

Appendix1

Establishing a baseline model with the relevant age structure for survival probabilities

Methods

We used the program RELEASE (Burnham *et al.*, 1987) to assess whether the data met the assumptions of CJS models, namely, (1) equal probability of being recaptured after initial capture at time t (TEST2), and (2) equal probability of surviving from time t to $t+1$ (TEST3) (Kéry, Masden & Lebreton, 2006). TEST 2 revealed no evidence of capture heterogeneity between individuals. Poor model fit for TEST 3, however, indicated the need to include age structure in survival sub-models to explain temporal variation in survival (Kéry, Masden & Lebreton, 2006).

For the African lion (*Panthera leo*) cubs are most vulnerable in their first year, and this age group often has the lowest probability of survival (Bertram 1975; Ogutu & Dublin, 2002; Rosenblatt *et al.*, 2014). During this time, cubs are completely dependent on their mothers, and are too young to defend themselves against predation and infanticide (Schaller, 1972; Metcalf, Hampson & Koons, 2007,1985). Cubs of this age also require large amounts of energy relative to their body size, and therefore also remain vulnerable to starvation resulting from low prey availability (Bertram, 2975). While cubs remain vulnerable to these influences during their second year, their survival probability improves (Schaller, 1972, Bertram, 1975, Ogutu & Dublin, 2002).

Lions between the age of two and four become independent, and males of this age will disperse in search of a new pride (Hanby & Bygott, 1987; Funston *et al.*, 2003, Elliot *et al.*,

2014). For subadult females, however, dispersal or recruitment depends on prevailing social circumstances such as natal pride size relative to habitat quality, or population density, which may influence the availability of vacant territories (Van der Waal, Mosser & Packer, 2009). For dispersing sub-adults, survival may be low during this period due to inexperience in hunting or conflict with neighbouring prides (Funston *et al.*, 2003; Elliot *et al.*, 2014). Lastly, apart from anthropogenic causes, adult survival tends to remain relatively constant, and is mostly influenced by social factors such as territorial conflict (Mosser & Packer, 2009), or stochastic events such as disease (Roelke-Parker *et al.*, 1996).

Given these patterns in age-specific survival, and in accordance with results from similar research on age-specific survival (Rosenblatt *et al.*, 2014, Ferreira *et al.*, 2020), we tested several survival sub-models with different age structures to determine which survival sub-model best fitted the data. The data was binned into different age classes which consisted of: young cubs (age 0 – 1 year), juveniles (age 1- 2 years), sub-adults (age 2 – 4 years), combined juvenile and sub-adults (1 – 4 years), young adults (age 4 – 8 years), old adults (age 8+ years) and a combined adult class (age 4 + years). As we were interested in relating changes in survival with annual changes in social and environmental covariates, all survival sub-models were fully time-varying.

Once the survival sub-model was finalized, the second step in the modelling process was to identify a sub-model that best described recapture probabilities (Emmerson & Southwell, 2011). We therefore modelled the fully time-dependent survival sub-model with a recapture sub-model that varied with time $p(t)$, or remained constant over the sampling period $p(.)$. To account for potential differences in survival between prides, pride was included as an

additive effect in the model structure for survival. Using Akaike's Information Criterion for small sample sizes (AICc), the best sub-models for survival and recapture probability was selected as the baseline model (Anderson & Burnham, 2002; Table 1).

Results

Test 2 results revealed no capture heterogeneity amongst individuals ($\chi^2 = 5.52$, $df = 4$, $p = 0.238$). However, Test 3 indicated the need to include age structure in modelling survival probabilities ($\chi^2 = 16.93$, $df = 7$, $p = 0.018$). The full-time varying model with three age classes for survival: cubs (0-1 year), combined class of juveniles and sub-adults (1-4 years) and the combined class for adults (>4 years; Table 1), outweighed other age structure models (AICc weight = 0.805), and was the only model with a change in AICc < 2. This model was thus used as the baseline model to assess goodness-of-fit and test for over-dispersion.

Table 1. Model selection table resulting from testing various age group structures for the survival probability sub-model, and testing temporal or constant trends in recapture probability sub-model for data from 5 African lion (*Panthera leo*) prides in the south-western Okavango Delta, Botswana.

Survival	Recapture	k	AICc	Δ AICc	w
$\varphi(\text{CY}(t) + \text{JSA}(t) + \text{AD}(t)) + \text{Pride}$	p(t)	17	514.12	0.00	0.8048
$\varphi(\text{CY}(t) + \text{JSA}(t) + \text{YAD}(t) + \text{OAD}(t)) + \text{Pride}$	p(t)	19	516.96	2.85	0.1938
$\varphi(\text{CY}(t) + \text{JU}(t) + \text{SA}(t) + \text{AD}(t)) + \text{Pride}$	p(t)	26	527.16	13.04	0.0012
$\varphi(\text{CY}(t) + \text{JSA}(t) + \text{AD}(t)) + \text{Pride}$	p(.)	12	531.98	17.86	0.0001
$\varphi(\text{CY}(t) + \text{JU}(t) + \text{SA}(t) + \text{YAD}(t) + \text{OAD}(t)) + \text{Pride}$	p(t)	28	531.99	17.87	0.0001
$\varphi(\text{CY}(t) + \text{JSA}(t) + \text{YAD}(t) + \text{OAD}(t)) + \text{Pride}$	p(.)	14	534.58	20.47	0.0000
$\varphi(\text{CY}(t) + \text{JU}(t) + \text{SA}(t) + \text{AD}(t)) + \text{Pride}$	p(.)	21	539.76	25.64	0.0000
$\varphi(\text{CY}(t) + \text{JU}(t) + \text{SA}(t) + \text{YAD}(t) + \text{OAD}(t)) + \text{Pride}$	p(.)	23	544.13	30.02	0.0000

CY = young cubs aged between 0 – 1 years old
JU = juveniles aged between 1 – 2 years old
JSA = combined class of juveniles and sub-adults aged 1 – 4 years old
SA = sub-adults aged 2 – 4 years old
YA = adult aged 4 – 8 years old
OA = older adult aged 8+ years
AD = combined adult age class aged 4 + years
t = denotes probability varies with time
. = denotes probability remains constant

φ = indicates survival probability sub-model
p = indicates capture probability sub-model
k = number of model parameters
AICc = Aikaike's Information Criterion for small sample sizes
 Δ AICc = change in AICc score
w = AICc model weight

References

- Anderson, D.R. & Burnham, K.P. (2002). Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management*, 66, 912-918.
- Bertram, B.C.B. (1975). Social factors influencing reproduction in wild lions. *Journal of Zoology* 177, 463–482.
- Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C. & Pollock, K. H. (1987). Design and analysis methods for fish survival experiments based on release-recapture. *American Fisheries Society Monographs*, 5, 1-437.
- 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, 1049-1056.
- Emmerson, L. & Southwell, C. (2011). Adélie penguin survival: age structure, temporal variability and environmental influences. *Oecologia*, 167, 951-965.

- Ferreira, S. M., Beukes, B. O., Haas, T. C., & Radloff, F. G. (2020). Lion (*Panthera leo*) demographics in the south-western Kgalagadi Transfrontier Park. *African Journal of Ecology*. <https://doi.org/10.1111/aje.12728>.
- Funston, P. J., Mills, M. G., Richardson, P. R., & van Jaarsveld, A. S. (2003). Reduced dispersal and opportunistic territory acquisition in male lions (*Panthera leo*). *Journal of Zoology*, 259, 131-142.
- Hanby, J.P. & Bygott, J.D. (1987). Emigration of sub-adult lions. *Animal Behaviour*, 35, 161-169.
- Kéry, M., Masden, J., Lebreton, J-D. (2006). Survival of Svalbard pink-footed geese *Anser brachyrhynchus* in relation to winter climate, density and land-use. *Journal of Animal Ecology*, 75, 1172-1181.
- Metcalf, C. J. E., Hampson, K., & Koons, D. N. (2007). What happens if density increases? Conservation implications of population influx into refuges. *Animal Conservation*, 10, 478-486.
- Mosser, A. & Packer, C. (2009). Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. *Animal Behaviour*, 78, 359-370.
- Ogutu, J. O. & Dublin, H.T. (2002). Demography of lions in relation to prey and habitat in the Masai Mara National Reserve, Kenya. *African Journal of Ecology*, 40, 120-129.
- Roelke-Parker, M.E., Munson, L., Packer, C., Kock, R., Cleveland, S., Carpenter, M., O'Brien, S.J., Popsichil, A., Hofmann-Lehmann, R., Lutz, H., Mwamengele, G.L.M., Mgasa, M.N., Machange, G.A., Summers, B.A. & Appel, M.J.G. (1996). A canine distemper virus epidemic in Serengeti lions (*Panthera leo*). *Nature*, 379, 441-445.

- Rosenblatt, E., Becker, M. S., Creel, S., Droge, E., Mweetwa, T., Schuette, P. A., Watson, F., Merkle, J., & Mwape, H. (2014). Detecting declines of apex carnivores and evaluating their causes: an example with Zambian lions. *Biological Conservation*, 180, 176-186.
- Schaller, G. B. (1972). *The Serengeti lion: a study of predator prey relations*. Chicago: Chicago University Press.
- Van Der Waal, K.L., Mosser, A. & Packer, C. (2009). Optimal group size, dispersal decisions and post-dispersal relationships in female African lions. *Animal Behaviour*, 77, 949-954.