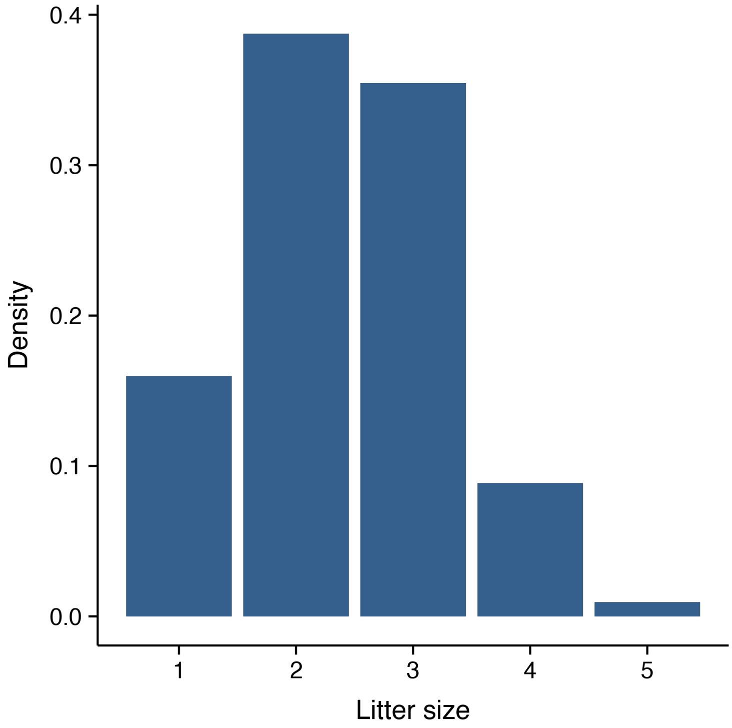


Figure S1 – Distribution of female litter size in the dataset. We used data on cubs with a single assigned mother to create an observed distribution of litter size (i.e., number of cubs per female including cubs lost before their first birthday) and assign mothers to cubs with no or several potential mothers.

To obtain the recruitment per reproducing female (i.e., the number of yearlings), we followed the life history of each cub and removed it from the litter if it died before its first birthday. In addition, we assigned zero cubs to females who lost their litter (recognized by lactation stains with no cubs observed; Packer 2023). In some cases, the number of cubs observed in a given pride was too high for the litter size per female to be kept at the maximum observed litter size (i.e., five cubs). This is likely because some females in the focal pride were not observed in the birth season of the cubs, and we therefore did not assign those cubs to any female (<1% of the total number of cubs). The resulting distribution of female recruitment (i.e., number of cubs ≥1 year old per reproducing female) on the whole dataset resembles that of the observed recruitment (Fig. S2).

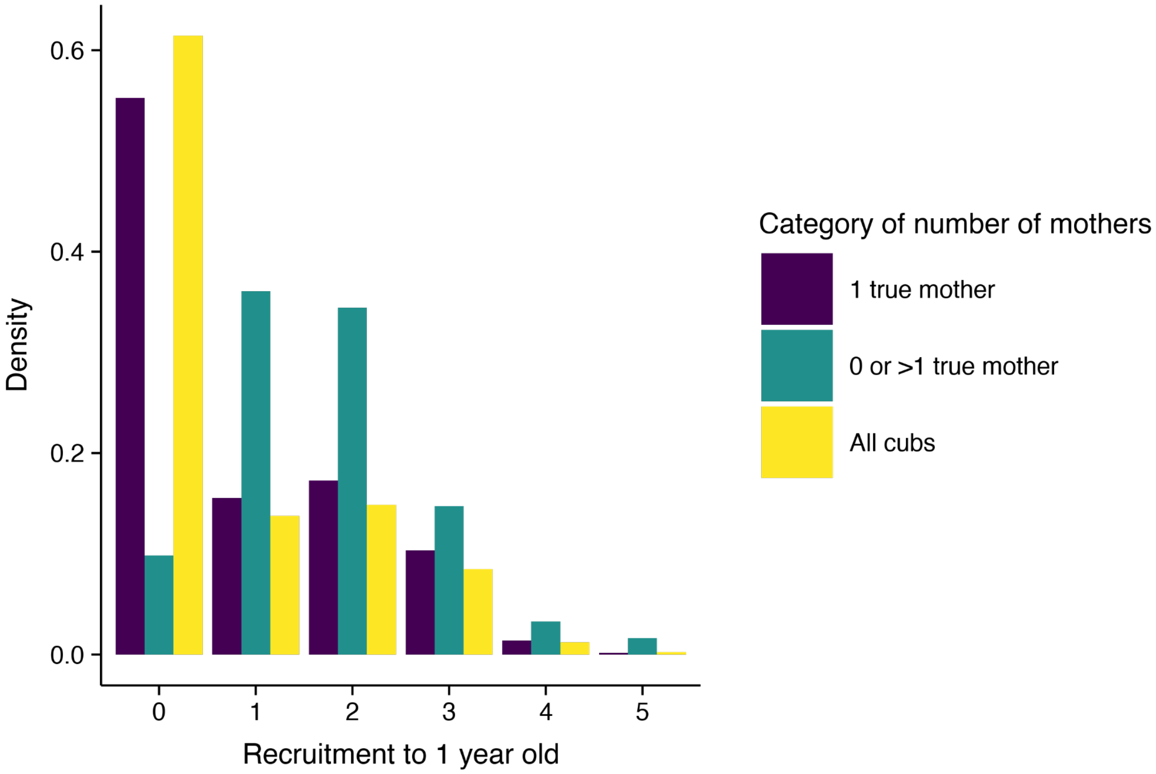


Figure S2 – Distribution of female recruitment in the dataset. We used data on cubs with a single assigned mother (1 true mother) to create an observed distribution of litter size (i.e., number of cubs per female including cubs lost before their first birthday) and assign mothers to cubs with no or several potential mothers (0 or >1 true mother). Although the distribution for cubs with no or more than one potential mother does not match that for the cubs with a single potential mother, the final distribution of recruitment (i.e., number of yearlings per female) in the full dataset (all cubs) matches it quite well.

References – Appendix S3

Packer, C. (2023). The lion: Behavior, ecology, and conservation of an iconic species. Princeton University Press.

Packer, C., Pusey, A. E., & Eberly, L. E. (2001). Egalitarianism in female African lions. *Science, 293(5530)*, 690–93. https://doi.org/10.1126/science.1062320.

Appendix S4 – Number of nomadic coalitions in the home range of a pride

The effect of nomadic males on lion demography has previously been assessed by looking at the number of nomadic coalitions entering the study area, that is, at the population level (Borrego et al. 2018). Throughout the study period (1984–2014), nomadic coalitions (i.e., coalitions of males above 2 years old that do not belong to a pride) in the study area have been recorded through opportunistic sightings during monitoring of prides (Borrego et al. 2018).

In our study, we assessed the response of survival, stage transitions, and reproductive rates to the presence of nomadic males by testing for the effect of the number of nomadic coalitions within any given pride home range. Because resident males spend only about 15% of their time with females of the pride (Packer 2023), we calculated separate home ranges for resident males and for other pride individuals (i.e., subadults, young males, and adult females of the same pride). That is, we used the GPS locations of individuals in a given male coalition or pride to compute the 95% kernel utilization distribution using the *kernelUD* and *getverticesHR* functions of the *adehabitatHR* R package (version 0.4.20; Calenge 2006)—with the *ad hoc* method "href" for the smoothing parameter of the bivariate normal kernel. Using the utilization distribution of each group (i.e., resident-male coalition or pride), we assessed the presence of nomadic coalitions by computing the overlap between the home range of a group and the GPS locations of nomads in a given coalition, using the *over* function of the *sp* R package (version 1.4-7; Pebesma & Bivand 2005; Bivand et al. 2013). We added a nomadic coalition to the list of coalitions in a home range if the overlap was >0, that is, if at least one individual in the focal nomadic coalition was observed in the home range of a coalition or pride. We could not calculate a home range for resident coalitions or prides for which we only had five or less locations and thus assigned NA to the number of nomadic coalitions in the home range of these groups.

References – Appendix S4

Bivand, R. S., Pebesma, E., & Gómez-Rubio, V. (2013). Applied Spatial Data Analysis with R. 2nd edition. UseR! Series. Springer. https://doi.org/10.1007/978-1-4614-7618-4.

Borrego, N., Ozgul, A., Slotow, R., & Packer, C. (2018). Lion population dynamics: Do nomadic males matter? *Behavioral Ecology, 29(3)*, 660–66. https://doi.org/10.1093/beheco/ary018.

Calenge, C. (2006). The package ‘adehabitat’ for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling, 197(3)*, 516–19. https://doi.org/10.1016/j.ecolmodel.2006.03.017.

Packer, C. 2023. The lion: Behavior, ecology, and conservation of an iconic species. Princeton University Press.

Pebesma, E., & Bivand, R. S. (2005). Classes and methods for spatial data in R. *R News, 5(2)*, 9–13.

Appendix S5 – Additional results, parameter identifiability, and posterior predictive checks

Effects of density-dependent factors and habitat on lion vital rates

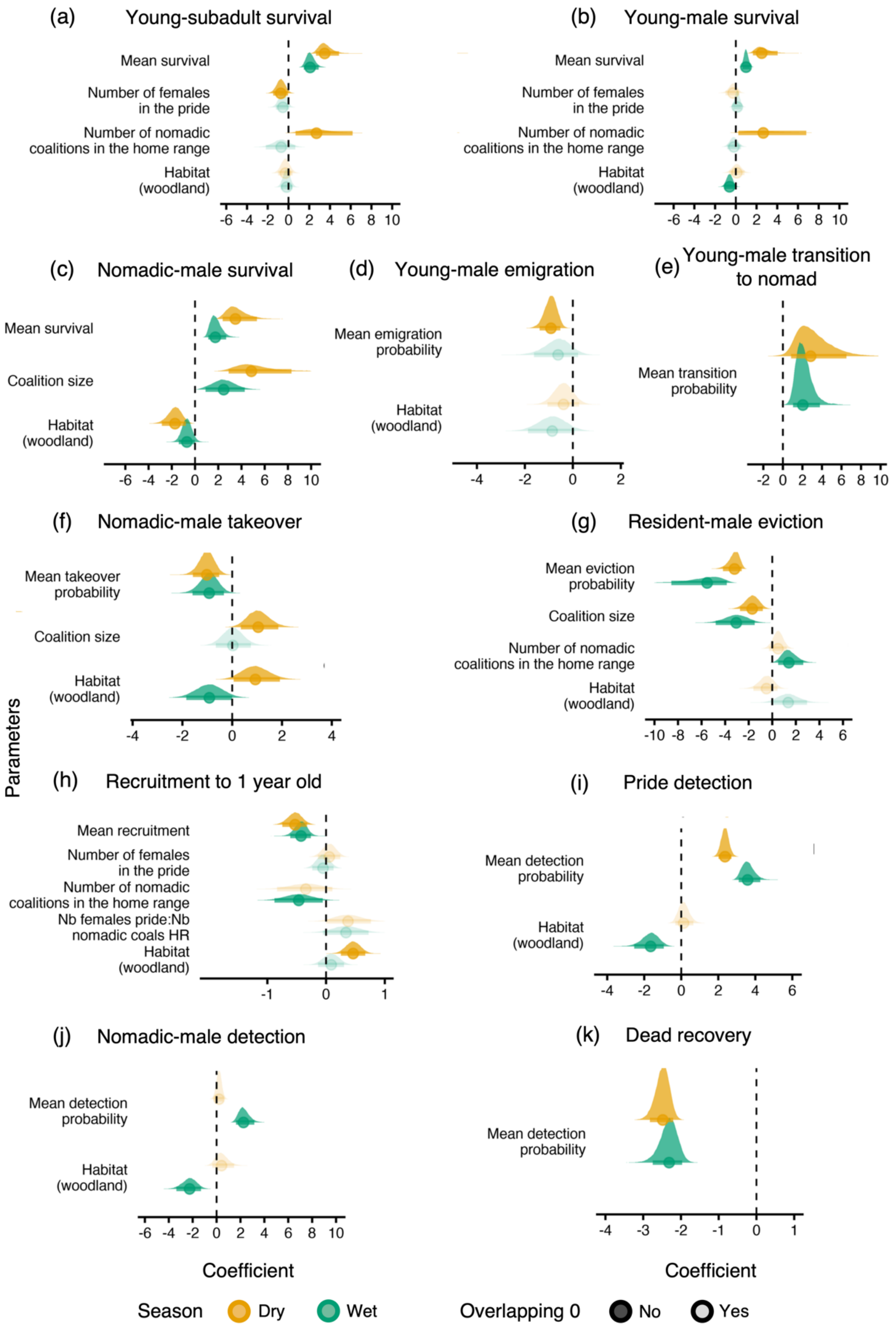


Figure S1 - Seasonal effects of habitat and within- and among-group density variables on lion vital rates. We investigated season-specific effects of within-group density (number of adult females and coalition size), the number of nomadic males in the home range, and habitat (plains or woodland) on the survival of (a) young subadults, (b) young males, and (c) nomadic males; (d) young-male emigration probability and (e) their probability to become nomadic after emigrating; probabilities of (f) nomadic-male takeover and (g) resident-male eviction; (h) recruitment to 1 year old; and detection probabilities of (i) pride individuals, (j) nomads, and (k) dead individuals. On each plot, the median (dots) and 90% Credible Interval (CRI; lines) of each coefficient (on the logit scale) were obtained from the posterior samples of the multistate capture-recapture model and the GLMMs. Density plots show the posterior distribution of each parameter. Shaded dots and CRIs are used for coefficients of effects for which there was little evidence in the data (i.e., 90% CRI overlapping with zero).

Posterior distributions for random year effects

The season-specific yearly random-effect parameters showed seasonal differences in most years for most vital rates and detection probabilities (Fig. S2), indicating a potential effect of a seasonal variable our models did not explicitly account for. While we did not find any noticeable temporal trend in the random effects, their variation was higher in the wet season for most survival rates, and in the dry season for most transition rates. This stronger yearly variation in specific seasons for specific groups of vital rates could be an indicator of important seasonal factors that were not included in our model. Young- to nomadic-male transition was an exception to this pattern, as the variability in random effects was much greater in the wet season. While the lack of data on this transition rate prevented us from testing for the effect of density, this variability is likely due to a covariate linked especially to the wet season that we did not explicitly account for.

Because of the complexity of our models and our decision to focus on the effect of socially-explicit density measures, we could not include effects of overall population size and rainfall in our multistate capture-recapture model and GLMMs. However, to assess a potential effect of these two variables, we calculated the Pearson correlation coefficients between both variables and every posterior sample of every vital rate and detection parameter. The distribution of correlation coefficients enables us to identify vital rates for which variation might be associated with changes in population size or rainfall (no or a small overlap with 0, represented by the orange line), or not (large overlap with 0). The resulting posterior distributions of correlation coefficients do not indicate additional effects of seasonal rainfall for any vital rate (Fig. S3). However, while our models did not reveal any effect of the considered density measures on adult-female survival, we find evidence for potential effects of overall population size on this vital rate. Additionally, we find a potential association between population size and young-male emigration, resident-male eviction, and pride detection probability (Fig. S3).

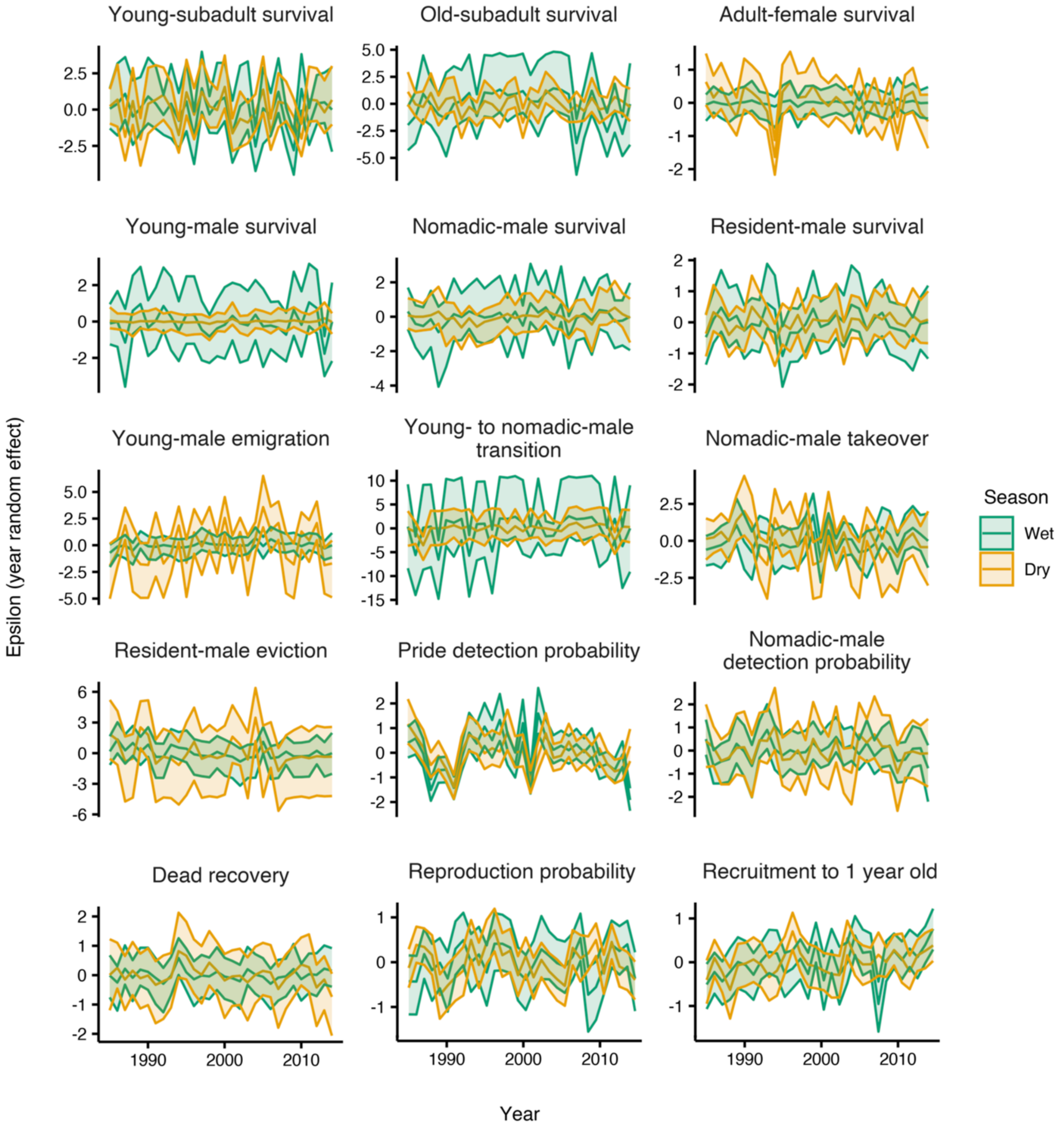


Figure S2 - Season-specific yearly random effects. In each model, we included a season-specific yearly random effect. For old-subadult survival, while the intercept depends on the sex, the random effect is shared for both males and females. The figure shows the season-specific mean random effect value (line) and the 90% credible interval (shaded ribbon) as a function of the year.

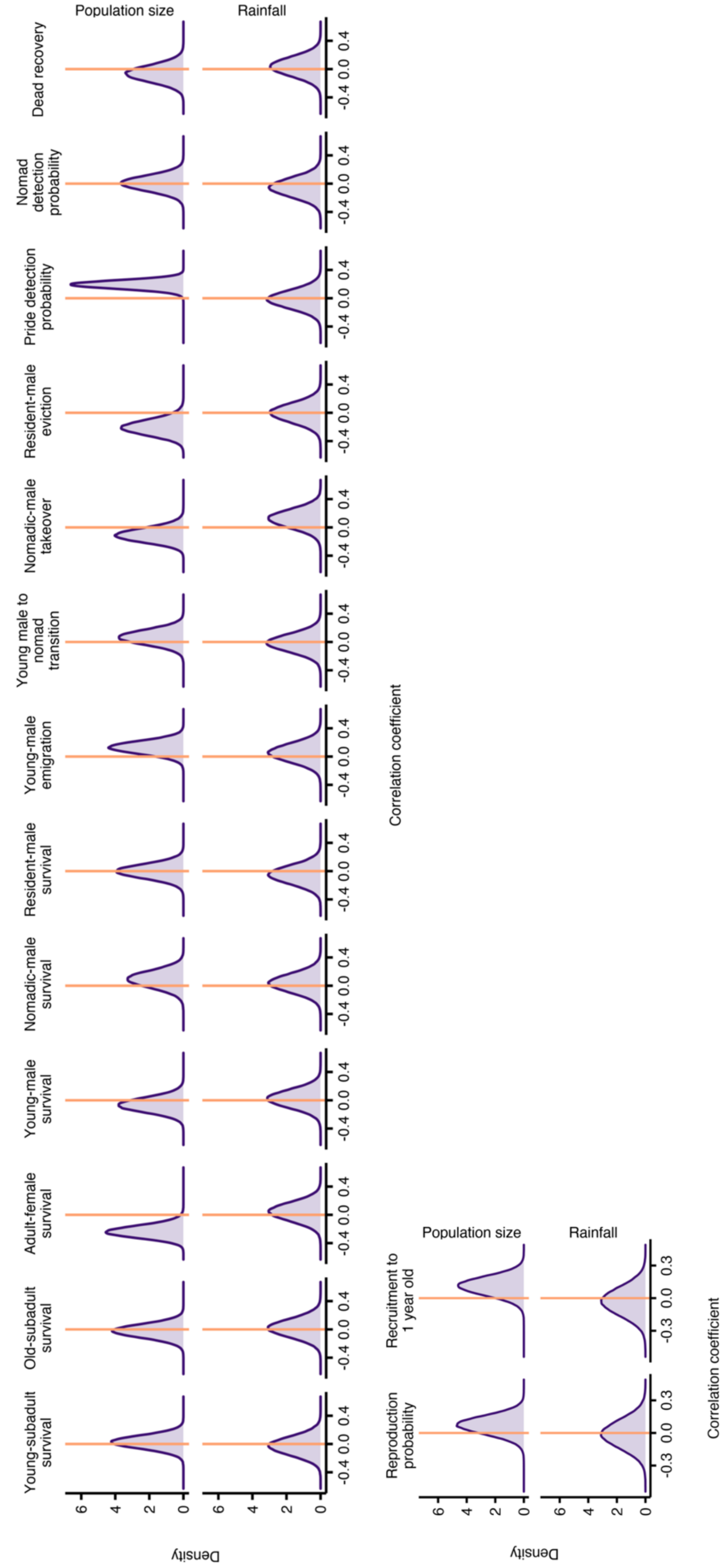


Figure S3 - Distribution of the Pearson correlation coefficients between the season-specific random effects of each vital rate model and two covariates: rainfall and population size. Posterior distributions (purple) of Pearson correlation coefficients between each MCMC sample of season-specific yearly random effects and potential additional covariates overall population size and seasonal rainfall. The orange vertical line marks “no correlation” (i.e., correlation coefficient = 0). The distribution of correlation coefficients enables us to identify vital rates for which variation might be associated with changes in population size or rainfall (no or a small overlap with 0, represented by the orange line), or not (large overlap with 0).

Additional discussion

In contrast with the other vital rates, which were affected by at least one measure of density (Fig. S1), our results suggest that adult-female survival is affected only by the habitat and age, and not by the density measures we considered. However, previous findings have indicated negative effects of neighbours on female survival due to higher wounding rates (Mosser & Packer 2009). In their study, Mosser and Packer investigated the response of adult-female survival to the number of individual neighbours (males or females only, or both), while we focused exclusively on the effect of nomadic males by calculating the number of nomadic coalitions in the home range of a pride without regard to the number of neighbours; this could explain the discrepancies between our results and that of previous studies. Importantly, however, our results indicate a potential negative effect of population size—which might be correlated with the number of neighbours—on adult-female survival (Fig. S3). Therefore, in this specific case, the lower-level density measures we included in our models might not be able to provide additional insights on the response of adult-female survival to density. Additionally, effects of neighbours could, be grasped by the habitat. Our results indicate a lower wet-season survival rate of adult females in the woodland than in the plains. While lions in both habitats can profit from a high prey availability in the wet season, lion—and thereby neighbour—densities can strongly increase in good quality habitats such as the woodland, where prey availability is more consistent between seasons (Hanby & Bygott 1979; VanderWaal et al. 2009). Therefore, neighbour lions in general might have stronger effects on female survival than nomadic coalitions specifically.

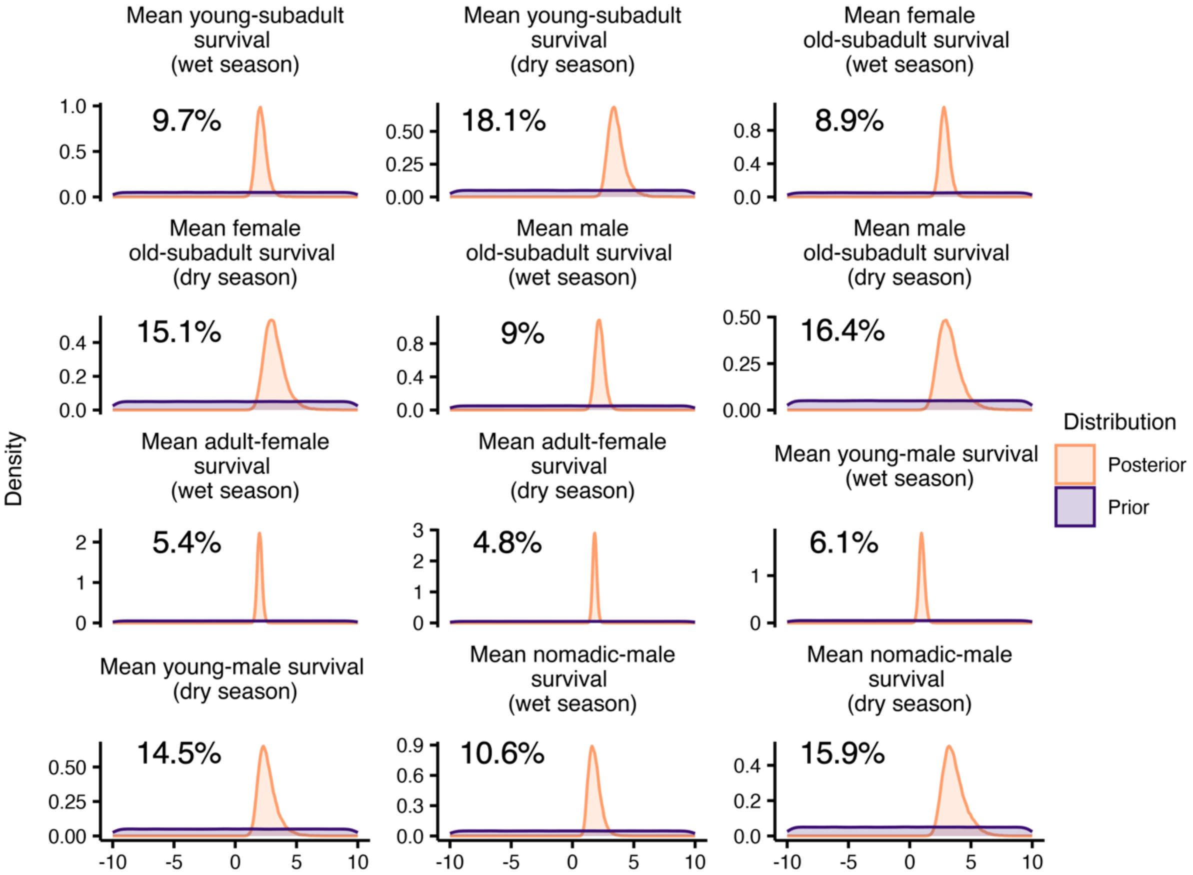
Previous studies showed notable effects of pride size on female reproductive output, with a higher number of cubs per female in average-sized prides (Packer et al. 1990; Packer 2023). However, while we found an effect of the number of females in a pride on the probability of a female reproducing in the wet season, our results showed no effect of females on recruitment (i.e., the number cubs surviving to one year old). Previous studies focused on female overall reproductive output, whereas we partitioned this output into two components: reproduction probability (i.e., the probability to become a reproducing female) and recruitment to 1 year old (i.e., the number of cubs reaching their first birthday per reproducing female). Although this approach enables us to assess the seasonal effects of density and habitat on each of these components, this partitioning potentially introduces a bias in the estimation of reproduction probability, which might be underestimated in our analyses. This is due to the lack of data on pregnancy resulting in lost litters for some females, especially solitary lionesses, who often fail to recruit cubs due to their limited access to high-quality territories (Packer 2023), and whose reproduction is seldom recorded. While females who were not seen reproducing (i.e., pregnant, with lactation stains, or with small cubs) had a recruitment of 0 in previous studies, we assigned them a reproduction of 0 and *NA* cubs. Many solitary females were thus considered as non-reproducing and excluded from the recruitment analysis despite some of them possibly having had unobserved cubs that did not survive until their first birthday. Our attribution of reproduction to adult females associated with the lack of an effect of pride size on recruitment indicates that solitary females struggle to raise cubs until their first birthday because they have to settle in poor-quality habitats and suffer more from wounding (Packer 2023). Consequently, belonging to a pride of at least two lionesses may be key to raising cubs until their first birthday, but two or ten females does not make any discernible difference.

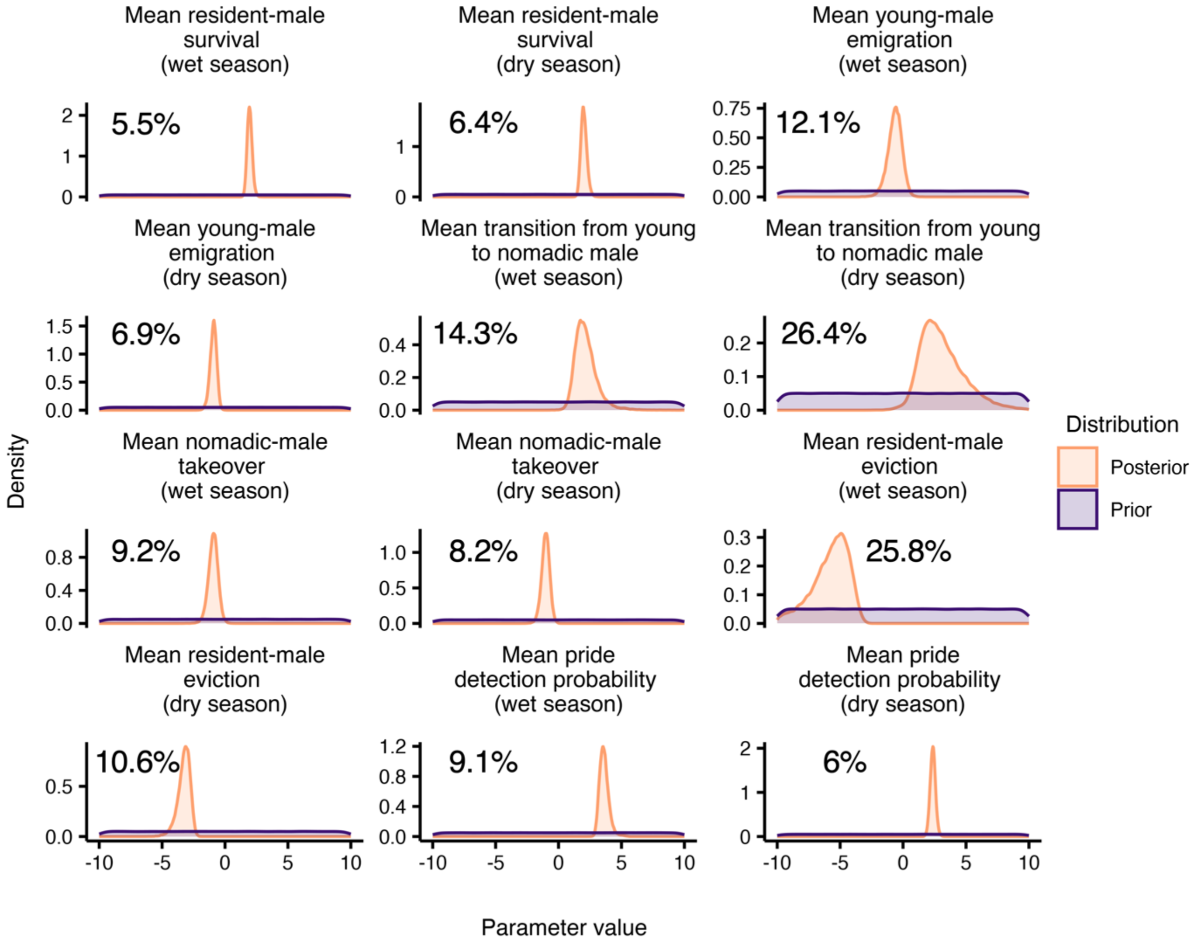
Overall, our definition of reproduction and recruitment leads to a lower number of females with 0 recruited cubs in our data, and any underestimation of reproduction probability subsequently leads to a corresponding overestimation in the recruitment per reproducing female. As a result, the combined reproductive output remains consistent with the measure used in previous analyses (e.g. Packer et al. 1990; Packer 2023), and investigating the season-specific effects of density and habitat on each component of reproduction is still possible—granted that the source of the bias is not correlated with these variables. Our results thus indicate that the effect of the number of females on overall reproduction might be more strongly influenced through probability of reproduction rather than recruitment. Alternatively, the discrepancies between previous results and ours might arise because, while our model does not account for differences in density effects between habitats or across time, effects of pride size are largely driven by habitat quality, which has varied over time (Packer 2023). Additionally—although we could not test for it—recruitment is driven to a considerable extent by the ability of the resident coalition to fend off rivals (Bygott et al. 1979; Pusey & Packer 1994).

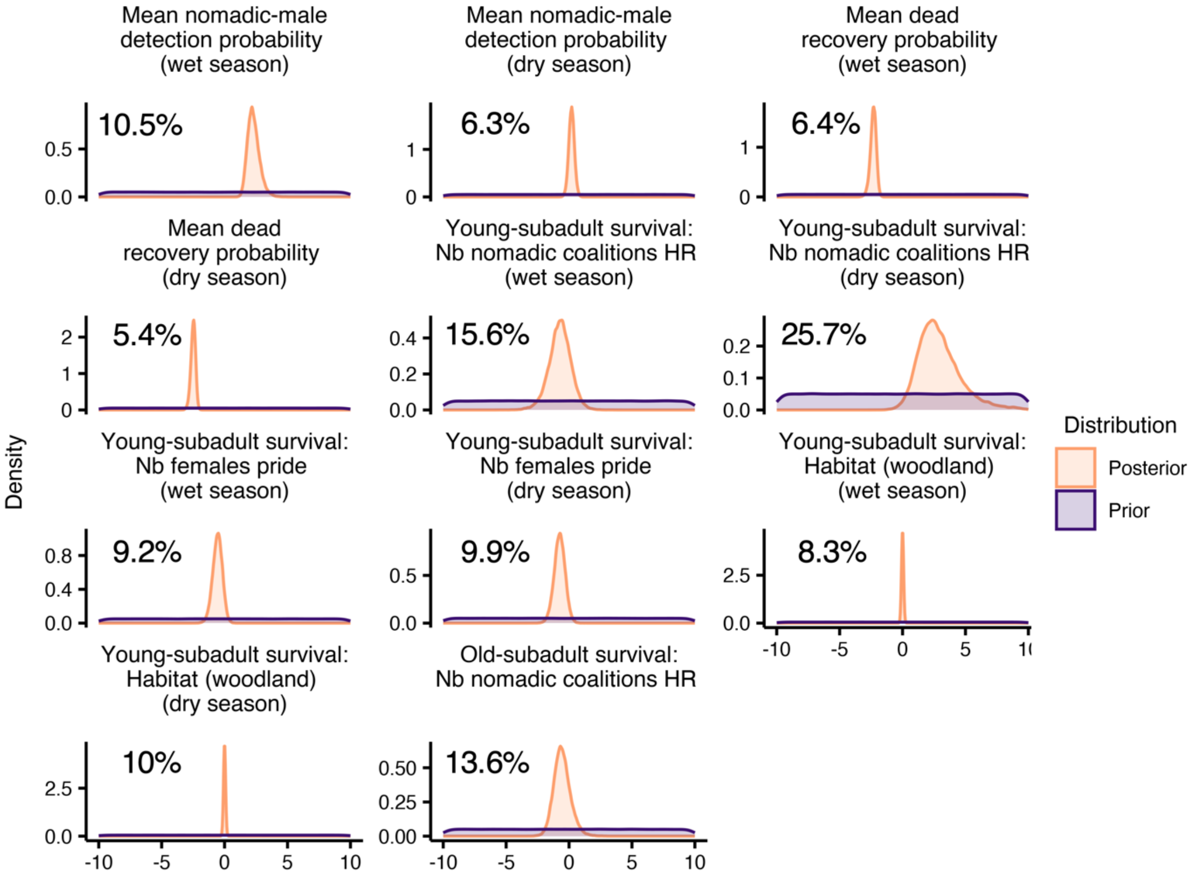
While results on male survival and takeover dynamics confirm previous findings, the estimates on nomadic- and resident-male vital rates should be interpreted cautiously. In our study population, lions are followed via the GPS localisation of prides and opportunistic sightings of isolated and nomadic individuals (Borrego et al. 2018). Although capture-recapture models enable to account for differences in detection probability (Lebreton et al. 1992; Lebreton & Pradel 2002), the lack of observed data—here more specifically on nomad-resident transitions—can pose limitations on vital-rate estimations (Bailey et al. 2010; Griffith et al. 2016). Similarly, lack of data on specific life-history stages and transitions can limit the interpretation of density effects on demographic processes. For example, contrary to previous findings (Elliot et al. 2014; Packer 2023), our analysis unexpectedly indicates a positive effect of nomadic coalitions on the survival of young subadults and young males in the dry season. Because our model only estimates apparent survival (i.e., does not distinguish mortality from permanent emigration), an increase in young-male apparent survival might be a consequence of a decrease in permanent emigration due to the pressure exerted by high numbers of nomadic coalitions. However, changes in the detection of nomads across the study period might bias the observed numbers of nomadic coalitions, as nomadic males are only found opportunistically in the study area (Borrego et al. 2018). Such limitations could be overcome by the use of combined capture-recapture and telemetry data (e.g. Johnson et al. 2010; Bird et al. 2014), or of auxiliary data sources such as previous publications or expert knowledge (e.g. Bauduin et al. 2020). Nevertheless, the interpretation of current vital-rate predictions and population projections relying on them needs to take into account the uncertainty in estimates (Fieberg & Ellner 2001; Ellner et al. 2002).

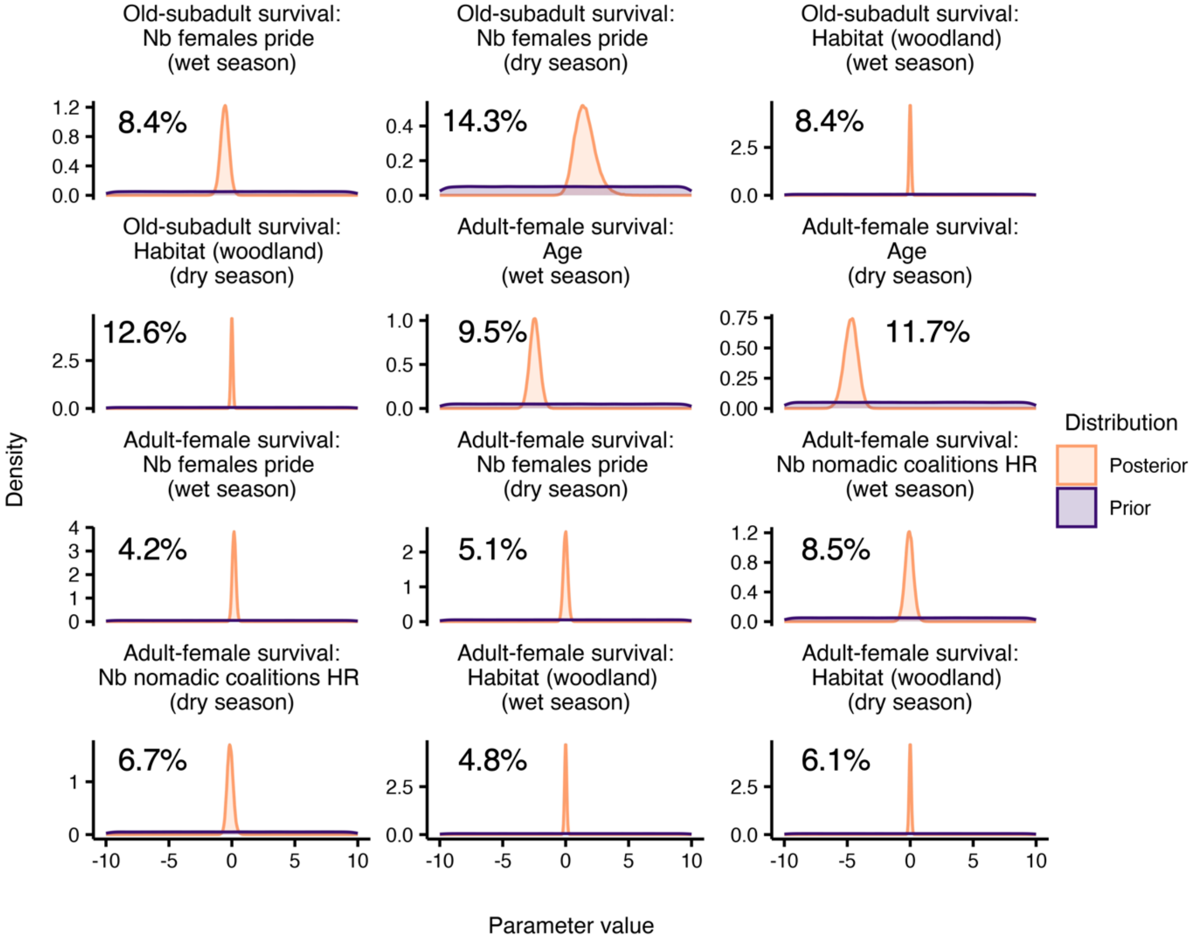
Extrinsic identifiability

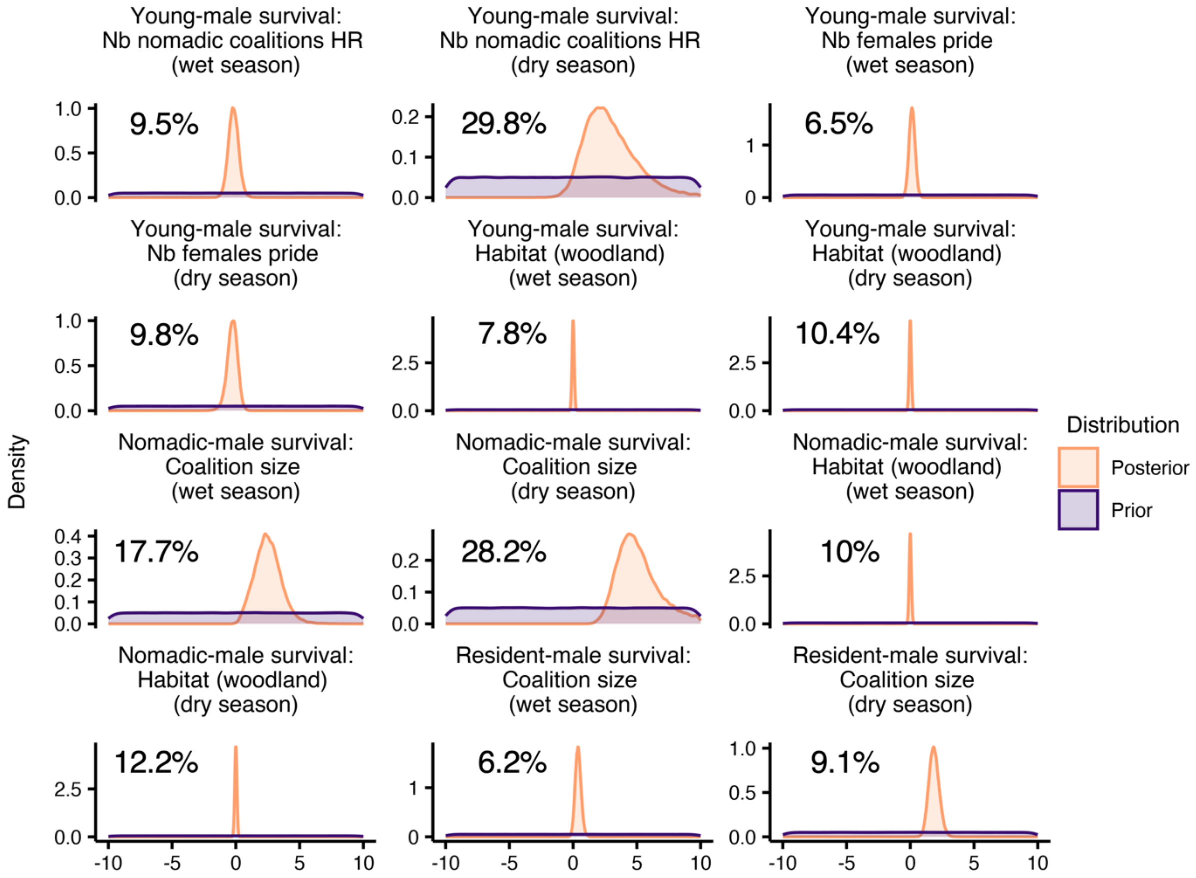
We assessed parameter extrinsic identifiability to detect near-redundancy in our model parameters by calculating the overlap between the prior and posterior distributions (following Garrett & Zeger 2000). For various classes of models, a parameter is commonly considered as weakly identifiable when its prior and posterior distributions overlap by more than 35% (Garrett & Zeger 2000; Gimenez et al. 2009). In our case, this threshold was reached for none of the estimated parameters (Fig. S4), suggesting no major issues with extrinsic identifiability for any of the parameters.

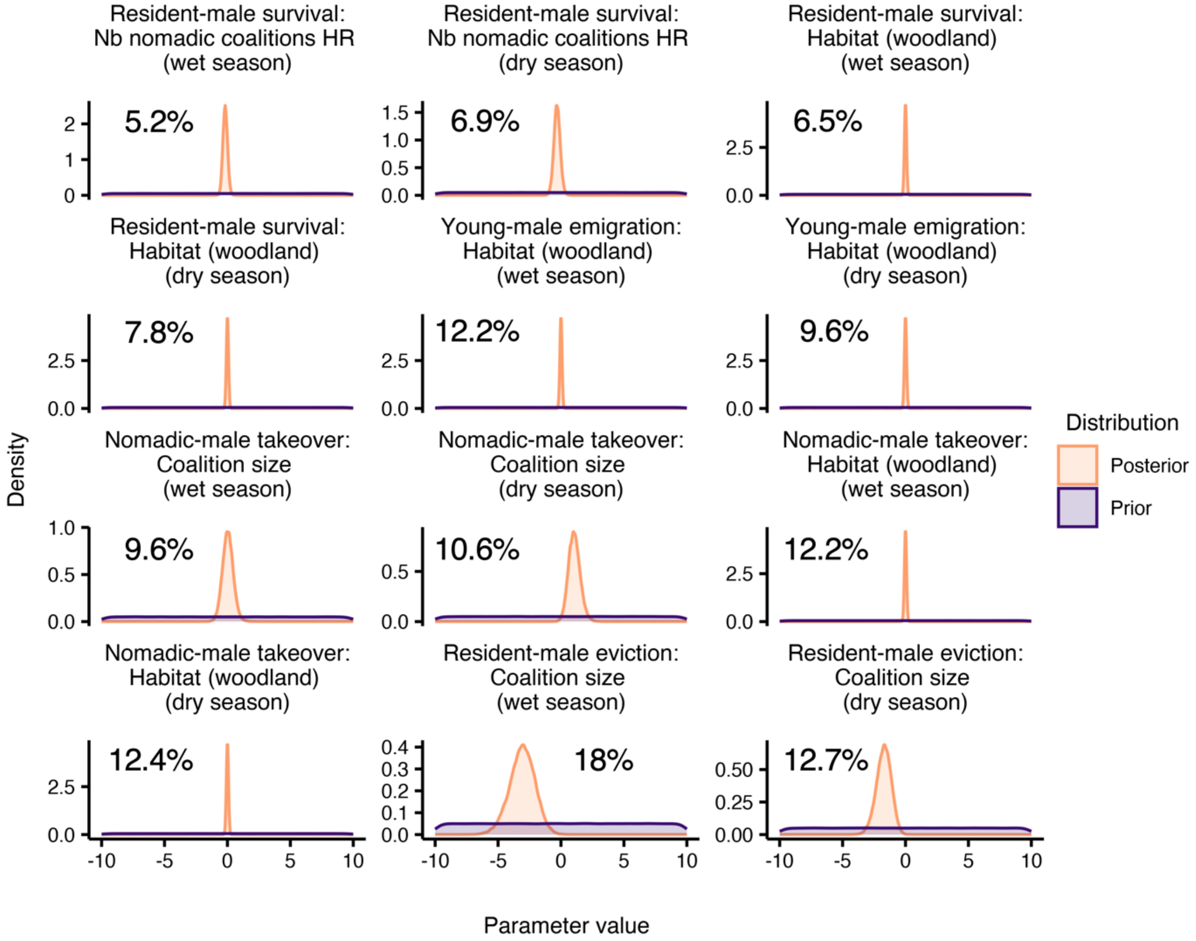

Mean young-subadult survival (wet season)
9.7%
Mean young-subadult survival (dry season)
18.1%
Mean female old-subadult survival (wet season)
8.9%
Mean female old-subadult survival (dry season)
15.1%
Mean male old-subadult survival (wet season)
9%
Mean male old-subadult survival (dry season)
16.4%
Mean adult-female survival (wet season)
5.4%
Mean adult-female survival (dry season)
4.8%
Mean young-male survival (wet season)
6.1%
Mean young-male survival (dry season)
14.5%
Mean nomadic-male survival (wet season)
10.6%
Mean nomadic-male survival (dry season)
15.9%
Density
-10
-5
0
5
10
Distribution
Posterior
Prior

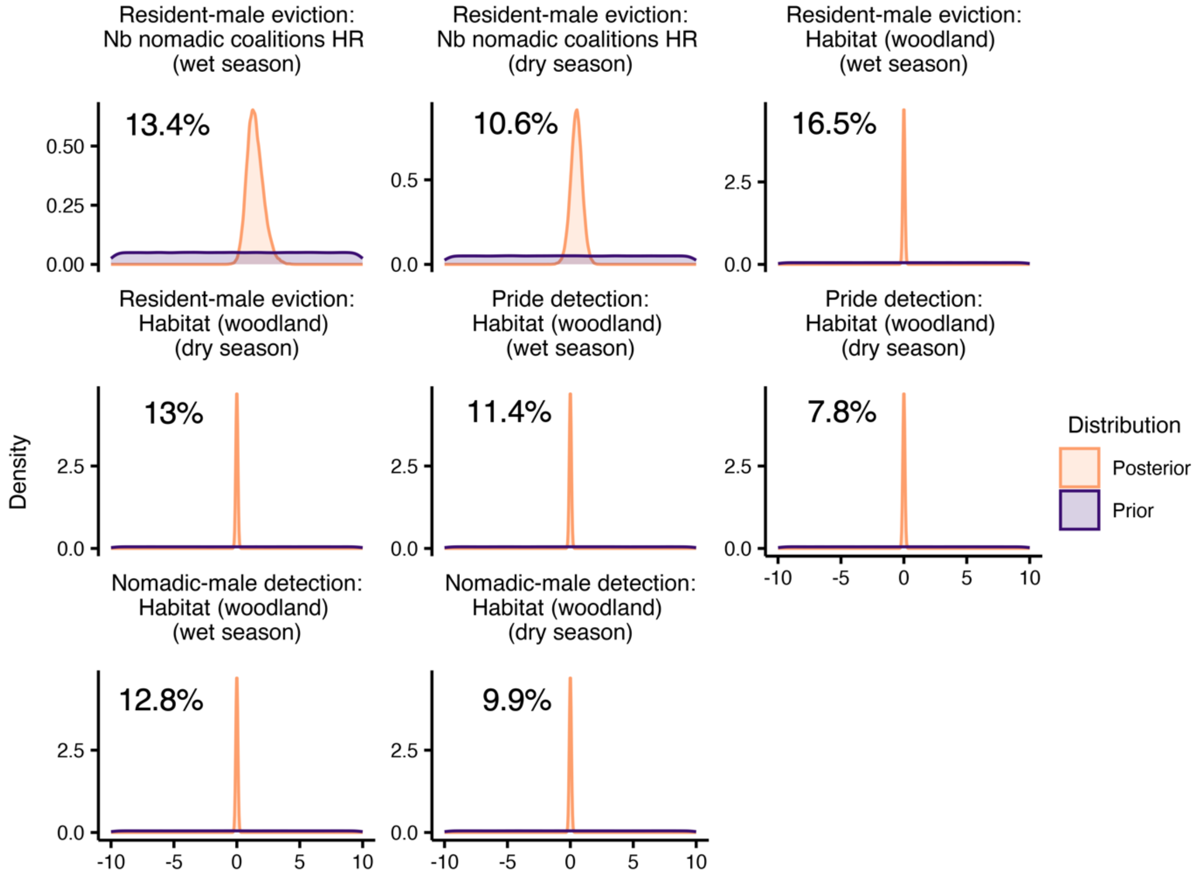

Mean resident-male survival (wet season)
5.5%
Mean resident-male survival (dry season)
6.4%
Mean young-male emigration (wet season)
12.1%
Mean young-male emigration (dry season)
6.9%
Mean transition from young to nomadic male (wet season)
14.3%
Mean transition from young to nomadic male (dry season)
26.4%
Mean nomadic-male takeover (wet season)
9.2%
Mean nomadic-male takeover (dry season)
8.2%
Mean resident-male eviction (wet season)
25.8%
Mean resident-male eviction (dry season)
10.6%
Mean pride detection probability (wet season)
9.1%
Mean pride detection probability (dry season)
6%
Density
-10
-5
0
5
10
Parameter value
Distribution
Posterior
Prior

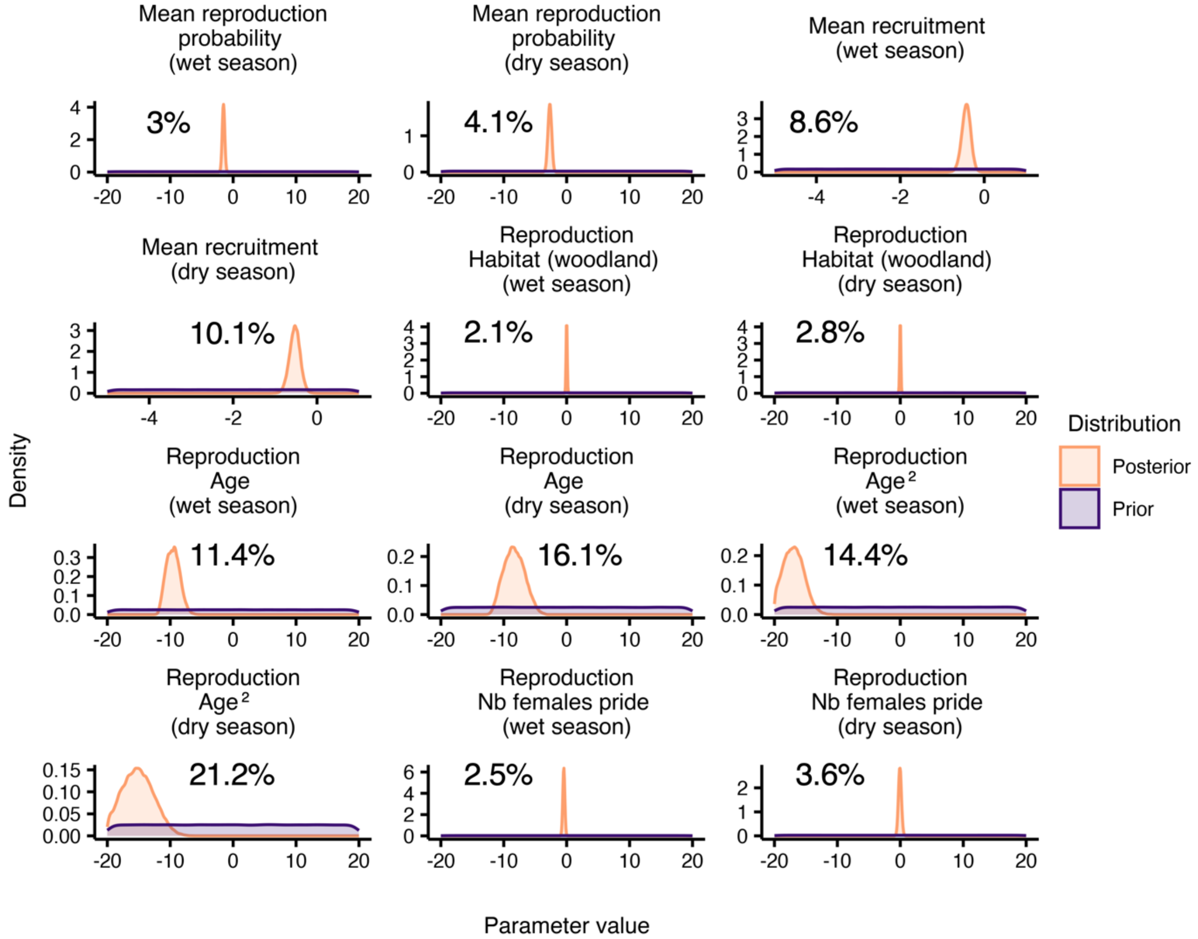

Mean nomadic-male detection probability (wet season)
10.5%
Mean nomadic-male detection probability (dry season)
6.3%
Mean dead recovery probability (wet season)
6.4%
Mean dead recovery probability (dry season)
5.4%
Young-subadult survival: Nb nomadic coalitions HR (wet season)
15.6%
Young-subadult survival: Nb nomadic coalitions HR (dry season)
25.7%
Young-subadult survival: Nb females pride (wet season)
9.2%
Young-subadult survival: Nb females pride (dry season)
9.9%
Young-subadult survival: Habitat (woodland) (wet season)
8.3%
Young-subadult survival: Habitat (woodland) (dry season)
10%
Old-subadult survival: Nb nomadic coalitions HR
13.6%
Density
Distribution
Posterior
Prior
-10
-5
0
5
10


Old-subadult survival: Nb females pride (wet season)
8.4%
Old-subadult survival: Nb females pride (dry season)
14.3%
Old-subadult survival: Habitat (woodland) (wet season)
8.4%
Old-subadult survival: Habitat (woodland) (dry season)
12.6%
Adult-female survival: Age (wet season)
9.5%
Adult-female survival: Age (dry season)
11.7%
Adult-female survival: Nb females pride (wet season)
4.2%
Adult-female survival: Nb females pride (dry season)
5.1%
Adult-female survival: Nb nomadic coalitions HR (wet season)
8.5%
Adult-female survival: Nb nomadic coalitions HR (dry season)
6.7%
Adult-female survival: Habitat (woodland) (wet season)
4.8%
Adult-female survival: Habitat (woodland) (dry season)
6.1%
Density
Distribution
Posterior
Prior
-10
-5
0
5
10
Parameter value


Young-male survival: Nb nomadic coalitions HR (wet season)
9.5%
Young-male survival: Nb nomadic coalitions HR (dry season)
29.8%
Young-male survival: Nb females pride (wet season)
6.5%
Young-male survival: Nb females pride (dry season)
9.8%
Young-male survival: Habitat (woodland) (wet season)
7.8%
Young-male survival: Habitat (woodland) (dry season)
10.4%
Nomadic-male survival: Coalition size (wet season)
17.7%
Nomadic-male survival: Coalition size (dry season)
28.2%
Nomadic-male survival: Habitat (woodland) (wet season)
10%
Nomadic-male survival: Habitat (woodland) (dry season)
12.2%
Resident-male survival: Coalition size (wet season)
6.2%
Resident-male survival: Coalition size (dry season)
9.1%
Density
-10
-5
0
5
10
Distribution
Posterior
Prior


Resident-male survival: Nb nomadic coalitions HR (wet season)
5.2%
Resident-male survival: Nb nomadic coalitions HR (dry season)
6.9%
Resident-male survival: Habitat (woodland) (wet season)
6.5%
Resident-male survival: Habitat (woodland) (dry season)
7.8%
Young-male emigration: Habitat (woodland) (wet season)
12.2%
Young-male emigration: Habitat (woodland) (dry season)
9.6%
Nomadic-male takeover: Coalition size (wet season)
9.6%
Nomadic-male takeover: Coalition size (dry season)
10.6%
Nomadic-male takeover: Habitat (woodland) (wet season)
12.2%
Nomadic-male takeover: Habitat (woodland) (dry season)
12.4%
Resident-male eviction: Coalition size (wet season)
18%
Resident-male eviction: Coalition size (dry season)
12.7%
Density
-10
-5
0
5
10
Parameter value
Distribution
Posterior
Prior


Resident-male eviction: Nb nomadic coalitions HR (wet season)
13.4%
Resident-male eviction: Nb nomadic coalitions HR (dry season)
10.6%
Resident-male eviction: Habitat (woodland) (wet season)
16.5%
Resident-male eviction: Habitat (woodland) (dry season)
13%
Pride detection: Habitat (woodland) (wet season)
11.4%
Pride detection: Habitat (woodland) (dry season)
7.8%
Nomadic-male detection: Habitat (woodland) (wet season)
12.8%
Nomadic-male detection: Habitat (woodland) (dry season)
9.9%
Density
0.00
0.25
0.50
0.0
0.5
2.5
-10
-5
0
5
10
Distribution
Posterior
Prior


Mean reproduction probability (wet season)
3%
Mean reproduction probability (dry season)
4.1%
Mean recruitment (wet season)
8.6%
Mean recruitment (dry season)
10.1%
Reproduction Habitat (woodland) (wet season)
2.1%
Reproduction Habitat (woodland) (dry season)
2.8%
Reproduction Age (wet season)
11.4%
Reproduction Age (dry season)
16.1%
Reproduction Age² (wet season)
14.4%
Reproduction Age² (dry season)
21.2%
Reproduction Nb females pride (wet season)
2.5%
Reproduction Nb females pride (dry season)
3.6%
Density
Parameter value
-20
-10
0
10
20
-4
-2
Distribution
Posterior
Prior

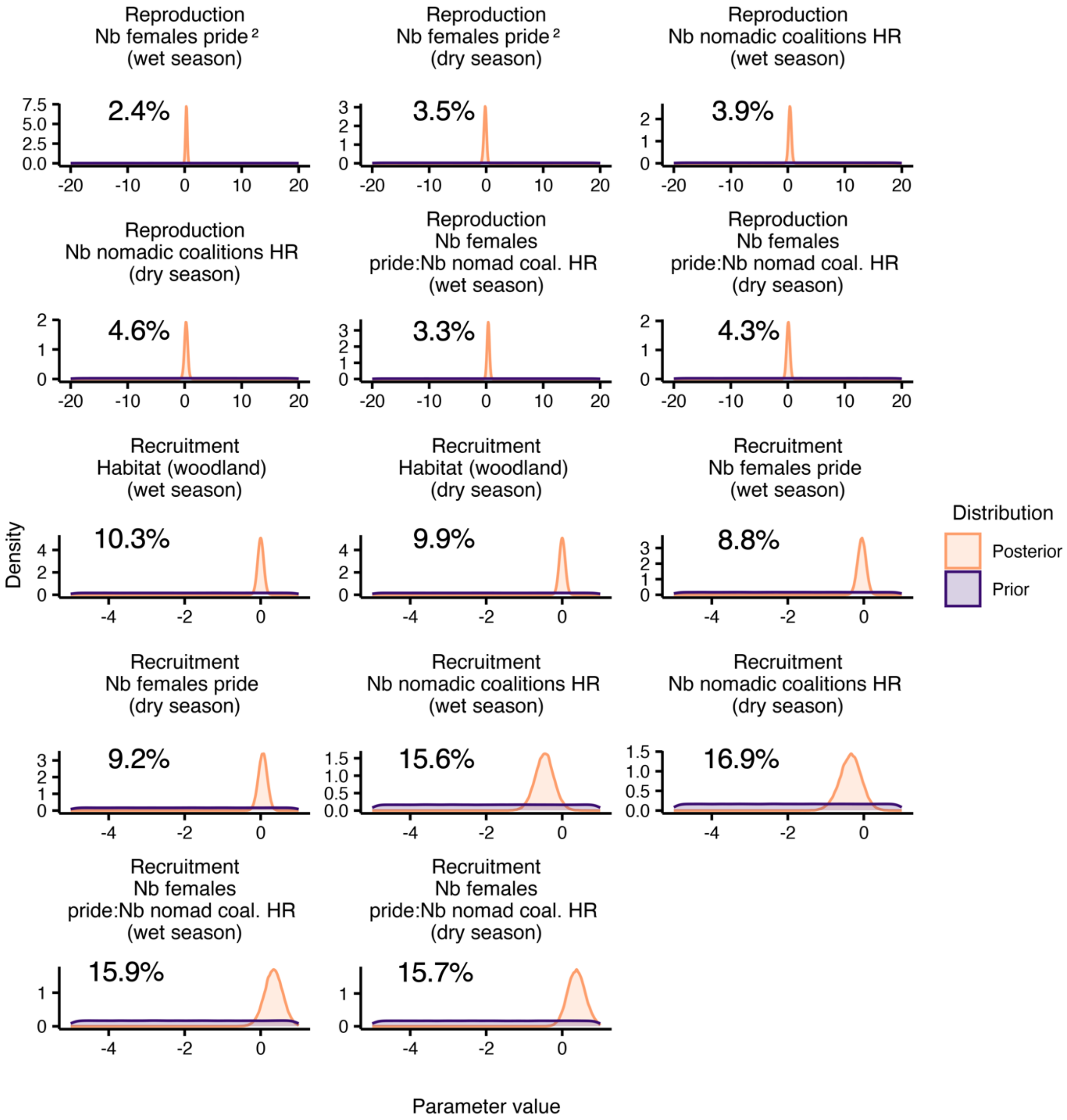


Figure S4 - Overlap between the prior and posterior distributions of each estimated parameter. For each estimated parameter, we assessed extrinsic identifiability by calculating the overlap between the prior (purple density plots) and the posterior distribution (orange density plots). A percentage of overlap above 35% indicates weak identifiability.

Posterior predictive checks

We assessed model fit for both the multistate capture-recapture model and the GLMMs by performing posterior predictive checks (Conn et al. 2018). We first defined a set of metrics to be calculated from the lion capture histories (e.g. total number of recaptures or number of recaptures in a given state *S*, see below) and from the reproduction and recruitment data (e.g. mean recruitment per female, see below). For each metric, we compared the observed value to the distribution of values obtained from simulated datasets. To produce these simulated datasets, we first sampled 500 sets of posterior values for each parameter of the corresponding model—including random effects, which we did not re-sample from the estimated standard deviations of the vital rate-specific random effects. For each sampled set of parameters, we used observed covariate values to simulate 10 new reproduction and capture-history datasets, for the latter starting from the true state of each individual on its first capture. We therefore obtained 5000 simulated datasets for each model and calculated, as for the observed data, the following metrics:

For the reproduction data:

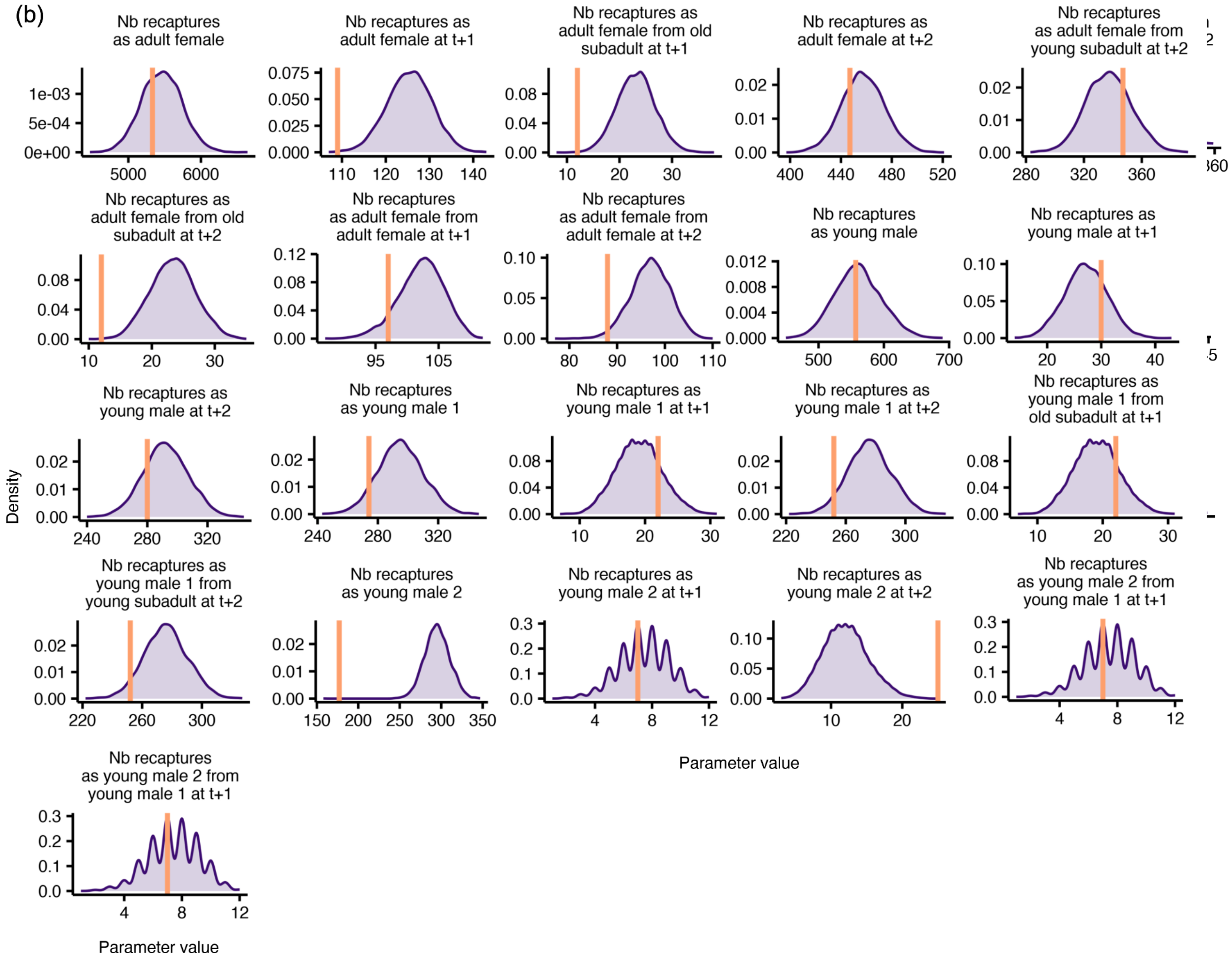
- Proportion of females reproducing
- Mean age of reproducing females
- Mean number of cubs (recruited to 1 year old) per reproducing female

For the capture histories:

- Total number of recaptures (overall, at *t*+1, and at *t*+2)
- Number of recaptures as female old subadult (overall and at *t*+1)
- Number of recaptures as male old subadult (overall and at *t*+1)
- Number of recaptures as young male (overall, at *t*+1, and at *t*+2)
- Number of recaptures in each of the four young-male stages (overall, at *t*+1, and at *t*+2)
- Number of male old subadults becoming young male 1 (at *t*+1)
- Number of young subadults becoming young male 1 (at *t*+2)
- Number of young male 1 becoming young male 2 (at *t*+1)
- Number of male old subadults becoming young male 2 (at *t*+2)
- Number of young male 2 becoming young male 3 (at *t*+1)
- Number of young male 1 becoming young male 3 (at *t*+2)
- Number of young male 3 becoming young male 4 (at *t*+1)
- Number of young male 2 becoming young male 4 (at *t*+2)
- Number of recaptures as nomadic male (overall, at *t*+1, and at *t*+2)
- Number of male old subadults becoming nomadic males (at *t*+2)
- Number of young male 1 becoming nomadic males (at *t*+1 and *t*+2)
- Number of young male 2 becoming nomadic males (at *t*+1 and *t*+2)

- Number of young male 3 becoming nomadic males (at *t*+1 and *t*+2)
- Number of young male 4 becoming nomadic males (at *t*+1 and *t*+2)
- Number of nomadic males becoming nomadic males (at *t*+1 and *t*+2)
- Number of resident males becoming nomadic males (at *t*+1 and *t*+2)
- Number of recaptures as resident male (overall, at *t*+1, and at *t*+2)
- Number of male old subadults becoming resident males at *t*+2
- Number of young male 1 becoming resident males (at *t*+1 and *t*+2)
- Number of young male 2 becoming resident males (at *t*+1 and *t*+2)
- Number of young male 3 becoming resident males (at *t*+1 and *t*+2)
- Number of young male 4 becoming resident males (at *t*+1 and *t*+2)
- Number of nomadic males becoming resident males (at *t*+1 and *t*+2)
- Number of resident males becoming resident males (at *t*+1 and *t*+2)
- Number of recaptures as adult female (overall, at *t*+1, and at *t*+2)
- Number of female old subadults becoming adult females (at *t*+1 and *t*+2)
- Number of young subadults becoming adult females (at *t*+2)
- Number of adult females becoming adult females (at *t*+1 and *t*+2)
- Number of dead recoveries

Comparing the observed and simulated values for each metric allowed us to determine which vital rate in the lion life cycle was poorly estimated by the two models and to improve the model accordingly. For example, an earlier model assuming an even (i.e. 0.5) female-to-male sex ratio led to an underestimated number of females in the simulated datasets compared to the observed capture histories (Fig. S5a). Adjusting the sex ratio to 0.55 improved estimates of the number of females (Fig. S5b). In addition, a previous version of the model did not discriminate between male and female old subadults and assumed the same mean survival for both sexes. In that model, posterior predictive checks pointed to issues in transitions between subadults and adult females or young males. While estimating sex-specific mean survival rates for old subadults improved the precision and accuracy of predictions on the number of recaptured adult females, it did not improve predictions related to young males (Fig. S5c).


(b)

Nb recaptures as adult female

Nb recaptures as adult female at t+1

Nb recaptures as adult female from old subadult at t+1

Nb recaptures as adult female at t+2

Nb recaptures as adult female from young subadult at t+2

Nb recaptures as adult female from old subadult at t+2

Nb recaptures as adult female from adult female at t+1

Nb recaptures as adult female from adult female at t+2

Nb recaptures as young male

Nb recaptures as young male at t+1

Nb recaptures as young male at t+2

Nb recaptures as young male 1

Nb recaptures as young male 1 at t+1

Nb recaptures as young male 1 at t+2

Nb recaptures as young male 1 from old subadult at t+1

Nb recaptures as young male 1 from young subadult at t+2

Nb recaptures as young male 2

Nb recaptures as young male 2 at t+1

Nb recaptures as young male 2 at t+2

Nb recaptures as young male 2 from young male 1 at t+1

Nb recaptures as young male 2 from young male 1 at t+1

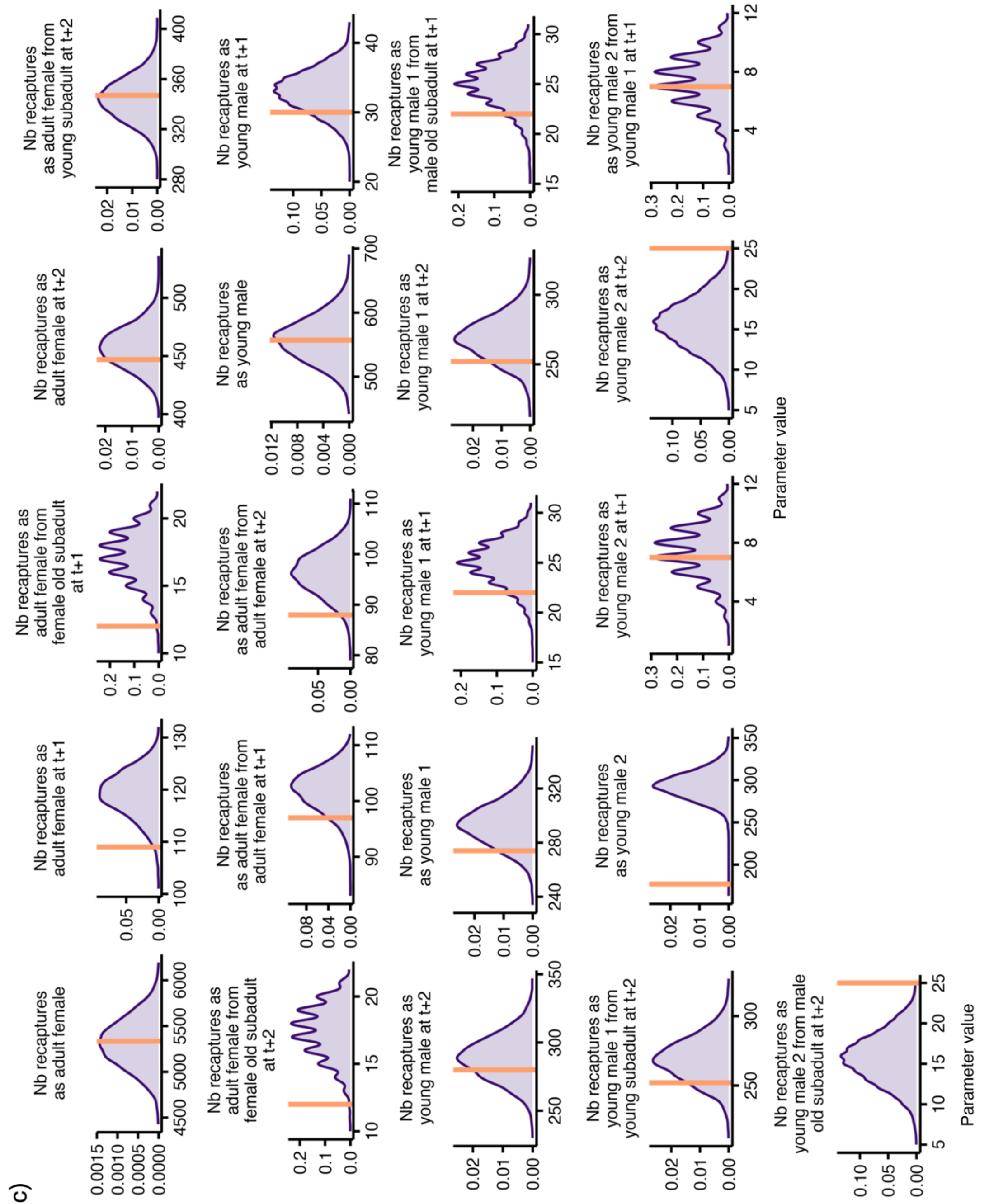
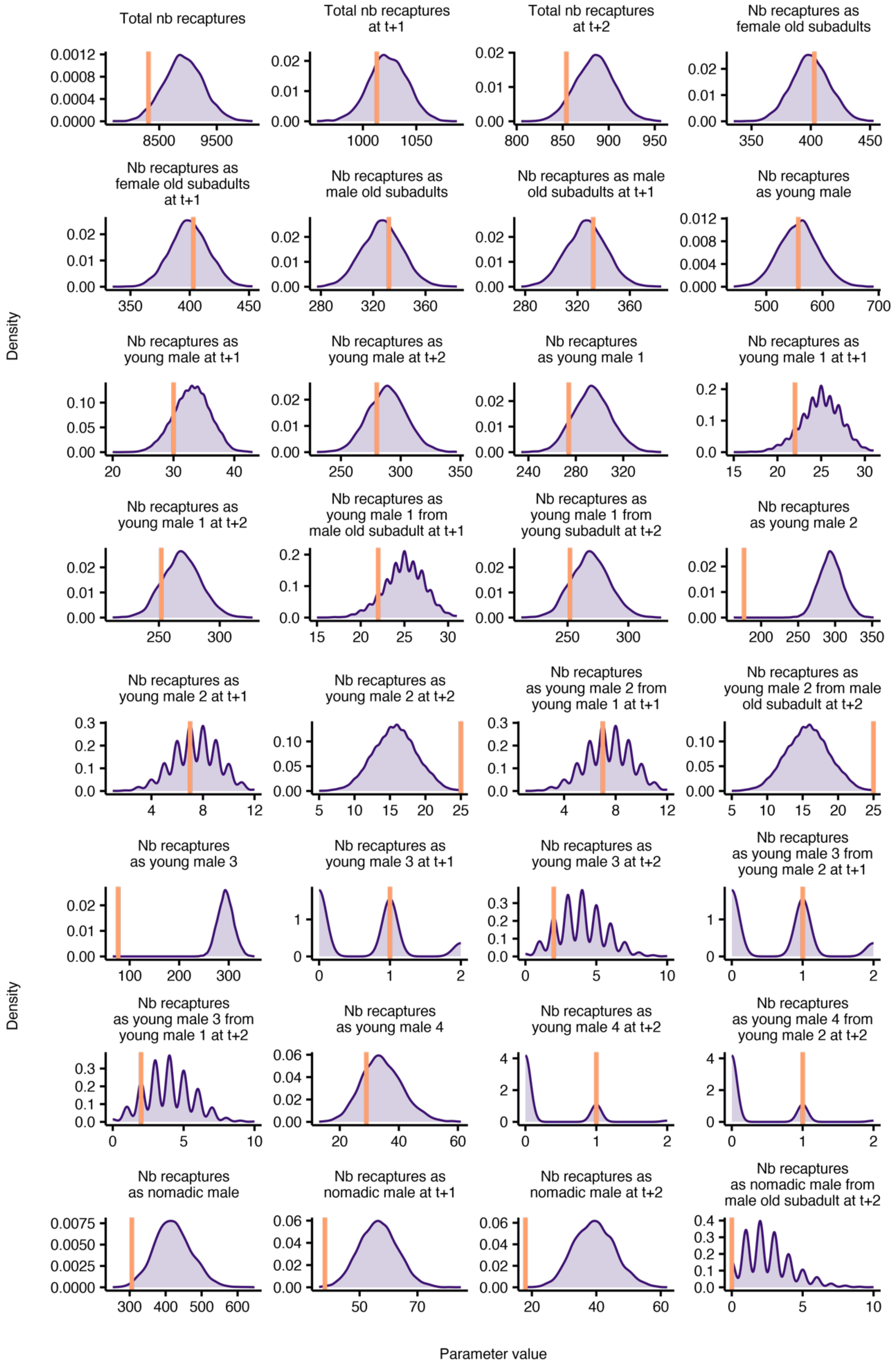
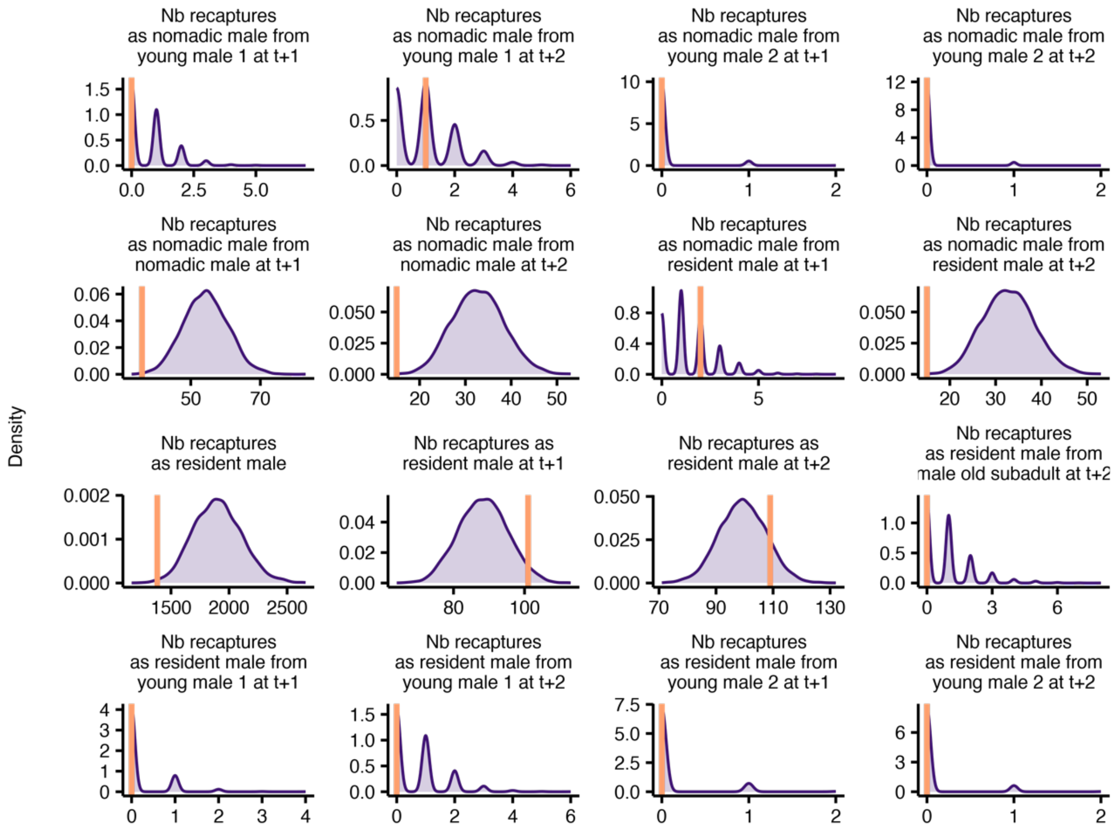


Figure S5 - Simulated and observed values of metrics calculated on capture histories for the posterior predictive checks in three models with different structures. We calculated a set of metrics on the observed data (orange vertical line) and the associated 5000 simulated datasets (corresponding to 10 datasets simulated for each of 500 sets of sampled parameters; purple density plots). This figure compares the posterior predictive checks of three model assumptions: (a) Sex ratio of 0.5; (b) sex ratio of 0.55; and (c) sex ratio of 0.55 and sex-specific intercepts for the survival of old subadults.

In the final model, for most metrics, the simulated distributions included the observed value (Fig. S6), and the Bayesian p-values (i.e., the proportion of simulated values higher than the observed value) were close to 0.5, indicating satisfactory fit (Fig. S7). However, some discrepancies remain and should be discussed; mainly, the number of individuals recaptured as young male 2–4 is greatly underestimated. This is likely a consequence of the limited amount of data on transitions to and from young-male stages leading to issues estimating the related parameters and thereby to discrepancies between the observed and simulated values. In addition, the number of resident males becoming nomadic is overestimated, while the number of nomadic males becoming resident is underestimated. This points to issues estimating the parameters linked to takeover dynamics, indicating that more data is needed to estimate such parameters properly. This could be achieved, for example, by integrating additional data sources, such as telemetry data, or expert knowledge to increase information about when males leave or join a pride (Johnson et al. 2010; Bird et al. 2014; Bauduin et al. 2020). Overall, parameters linked to young, resident, and nomadic males, as well as future population projections relying on the predictions of these vital rates should be interpreted with caution.

In addition, we used the posterior distributions of the parameters defining reproduction rates to predict the season-specific reproduction probability and recruitment in each year. The predicted values and 95% credible intervals do correspond to the observed values (Fig. S8), giving further indication of a good model fit.


Density
Density
Parameter value
Total nb recaptures
0.0012
0.0008
0.0004
0.0000
8500
9500
Total nb recaptures at t+1
0.02
0.01
0.00
1000
1050
Total nb recaptures at t+2
0.02
0.01
0.00
800
850
900
950
Nb recaptures as female old subadults
0.02
0.01
0.00
350
400
450
Nb recaptures as female old subadults at t+1
0.02
0.01
0.00
350
400
450
Nb recaptures as male old subadults
0.02
0.01
0.00
280
320
360
Nb recaptures as male old subadults at t+1
0.02
0.01
0.00
280
320
360
Nb recaptures as young male
0.012
0.008
0.004
0.000
500
600
700
Nb recaptures as young male at t+1
0.10
0.05
0.00
20
30
40
Nb recaptures as young male at t+2
0.02
0.01
0.00
250
300
350
Nb recaptures as young male 1
0.02
0.01
0.00
240
280
320
Nb recaptures as young male 1 at t+1
0.2
0.1
0.0
15
20
25
30
Nb recaptures as young male 1 at t+2
0.02
0.01
0.00
250
300
Nb recaptures as young male 1 from male old subadult at t+1
0.2
0.1
0.0
15
20
25
30
Nb recaptures as young male 1 from young subadult at t+2
0.02
0.01
0.00
250
300
Nb recaptures as young male 2
0.02
0.01
0.00
200
250
300
350
Nb recaptures as young male 2 at t+1
0.3
0.2
0.1
0.0
4
8
12
Nb recaptures as young male 2 at t+2
0.10
0.05
0.00
5
10
15
20
25
Nb recaptures as young male 2 from young male 1 at t+1
0.3
0.2
0.1
0.0
4
8
12
Nb recaptures as young male 2 from male old subadult at t+2
0.10
0.05
0.00
5
10
15
20
25
Nb recaptures as young male 3
0.02
0.01
0.00
100
200
300
Nb recaptures as young male 3 at t+1
1
0
0
1
2
Nb recaptures as young male 3 at t+2
0.3
0.2
0.1
0.0
0
5
10
Nb recaptures as young male 3 from young male 2 at t+1
1
0
0
1
2
Nb recaptures as young male 3 from young male 1 at t+2
0.3
0.2
0.1
0.0
0
5
10
Nb recaptures as young male 4
0.06
0.04
0.02
0.00
20
40
60
Nb recaptures as young male 4 at t+2
4
2
0
0
1
2
Nb recaptures as young male 4 from young male 2 at t+2
4
2
0
0
1
2
Nb recaptures as nomadic male
0.0075
0.0050
0.0025
0.0000
300
400
500
600
Nb recaptures as nomadic male at t+1
0.06
0.04
0.02
0.00
50
70
Nb recaptures as nomadic male at t+2
0.06
0.04
0.02
0.00
20
40
60
Nb recaptures as nomadic male from male old subadult at t+2
0.4
0.3
0.2
0.1
0.0
0
5
10


Density
Nb recaptures as nomadic male from young male 1 at t+1
1.5 1.0 0.5 0.0
0.0 2.5 5.0
Nb recaptures as nomadic male from young male 1 at t+2
0.5 0.0
0 2 4 6
Nb recaptures as nomadic male from young male 2 at t+1
10 5 0
0 1 2
Nb recaptures as nomadic male from young male 2 at t+2
12 8 4 0
0 1 2
Nb recaptures as nomadic male from nomadic male at t+1
0.06 0.04 0.02 0.00
50 70
Nb recaptures as nomadic male from nomadic male at t+2
0.050 0.025 0.000
20 30 40 50
Nb recaptures as nomadic male from resident male at t+1
0.8 0.4 0.0
0 5
Nb recaptures as nomadic male from resident male at t+2
0.050 0.025 0.000
20 30 40 50
Nb recaptures as resident male
0.002 0.001 0.000
1500 2000 2500
Nb recaptures as resident male at t+1
0.04 0.02 0.00
80 100
Nb recaptures as resident male at t+2
0.050 0.025 0.000
70 90 110 130
Nb recaptures as resident male from male old subadult at t+2
1.0 0.5 0.0
0 3 6
Nb recaptures as resident male from young male 1 at t+1
4 3 2 1 0
0 1 2 3 4
Nb recaptures as resident male from young male 1 at t+2
1.5 1.0 0.5 0.0
0 2 4 6
Nb recaptures as resident male from young male 2 at t+1
7.5 5.0 2.5 0.0
0 1 2
Nb recaptures as resident male from young male 2 at t+2
6 3 0
0 1 2

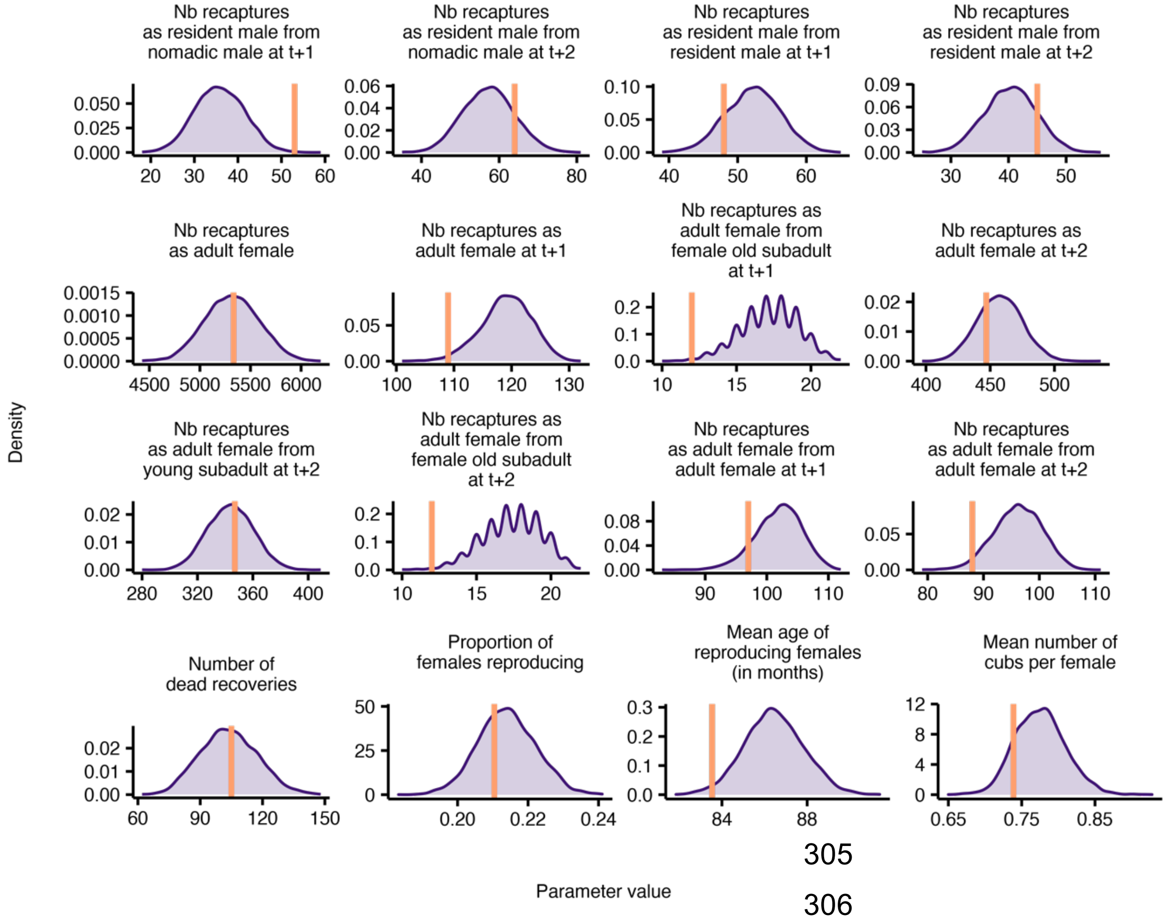

Density
Nb recaptures as resident male from nomadic male at t+1
0.050 0.025 0.000
20 30 40 50 60
Nb recaptures as resident male from nomadic male at t+2
0.06 0.04 0.02 0.00
40 60 80
Nb recaptures as resident male from resident male at t+1
0.10 0.05 0.00
40 50 60
Nb recaptures as resident male from resident male at t+2
0.09 0.06 0.03 0.00
30 40 50
Nb recaptures as adult female
0.0015 0.0010 0.0005 0.0000
4500 5000 5500 6000
Nb recaptures as adult female at t+1
0.05 0.00
100 110 120 130
Nb recaptures as adult female from female old subadult at t+1
0.2 0.1 0.0
10 15 20
Nb recaptures as adult female at t+2
0.02 0.01 0.00
400 450 500
Nb recaptures as adult female from young subadult at t+2
0.02 0.01 0.00
280 320 360 400
Nb recaptures as adult female from female old subadult at t+2
0.2 0.1 0.0
10 15 20
Nb recaptures as adult female from adult female at t+1
0.08 0.04 0.00
90 100 110
Nb recaptures as adult female from adult female at t+2
0.05 0.00
80 90 100 110
Number of dead recoveries
0.02 0.01 0.00
60 90 120 150
Proportion of females reproducing
50 25 0
0.20 0.22 0.24
Mean age of reproducing females (in months)
0.3 0.2 0.1 0.0
84 88
Mean number of cubs per female
12 8 4 0
0.65 0.75 0.85
Parameter value

Figure S6 - Simulated and observed values of metrics calculated on capture histories and reproduction data for the posterior predictive checks. For the capture histories and the reproduction dataset, we calculated a set of metrics on the observed data (orange vertical line) and the associated 5000 simulated datasets (corresponding to 10 datasets simulated for each of 500 sets of sampled parameters; purple density plots).

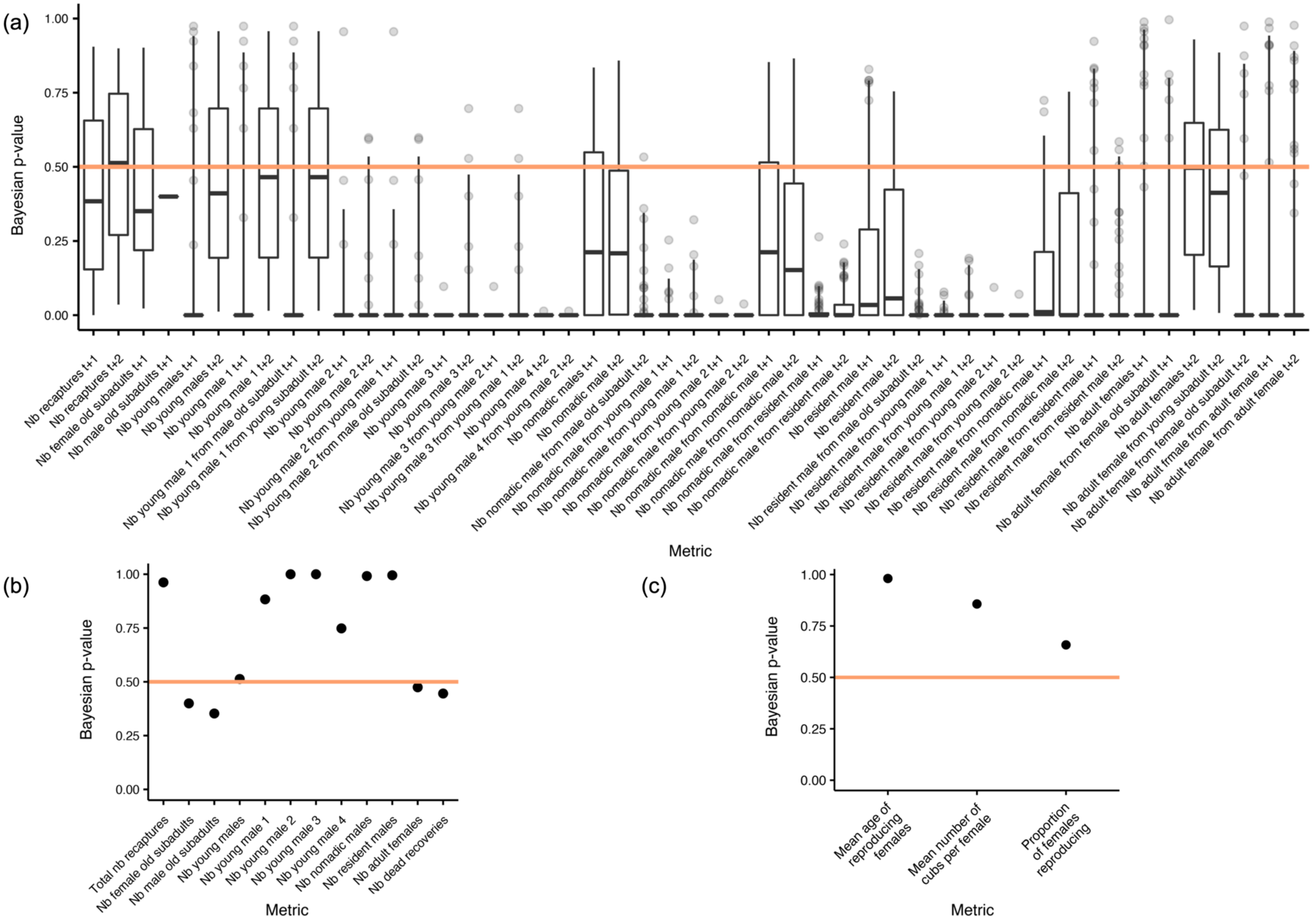

(a)
Bayesian p-value
1.00
0.75
0.50
0.25
0.00
Nb recaptures t+1
Nb recaptures t+2
Nb female old subadults t+1
Nb male old subadults t+1
Nb young males t+1
Nb young males t+2
Nb young male 1 t+1
Nb young male 1 t+2
Nb young male 1 from male old subadult t+1
Nb young male 1 from young subadult t+2
Nb young male 2 t+1
Nb young male 2 t+2
Nb young male 2 from young male 1 t+1
Nb young male 2 from male old subadult t+2
Nb young male 3 t+1
Nb young male 3 t+2
Nb young male 3 from young male 2 t+1
Nb young male 3 from young male 1 t+2
Nb young male 4 t+2
Nb young male 4 from young male 2 t+2
Nb nomadic males t+1
Nb nomadic male t+2
Nb nomadic male from male old subadult t+2
Nb nomadic male from young male 1 t+1
Nb nomadic male from young male 1 t+2
Nb nomadic male from young male 2 t+1
Nb nomadic male from young male 2 t+2
Nb nomadic male from nomadic male t+1
Nb nomadic male from nomadic male t+2
Nb nomadic male from resident male t+1
Nb nomadic male from resident male t+2
Nb resident male t+1
Nb resident male t+2
Nb resident male from male old subadult t+2
Nb resident male from young male 1 t+1
Nb resident male from young male 1 t+2
Nb resident male from young male 2 t+1
Nb resident male from young male 2 t+2
Nb resident male from nomadic male t+1
Nb resident male from nomadic male t+2
Nb resident male from resident male t+1
Nb resident male from resident male t+2
Nb adult females t+1
Nb adult female from female old subadult t+1
Nb adult females t+2
Nb adult female from young subadult t+2
Nb adult female from female old subadult t+2
Nb adult frmale from adult female t+1
Nb adult female from adult female t+2
Metric
(b)
Bayesian p-value
1.00
0.75
0.50
0.25
0.00
Total nb recaptures
Nb female old subadults
Nb male old subadults
Nb young males
Nb young male 1
Nb young male 2
Nb young male 3
Nb young male 4
Nb nomadic males
Nb resident males
Nb adult females
Nb dead recoveries
Metric
(c)
Bayesian p-value
1.00
0.75
0.50
0.25
0.00
Mean age of reproducing females
Mean number of cubs per female
Proportion of females reproducing
Metric

Figure S7 - Bayesian p-values of each metric used for the posterior predictive checks. For each metric calculated on 5000 simulated capture histories and reproduction datasets, we computed the Bayesian p-value (i.e., the proportion of simulated values higher than the observed value). (a) For metrics associated with a given timestep *t* (i.e. *t*+1 and *t*+2), we calculated one p-value for each *t* of the capture history, obtaining 59 p-values for metrics calculated at *t*+1 and 58 for those calculated at *t*+2. (b) For metrics associated with the whole dataset, we only calculated one p-value. The orange horizontal line corresponds to a p-value of 0.5, indicating a perfect correspondence between the observed and simulated metric.

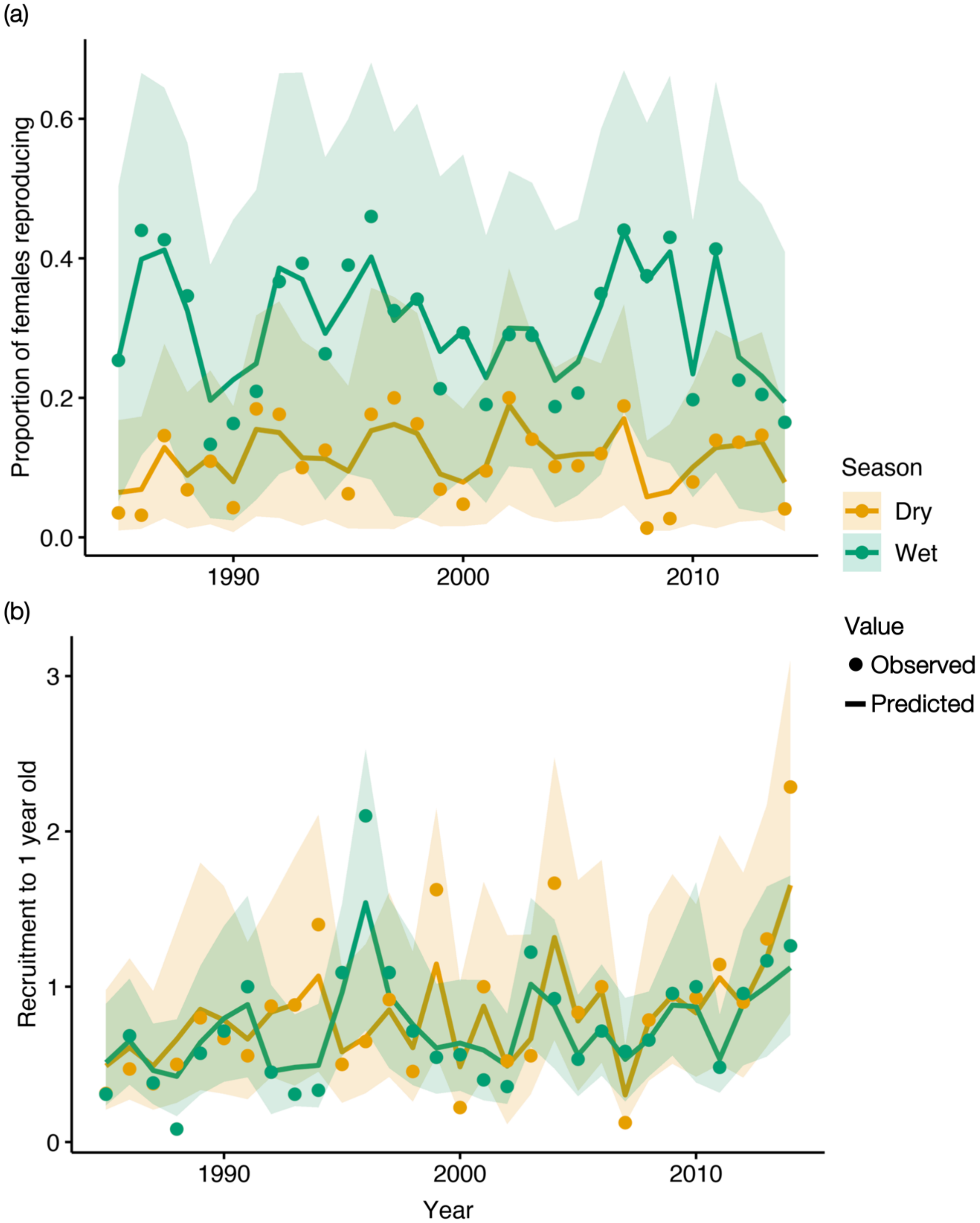


Figure S8 - Observed and predicted reproduction probability and recruitment. For each year, we predicted the season-specific proportion of (a) females reproducing in the population and (b) the season-specific recruitment (i.e., number of cubs reaching one year old per female) using the posterior distributions of the parameters defining these reproductive rates to compare our mean model predictions (lines) and their 95% credible intervals to the observed data (dots).

References – Appendix S5

Bailey, L. L., Converse, S. J., & Kendall, W. L. (2010). Bias, precision, & parameter redundancy in complex multistate models with unobservable states. *Ecology, 91(6)*, 1598–1604. https://doi.org/10.1890/09-1633.1.

Bauduin, S., Grente, O., Santostasi, N. L., Ciucci, P., Duchamp, C., & Gimenez, O. (2020). An individual-based model to explore the impacts of lesser-known social dynamics on wolf populations. *Ecological Modelling*, *433(October)*, 109209. https://doi.org/10.1016/j.ecolmodel.2020.109209.

Bird, T., Lyon, J., Nicol, S., McCarthy, M., & Barker, R. (2014). Estimating population size in the presence of temporary migration using a joint analysis of telemetry and capture–recapture data. *Methods in Ecology and Evolution, 5(7)*, 615–25. https://doi.org/10.1111/2041-210X.12202.

Borrego, N., Ozgul, A., Slotow, R., & Packer, C. (2018). Lion population dynamics: Do nomadic males matter? *Behavioral Ecology, 29(3)*, 660–66. https://doi.org/10.1093/beheco/ary018.

Bygott, J. D., Bertram, B. C. R., & Hanby, J. P. (1979). Male lions in large coalitions gain reproductive advantages. *Nature, 282(5741)*, 839–41. https://doi.org/10.1038/282839a0.

Conn, P. B., Johnson, D. S., Williams, P. J., Melin, S. R., & Hooten, M. B. (2018). A guide to Bayesian model checking for ecologists. *Ecological Monographs, 88(4)*, 526–42. https://doi.org/10.1002/ecm.1314.

Elliot, N. B., Valeix, M., Macdonald, D. W., & Loveridge, A. J. (2014). Social relationships affect dispersal timing revealing a delayed infanticide in African lions. *Oikos, 123(9)*, 1049–56. https://doi.org/10.1111/oik.01266.

Ellner, S. P., Fieberg, J., Ludwig, D., & Wilcox, C. (2002). Precision of population viability analysis. *Conservation Biology, 16(1)*, 258–61. https://doi.org/10.1046/j.1523-1739.2002.00553.x.

Fieberg, J., & Ellner, S. P. (2001). Stochastic matrix models for conservation and management: A comparative review of methods. *Ecology Letters, 4(3)*, 244–66. https://doi.org/10.1046/j.1461-0248.2001.00202.x.

Garrett, E. S., & Zeger, S. L. (2000). Latent class model diagnosis. *Biometrics, 56(4)*, 1055–67. https://doi.org/10.1111/j.0006-341X.2000.01055.x.

Gimenez, O., Morgan, B. J. T., & Brooks, S. P. (2009). Weak identifiability in models for mark-recapture-recovery data. In D. L. Thomson, E. G. Cooch, & M. J. Conroy (Eds.) *Modeling demographic processes in marked populations* (pp. 1055–67). Springer

US. https://doi.org/10.1007/978-0-387-78151-8_48.

Griffith, A. B., Salguero-Gómez, R., Merow, C., & McMahon, S. (2016). Demography beyond the population. *Journal of Ecology, 104(2)*, 271–80. https://doi.org/10.1111/1365-2745.12547.

Hanby, J. P., & Bygott, J. D. (1979). Population changes in lions and other predators. In A. R. E. Sinclair, & M. Norton-Griffiths (Eds.) *Serengeti: Dynamics of an ecosystem* (pp. 249–62). University of Chicago Press.

Johnson, H. E., Scott Mills, L., Wehausen, J. D., & Stephenson, T. R. (2010). Combining ground count, telemetry, and mark–resight data to infer population dynamics in an endangered species. *Journal of Applied Ecology, 47(5)*, 1083–93. https://doi.org/10.1111/j.1365-2664.2010.01846.x.

Lebreton, J.-D., Burnham, K. P., Clobert, J., & Anderson, D. R. (1992). Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecological Monographs, 62(1)*, 67–118. https://doi.org/10.2307/2937171.

Lebreton, J.-D., & Pradel, R. (2002). Multistate recapture models: Modelling incomplete individual histories. *Journal of Applied Statistics, 29(1–4)*, 353–69. https://doi.org/10.1080/02664760120108638.

Mosser, A., & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour, 78(2)*, 359–70. https://doi.org/10.3389/fevo.2023.983266.

Packer, C. (2023). The lion: Behavior, ecology, and conservation of an iconic species. Princeton University Press.

Packer, C., Scheel, D., & Pusey, A. E. (1990). Why lions form groups: Food is not enough. *The American Naturalist, 136(1)*, 1–19. https://doi.org/10.1086/285079.

Pusey, A. E., & Packer, C. (1994). Infanticide in lions: consequences and counterstrategies. In S. Parmigiani, & F. vom Saal (Eds.) *Infanticide and Parental Care* (pp. 277–99). Taylor & Francis.

VanderWaal, K. L., Mosser, A., & Packer, C. (2009). Optimal group size, dispersal decisions and postdispersal relationships in female African lions. *Animal Behaviour, 77(4)*, 949–54. https://doi.org/10.1016/j.anbehav.2008.12.028.