

RESEARCH ARTICLE

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

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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 generalized linear mixed models 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 with 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.

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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

Bayesian models, demographic rates, density dependence, density–environment interactions, multistate capture–recapture models, sociality

1 | 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; Behr et al., 2020; Maag et al., 2018; Packer & Pusey, 1983a), 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 into the role of density feedbacks in shaping population demography.

Socially structured populations are often more susceptible to multifaceted density effects (e.g. Ausband & Mitchell, 2021; Behr et al., 2020). 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 (Borrego et al., 2018; Bygott et al., 1979; Elliot et al., 2014; Packer & Pusey, 1987). 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) (Packer, 2023; Schaller, 1972). Young males in the Serengeti system disperse from their natal pride by 4 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; Hanby & Bygott, 1987; Packer & Pusey, 1982, 1987). Nomadic males play a key role in shaping lion demography (Borrego et al., 2018; Whitman et al., 2004). 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; Borrego et al., 2018; Elliot et al., 2014) 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 (Packer et al., 1990; Schaller, 1972), 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 into 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. We estimated 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.

2 | MATERIALS AND METHODS

2.1 | Study species

2.1.1 | Demographic data

We used individual-based life-history data of 1347 lions (65 prides and 242 male coalitions ranging size from 1 to 8 individuals), collected

between 1984 and 2014 during a consistent monitoring in a 2000-km² 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 (Packer, 2023; VanderWaal et al., 2009). Each pride was then visited at least once every 2 weeks by locating the collared females (Borrego et al., 2018; VanderWaal et al., 2009). Additionally, lions or groups of lions away from their pride, as well as nomadic males, were observed and recorded opportunistically during the monitoring. The fieldwork research was conducted with the approval of the Institutional Animal Care and Use Committee (IACUC) of the University of Minnesota (protocol number 1207A16868). The monitoring and collaring of animals within the SNP were conducted with permission from the Tanzanian Wildlife Research Institute (TAWIRI), ensuring compliance with local wildlife research regulations and facilitating the fieldwork necessary for this study.

Lions were identified by eye based on photographs of features such as scars and individual-specific whisker spots recorded at the first sighting (Packer & Pusey, 1993; Pennycuik & Rudnai, 1970). 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—that is, not killed by humans—opportunistically during the regular pride surveys to provide the model with additional insights into the difference between mortality and lack of observation, thereby better informing the survival process and obtaining more accurate survival estimates.

2.1.2 | Life history

We divided the lion life history into 10 stages based on age, sex and social status (Figure 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: YM₁ (2–2.5 years), YM₂ (2.5–3 years), YM₃ (3–3.5 years), and YM₄ (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

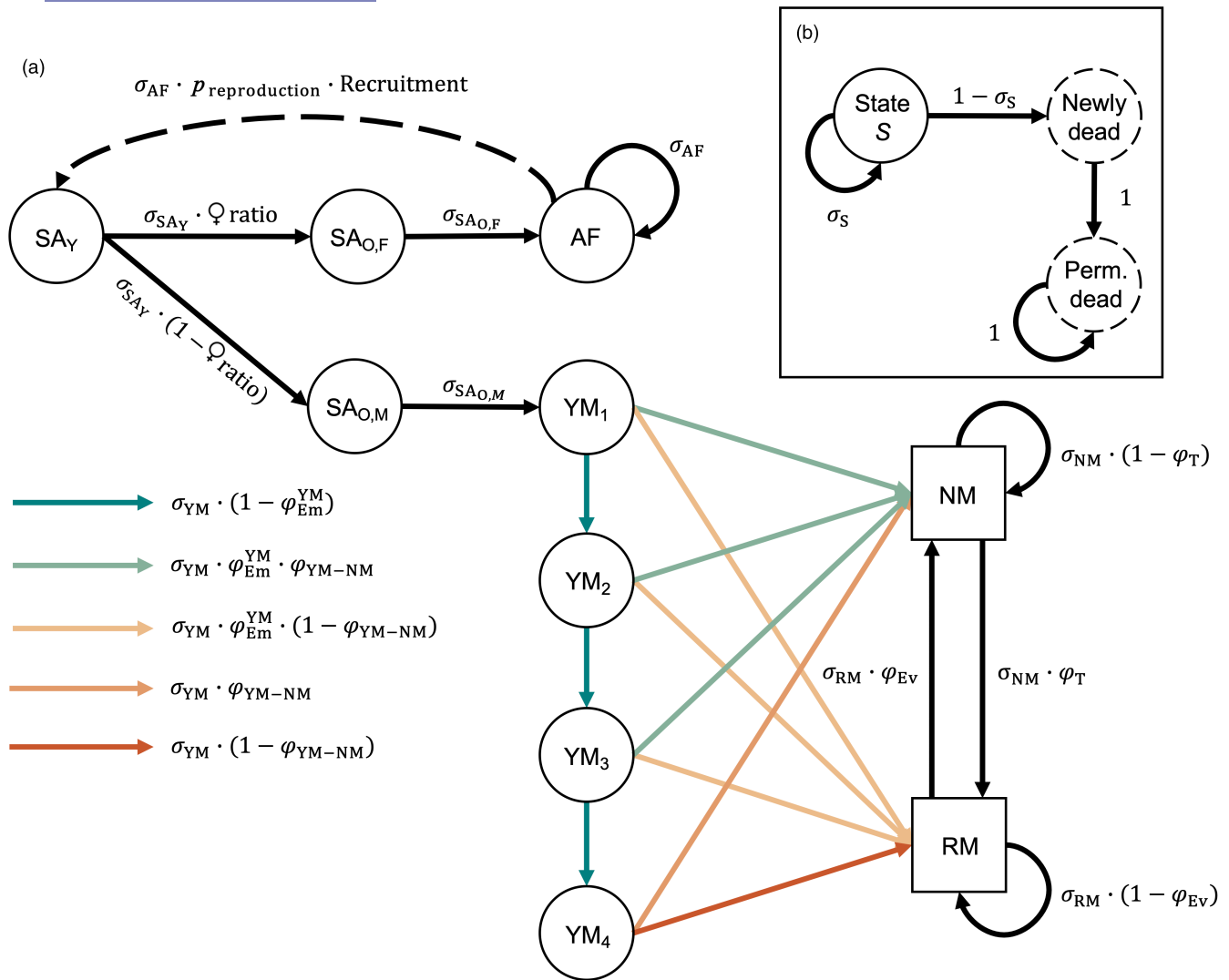


FIGURE 1 Lion life cycle. (a) The life cycle represents seasonal transitions between stages (solid arrows) and reproduction (dashed arrow); all transitions are conditional on survival (σ). The first stage, young subadult (SA_Y ; 12–18 months), is sex-independent. Young subadults transition to female ($SA_{O,F}$) or male ($SA_{O,M}$) 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 (φ_{Em}^{YM} ; except for YM_4) and probability of transitioning to nomadic male (φ_{YM-NM}). 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 ($p_{\text{reproduction}}$) 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.

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 φ_{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-NM}). 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 ($p_{\text{reproduction}}$), 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.

2.2 | Estimation of lion vital rates

2.2.1 | 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) (Figure 1b). Overall, we estimated the following parameters: state-specific survival (σ_S), young-male emigration and transition to nomadic male (φ_{Em}^{YM} and φ_{YM-NM}), 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.

2.2.2 | 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 Bayesian generalized linear mixed models. 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—that is, 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 GLMMs fitted in a Bayesian framework (Kéry & Royle, 2016).

2.3 | Effects of density, season and habitat on vital rates

2.3.1 | 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. 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: Figure 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 focussed 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: Figure 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).

2.3.2 | 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 (Borrego et al., 2018;

TABLE 1 Socially and spatially explicit density covariates included in the various vital-rate models.

Covariate	Vital rate	Motivation
Number of adult females in the pride	Young-subadult survival 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)	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 (Elliot et al., 2014; Packer & Pusey, 1987; Pusey & Packer, 1994), 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 (Packer & Pusey, 1997; Pusey & Packer, 1994).
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 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 Resident-male survival Nomadic male takeover Resident-male eviction	Successful takeovers are affected by the size of both resident and nomadic coalitions (Borrego et al., 2018; Bygott et al., 1979; Packer & Pusey, 1983a).
Number of nomadic coalitions in the home range	Young-subadult survival Old-subadult survival Young-male survival Adult-female survival Resident male survival Resident-male eviction Reproduction probability Recruitment (number of cubs surviving to their first birthday per female, conditional on reproduction)	Nomadic coalitions taking over prides can increase the mortality of subadults and older young through infanticide and forced dispersal (Elliot et al., 2014; Packer, 2023; Packer & Pusey, 1987). Protective encounters by mothers with nomadic coalitions can lead to injuries and lower survival of adult females (Packer & Pusey, 1997; Pusey & Packer, 1994). 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. Higher numbers of nomadic coalitions in the population can lead to more takeovers, increasing cub mortality due to infanticide (Bertram, 1975; Borrego et al., 2018; Pusey & Packer, 1994; Whitman et al., 2004).
Number of adult females in the pride × Number of nomadic coalitions in the home range	Reproduction probability Recruitment (number of cubs surviving to their first birthday per female, conditional on reproduction)	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.
Age	Adult-female survival Reproduction probability	Testing for senescence and age-dependent reproduction.
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.

Note: 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).

Packer et al., 2005). To understand whether seasonal environmental patterns lead to seasonal density feedbacks, we estimated season-specific vital rates—that is, 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: Figure S3).

2.3.3 | 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 (Packer et al., 2005; Schaller, 1972; Sinclair et al., 2013; Sinclair & Norton-Griffiths, 1995). On the other hand, lions in the woodland benefit from a somewhat continuous food availability throughout the whole year (Hanby & Bygott, 1979; Packer et al., 2005; VanderWaal et al., 2009). 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-NM}), 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 pride and nomadic-male detection probabilities.

2.3.4 | Correlation among covariates and year random effect

We checked for correlations between covariates using the Pearson's 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 *lrm* 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.

2.3.5 | Standardization of continuous covariates

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

$$\text{covariate}_{\text{scaled}} = \frac{(\text{covariate}_{\text{unscaled}} - \mu_{\text{covariate}_{\text{unscaled}}})}{2 \times \sigma_{\text{covariate}_{\text{unscaled}}}}, \quad (1)$$

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 approach enables the comparison

of the effect sizes of both categorical (i.e. habitat) and continuous covariates (i.e. density-dependent variables).

2.3.6 | 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 GLMMs 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. (Nater et al., 2020; see Appendix S2 for details). We used noninformative 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 for 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 Appendices S2 and S5. 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 (Conquet et al., 2024) and on GitHub at <https://github.com/EvaCnqt/LionsDensity>.

3 | RESULTS

3.1 | 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 (Figures 2–4; Appendix S5: Figure 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 (Figure 2; Appendix S5: Figure S1). In Figures 2 and 3, we highlight the lack of response of adult-female survival to the density measures we considered (Figure 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; Figures 2b–d and 3a–d) and home-range levels (recruitment and reproduction probability; Figure 3e,f). We also show notable examples of seasonal differences in density effects on lion vital rates (old-subadult and resident-male survival; Figures 2c,d and 3b,c). 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 (Figure 2a; Appendix S5: Figure S3). Otherwise, many vital rates were largely affected by density variables at the group level (Figure 2; Appendix S5: Figure 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; Figures 2b and 3a). The effect of the number of females in the pride on old-subadult survival strongly differed between seasons (Figures 2c and 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

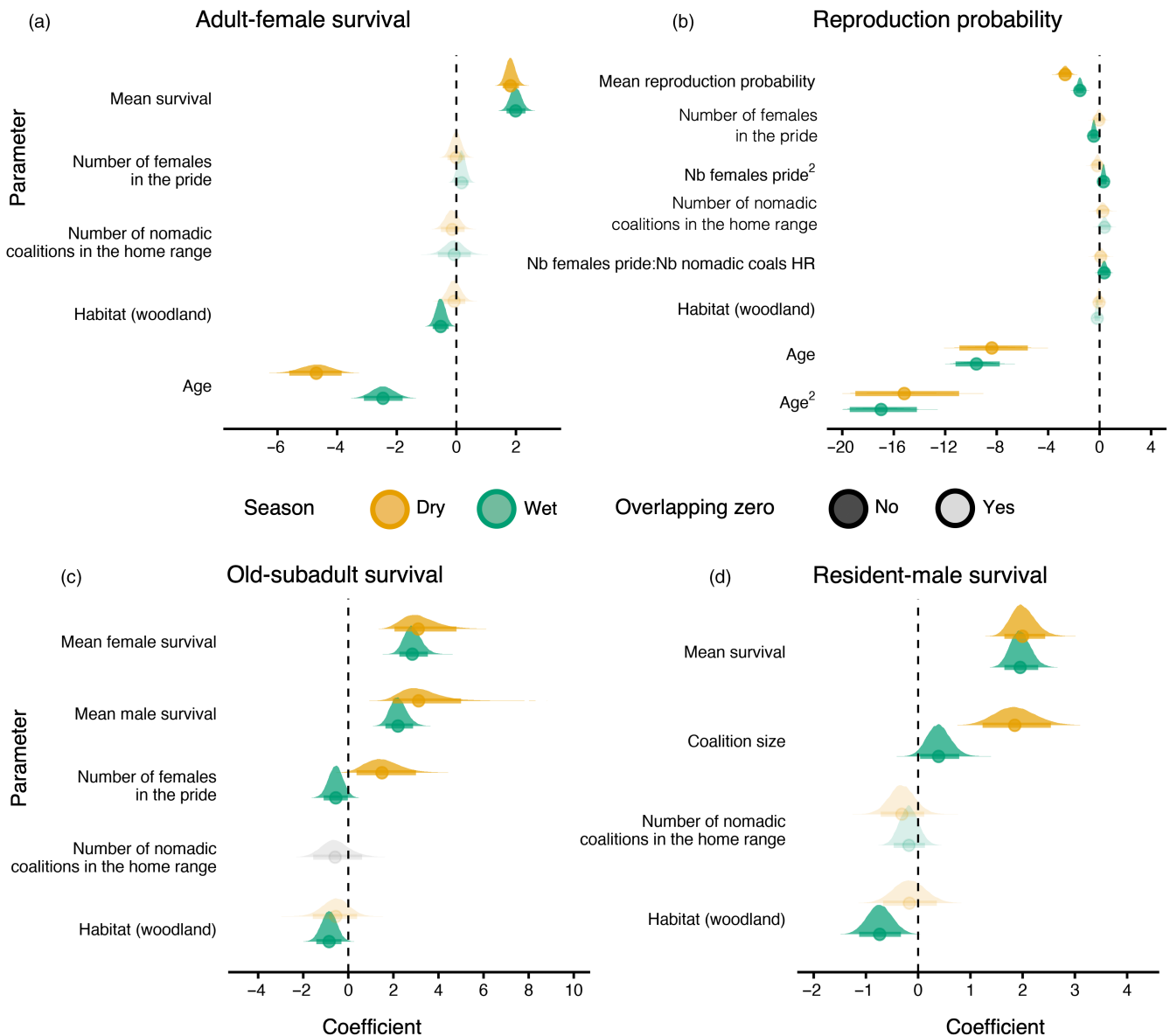


FIGURE 2 Seasonal effects of habitat and density variables at the group and home-range level on lion vital rates. Using a Bayesian multistate capture-recapture and Bayesian generalized linear mixed models (GLMMs), we investigated the presence of seasonal patterns in the response of lion survival, transition 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.

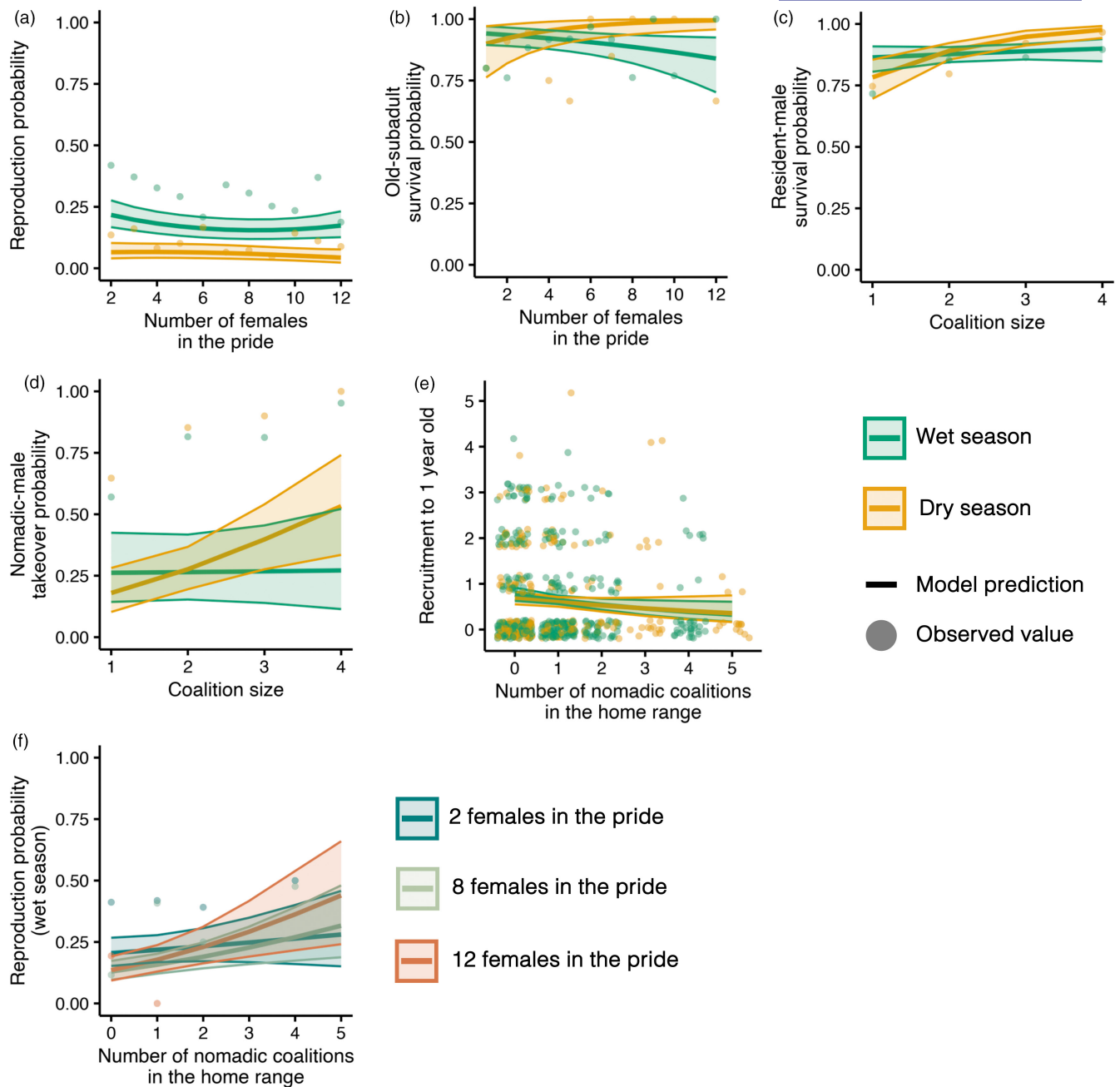
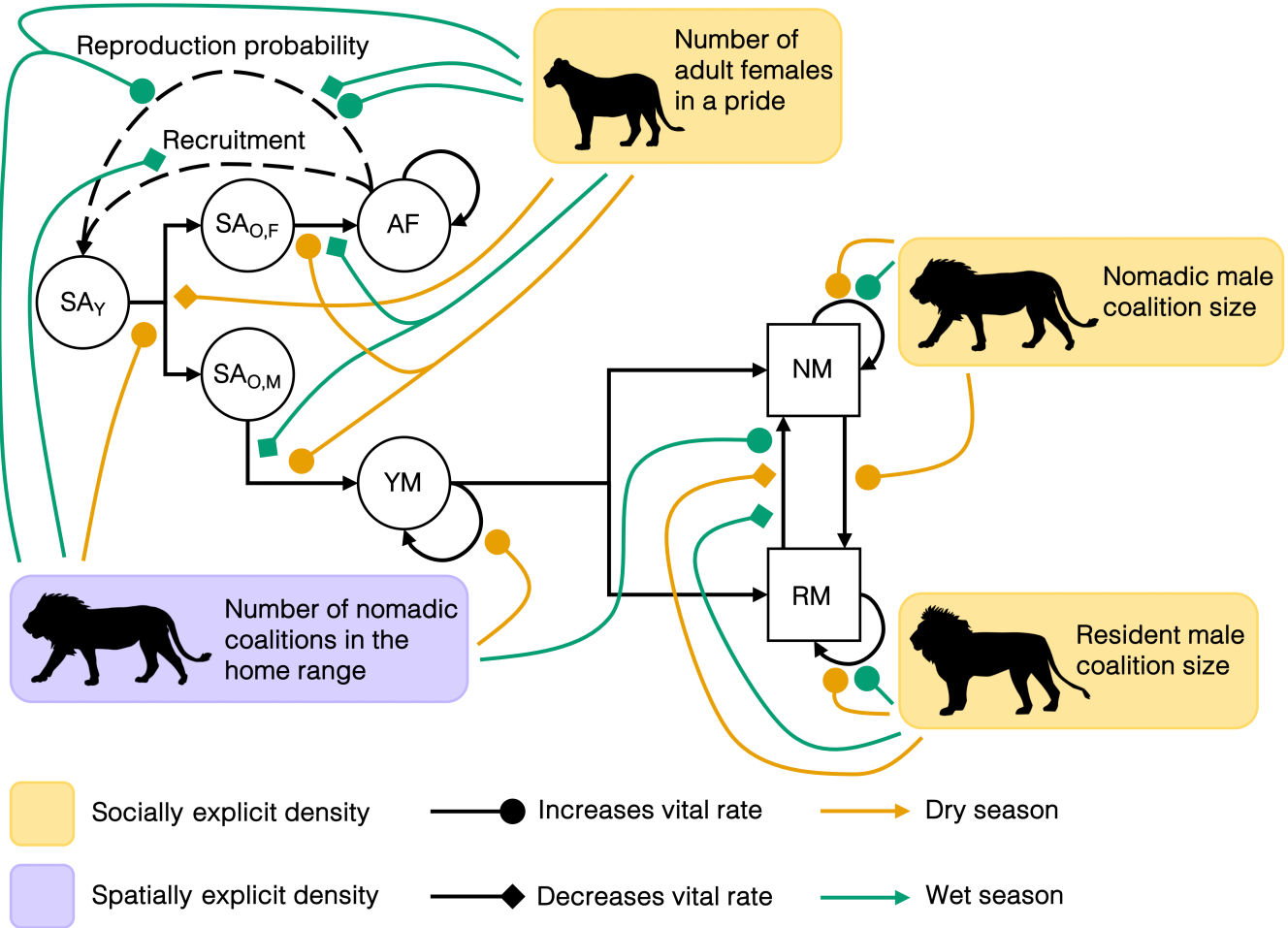


FIGURE 3 Seasonal effects of socially and spatially explicit density measures on lion vital rates. Using a Bayesian multistate capture–recapture and Bayesian generalized linear mixed models (GLMMs), we investigated the presence of seasonal patterns in the response of lion survival, transition, and reproductive rates to the habitat type (woodland or plains), 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 of (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.

number of adult females in the pride did not affect young-male survival or recruitment (Appendix S5: Figure 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: Figure S1). Resident-male survival increased with coalition size in both seasons but showed large differences in the seasonal response to coalition size (see Figures 2d



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 90% CRIs of the coefficient 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.

and 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; Figure 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: Figure 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; Figure 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: Figure 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; Figures 2b and 3f). However, we found no effect of nomadic coalitions on the survival of old subadults and resident males (Figure 2c,d).

3.2 | 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 (Figure 2; Appendix S5; Figure S1). 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 Figure 2c,d). 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 (Figure 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; Figure 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 Figure 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; Figure 2b).

3.3 | Parameter identifiability and model fit

We found no strong evidence of nonidentifiability for either the multistate capture-recapture model or the GLMMs (Appendix S5; Figure 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.

4 | 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 (Figure 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 & 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 (Conquet et al., 2023; Gamelon et al., 2017).

4.1 | 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 and Mitchell (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) (Borrego et al., 2018; Bygott et al., 1979; Packer & Pusey, 1983a). 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 1 year old). This is contrary to previous studies, which found notable effects of pride size on female reproductive output (Packer, 2023; Packer et al., 1990). 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 10 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. Paniw et al., 2019; Reed et al., 2013) 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., Conquet et al., 2023; Vinks et al., 2021). 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: Figure S3). These findings thus emphasize the need for a systematic assessment of the effects of a socially- and spatially-explicit consideration of density.

4.2 | Vital-rate responses to season–density interactions

Context dependence in density effects have been widely described in various species, with age- 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 (Conquet et al., 2023; Letcher et al., 2015; Payo-Payo et al., 2022). 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).

4.3 | 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 with the plains. However, the survival of most stages was lower in the wet season in the woodland compared with 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., Marra et al., 2015; Pärn et al., 2012), 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.

5 | CONCLUSIONS

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; Qu  rou   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.

AUTHOR CONTRIBUTIONS

Eva Conquet was involved in conceptualization, methodology, software, validation, formal analysis, data curation, writing—original draft, writing—review and editing, and visualization. Maria Paniw was involved in conceptualization, writing—review and editing, supervision and funding acquisition. Natalia Borrego was involved in conceptualization, investigation, resources, data curation, and writing—review and editing. Chlo   R. Nater was involved in methodology, validation, resources, writing—review and editing. Craig Packer was involved in investigation, resources, data curation, writing—review and editing. Arpat Ozgul was involved in conceptualization, resources, writing—review and editing, supervision, project administration, and funding acquisition (see Allen et al., 2019 for a definition of each term).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The processed data and MCMC samples necessary for reproducing results and graphs presented in the study are available on Zenodo <https://doi.org/10.5281/zenodo.12722523> (Conquet et al., 2024). Original data can be requested from Craig Packer (packer@umn.edu). Data and code for implementing and running models and analyses, and plotting results are available on GitHub: <https://github.com/EvaCnqt/LionsDensity>. The version of code used for this study is archived on Zenodo <https://doi.org/10.5281/zenodo.12722523> (Conquet et al., 2024).

STATEMENT ON INCLUSION

Our study does not include scientists based in the country where the study was carried out. We recognize 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.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1: Study area and habitat types.

Appendix S2: Details on the model structure and custom likelihood distribution.

Appendix S3: Female recruitment.

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

Appendix S5: Additional results, parameter identifiability, and posterior predictive checks.

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