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Rainfall driven changes in behavioural responses confound measuring trends in lion population size

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Population size estimates must be comparable through time to interpret trends in threatened carnivore populations. Because prey distribution and dynamics drive carnivore distribution, and sampling methods often utilise behavioural responses to attractants, habitat variability among sampling occasions may confound such estimates. We explored whether a marked and unexpected reduction in lion *Panthera leo* population size estimates in Kruger National Park, was real or represented changes in behavioural responses to call-up stations given reduced rainfall between sampling periods. Rainfall drives savannah landscape heterogeneity, surface water and lion prey food availability. Hence landscape factors should more strongly influence lion behaviour during dryer conditions. We compared proportion of stations visited and mean numbers visiting stations, among three sampling years (2005, 2006 and 2008) belonging to the two sampling periods 2005/2006 and 2008. We then modelled the influence of landscape factors and spotted hyena *Crocuta crocuta* presence on visits and numbers. We distinguished behavioural from real changes by simulating pseudo-absences of cubs (these are observations of females which do have cubs but did not show up with them at calling stations) and comparing observed with predicted population estimates. Adult males responded similarly among sampling years. However, in 2008 the driest year, adult females and those with cubs visited a lower proportion of stations, and landscape influences on these groups was stronger. A switch from rainfall explaining adult females with cubs visiting stations during wetter sampling years, to distance to rivers in 2008 confirmed landscape driven changes in lion responses consistent with prey distribution in dry conditions. However, simulations indicated that while behavioural responses accounted for some population reduction, some was real. Reduced rainfall induced behavioural effects were difficult to unravel from real population size changes. We advocate caution when interpreting trends from lion population estimates reliant on behavioural responses subject to variability in landscape factors. Particularly, for estimators sensitive to behavioural changes in females with cubs – the demographic component most affected by variable conditions.

Population size estimates form vital information for understanding the interactions between a species and its environment (Krebs 2003) and thus lie at the heart of many wildlife and conservation management strategies. This is especially the case for threatened carnivore species which often suffer from multiple stressors including human induced pressures (Ogutu and Dublin 2002, Ogutu et al. 2005, Woodroffe and Frank 2005, Loveridge et al. 2007, Kiffner et al. 2009, Packer et al. 2011) and disease (Mollel 1977, Brown et al. 1994, Roelke-Parker et al. 1996, Keet et al. 1997, Packer et al. 1999, Cleaveland et al. 2005). However, for carnivores, estimating and monitoring changes in population size is challenging (Funston et al. 2010). Carnivores are positioned at the top of the food chain, such that their distribution and behavioural responses are influenced by the distribution of their prey in relation to key resources, which in turn is modulated by the availability of structural and functional resources of systems to which they belong (Karanth et al. 2004, Valeix et al. 2011). Hence, variation in these resources can markedly influence population

estimates. This may be especially true when utilising sampling designs for one-off surveys that rely on carnivore behavioural responses (Ogutu and Dublin 1998, Ferreira and Funston 2010) because flow-on effects from prey responses to the distribution of food and water may alter lion responses to attractant stimuli. This is important, because variation in responses between sampling occasions may lead to incorrect estimates of population size, with serious consequences for conservation management decisions.

We explored if this was the case for African lions *Panthera leo* in Kruger National Park, South Africa (Kruger). Although Kruger hosts one of the largest lion populations in Africa (Chardonnet 2002, Bauer and van der Merwe 2004), emerging bovine tuberculosis (bTB) was flagged as a potential threat to the wellbeing of lions there (Keet et al. 1996). However, although no population level effects suggest threats to lion persistence (Ferreira and Funston 2010), two recent population estimates noted a decline of 19–31% per annum from 1684 lions (95% CI: 1617–1751) in 2005/2006 (Ferreira and Funston 2010) to 1016 lions (95% CI: 862–1180) in

2008 (SANParks, unpubl.data). If real, such a decline raises a key concern. Lions are vulnerable (Packer et al. 2013) and now only exist in 67 populations across Africa, of which Kruger is one of ten conservation strongholds for this species (Riggio et al. 2013). In this study, we assessed whether this decline was real, or the product of variation in behavioural responses to variation in structural and functional landscape factors between sampling years. Note that our two sampling periods of 2005/2006 and 2008 and respective population estimates comprised data from three sampling years 2005, 2006 and 2008.

Call-up stations are a preferred survey technique for lions in mesic savannah (Ogutu and Dublin 1998, Ferreira and Funston 2010) and were used in all our sampling years. Because this method relies on lion responses to prey-distress calls, we were concerned that the two population estimates may have been sensitive to a marked reduction in rainfall and/or an inadvertent increased distance to waterholes noted for the latter sampling period (SANParks, unpubl. data).

Rainfall and the distribution and availability of water sources influence lion behaviour. Rainfall drives the spatial arrangement, quality and quantity of limiting food and water in savannah systems at the landscape scale, with flow-on effects on carnivore distribution and density (Hopcroft et al. 2005, Mosser et al. 2009, De Boer et al. 2010, Valeix et al. 2010). Indeed, in woodlands, lion kills are typically closer to rivers (Mosser et al. 2009) and to artificial water points than expected (De Boer et al. 2010) particularly in the dry season when lions may prefer wooded areas for shade and cover for cubs, and when prey species are spatially restricted to areas where surface water is available (Hopcroft et al. 2005, Mosser et al. 2009, De Boer et al. 2010, Valeix et al. 2010). Moreover vegetation cover associated with rivers may render these areas more favourable for hunting by lions (Mosser et al. 2009). We therefore hypothesised that decreased rainfall between surveys and/or the increased distance of call-up stations to waterholes influenced the behavioural response of adult female lions with cubs. This in turn influenced calculated population estimates according to the response estimator derived for lions in Kruger (Ferreira and Funston 2010).

To test our hypothesis, we explored the influence of rainfall, distance to closest waterholes, distance to closest river and prey food availability on lion responses to call up stations. We expected the relationships between these structural and functional landscape factors and lion responses would be stronger during periods of low rainfall when lions take advantage of their prey being limited to available water sources (Hopcroft et al. 2005, De Boer et al. 2010, Valeix et al. 2010) and/or more easy to target (Mosser et al. 2009). In addition to these landscape level factors, we also explored the local influence of the presence of spotted hyena *Crocuta crocuta* (hereafter hyena) on lion responses. Because hyenas are competitors of lions (Owen-Smith and Mills 2008) and thus may modulate lion behaviour, we asked if the presence of hyenas differed among sampling years, and whether their presence modulated the response of lions to our call up stations. Finally, to distinguish between changes in behavioural responses and real changes in the number of females, and/or number of females with cubs, we also explored the effect on population estimates if behavioural

choices resulted in pseudo-observations of females without cubs. We reasoned that if predicted estimates differed from observed estimates during 2008, changes other than, or in addition to, female behavioural changes had occurred.

Our study highlights the need for caution when estimating lion population sizes from one-off surveys that rely on behavioural responses. We argue that variation in structural and functional landscape factors among sampling years can generate flow-on effects in prey dynamics and lion behavioural responses that need to be accounted for when interpreting trends in population size among surveys.

Material and methods

Study area

The Kruger National Park (Kruger) is situated in the low-lying savannah of the eastern parts of the Limpopo and Mpumalanga Provinces, South Africa. Mozambique abuts the Park in the east, while Zimbabwe forms the boundary to the north. The Park covers an area of 19 485 km² and has a mean annual rainfall that varies from 750 mm in the south to 450 mm in the north, with ~80% of rain falling during October to March (Gertenbach 1980). Granite and gneiss soils dominate Kruger's western half and nutrient-rich basalt soils dominate the eastern half, with a narrow band of Karoo sediment occurring at the junction of the granite and basalt (Schutte 1986).

The vegetation on the southern basalts is largely wooded savannah, with *Sclerocarya caffra* and *Acacia nigrescens* dominating the tree canopy. Mixed *Combretum* spp. and *Acacia* spp. dominate the southern granites. In the north *Colophospermum mopane* dominates both the basalt and granite substrates. However, taller *C. mopane* as well as *Combretum* spp. and *Acacia* spp. occur more often on the granites, while stunted or shrub like *C. mopane* sparsely interspersed by *S. caffra* are found on the basalts (Gertenbach 1983).

Large herbivore densities closely match substrate and vegetation patterns with higher densities on the fertile basalts than the granites, and at markedly lower densities in the dry north than the south irrespective of substrates (Ferreira and Funston 2010). In addition, there are zonal bTB prevalence differences within buffalo with 38.0%, 16.0% and 1.5% in the southern, central and northern regions of the Park respectively (Rodwell et al. 2000). The Olifants River is the boundary between the northern and central region while the Sabie River is the boundary between the central and southern zones. Ferreira and Funston (2010) originally defined six zones: low prey – low disease, medium prey – low disease, high prey – medium disease, very high prey – medium disease, high prey – high disease, and very high prey – high disease zones.

Data collection

Lion responses

We used three datasets collected across the Park in 2005, 2006 and 2008. Each dataset was collected in the dry season months (May, June, July, August and September). Because

the survey in 2005 focused primarily in the south of the park, and in 2006 from the middle to northern reaches of the park (thus together forming a total coverage of Kruger, Ferreira and Funston 2010), we analysed datasets for 2005 and 2006 both individually, and as a combined dataset. We note that this approach makes our reporting of results and discussion complicated. However, it provided us with the ability to interpret results collectively across the park, but also independently among years with relevance to the difference between the population estimates of concern. Hence, to assist the flow of reading, hereinafter we refer to 2005, 2006 and 2008 as sampling years, and 2005/2006 combined and 2008 as sampling periods. Note that the sampling year and period for 2008 are therefore one and the same and may be referred to twice for ease of reading.

All sampling locations were stratified according to a combination of prey biomass and tuberculosis incidence (Ferreira and Funston 2010). For our 2005 ($n = 101$ call-up stations) and 2006 ($n = 124$ call-up stations) sampling years, stations were placed no closer than 10 km apart in a systematic grid design (≈ 12 per 1000 km²). For our 2008 sampling year (127 call-up stations) stations were placed no closer than 11.5 km apart (≈ 8 per 1000 km² as per recommendation by Ferreira and Funston 2010), following the same sampling design as before (i.e. also stratified by prey biomass and tuberculosis incidence). This latter sampling intensity was based on optimal requirements that stabilized variance in estimates (Ferreira and Funston 2010). Call-ups comprised a buffalo distress call and were played for one hour at night (Ferreira and Funston 2010). For each call-up station, we recorded whether the station was visited, the total number of lions that visited the station, the total number of males, the total number of females, and whether cubs visited the station within the hour play period. We also recorded the presence of spotted hyenas, but did not record their numbers. Call-up station response rates have been calibrated by Ferreira and Funston (2010) providing for the effective area over which lions may respond, the probability that a group within that area will respond, and the probability that an individual within a responding group will respond. They also calibrated the efficiency of call-up stations by defining the survey effort required to achieve estimates with known precision in Kruger National Park, South Africa. Together these calculations render call-up station data similar to that of block counts (Ferreira et al. 2011) albeit with a circular sampling area.

Structural and functional landscape explanatory factors

For each call up station, we assigned prey biomass as low, medium, high and very high as per Ferreira and Funston (2010) based on data from the 2006 census (Judith Kruger, Scientific Services, SANParks, unpubl. data) from which we calculated the biomass of eight key prey species that make up >95% of the lion's prey in Kruger (Mills and Shenk 1992, Radloff and du Toit 2004).

We used the normalised difference vegetation index (NDVI) as an index of prey food availability. NDVI is good proxy for vegetation productivity (Pettorelli et al. 2005) and prey food availability because ungulate abundance associates with productivity (Verlinden and Masogo 1997, van Bommel et al. 2006, Pettorelli et al. 2009). We downloaded NDVI values for July 2005, July 2006 and July 2008 from

<http://free.vgt.vito.be/>. Data were at the resolution of 1 km², with NDVI-values calculated from 10-day composites of remotely sensed images from the VEGETATION sensor aboard the SPOT4 and SPOT5 satellites for July of each year. For each of July 2005, 2006 and 2008, three 10-day composites were available so we used the middle composite from 11–21 July to represent NDVI values of July that year. We then calculated the sum of total NDVI within an assumed effective operating area we calculated for each call-up station based on the probability of a lion to respond within that area as calculated by Ferreira and Funston (2010). Lions respond to call-up stations from a mean distance of 4.5 km (Ferreira and Funston 2010). Using this distance as a radius, we assumed an effective operating area of 64 km² about each call-up station location and, for each, created a round buffer of this size using the spatial analyses toolbox in ARCGIS ver 9.0. For each round buffer we calculated the total concurrent standing prey food availability (sum of NDVI of round buffer at time of call-up).

We also used the spatial analyses toolbox in ARCGIS ver 9.0 to calculate the Euclidian distance (in km) from each call-up station to the nearest waterhole (artificial or natural) and to the nearest river.

We calculated the total volume of rainfall in the twelve months prior to each respective July for each sampling station. To do this we used total rainfall recorded from 26 rainfall stations in 2005, 22 in 2006 and 19 in 2008 for the 12 month period prior to sampling. For each year we calculated a thin plate spline using a generalised additive model in the R-package 'fields' (http://pages.cs.wisc.edu/~xie/thin_plate_spline_tutorial.html) to predict rainfall across Kruger at a resolution of 1 km². We then extracted predicted rainfall values for each station in its respective sampling year.

Finally, rainfall increases in Kruger National Park in a north to south direction forming a distinct rainfall gradient (Gertenbach 1980). To assist in distinguishing between the influence of inter-annual variability and spatial-variation in rainfall on lion responses, we also used the latitude of each call-up station as an explanatory factor in our analyses.

The presence of hyenas

In addition to the explanatory factors above, we recorded the presence of hyena at each call up station. As per our introduction, the presence of hyena was treated as both a response variable (probability of visiting a station) and a localised explanatory factor for lion responses.

Analytical approach

We compared lion responses to call up stations among all three sampling years (2005, 2006 and 2008) and then between the 2005/2006 and 2008 sampling periods. We calculated the proportion of call up stations for each sampling year and sampling period that were visited by any lions, by adult males, by adult females (with and without cubs – hereinafter adult females), by adult females with cubs, and by hyena, and noted differences in these between sampling years (note that on only four occasions did cubs visit a station independent of an adult female so we did not calculate proportion of stations visited by cubs separately),

and between sampling occasions. We then used one way analyses of variance and Tukey's post hoc tests to compare mean group size, mean number of adult males, mean number of adult females and mean number of cubs per station between the three sampling years (2005, 2006 and 2008) and one way t-tests to compare between the two sampling periods (2005/2006 combined and 2008).

Next we compared the spatial distribution of sampling sites in relation to distance to closest waterhole, and distance to closest river, and also compared the sum of NDVI (our index of prey food availability) and total predicted rainfall in the twelve months prior to sampling between the three sampling years, and between the two sampling periods. As above, we used one way analysis of variance (ANOVA) and Tukey's post hoc tests to compare means between the sampling years, and one tailed t-tests to compare means between the sampling periods.

To establish the influence of our explanatory factors on lion responses and on the presence of hyenas, we modeled suites of alternative hypotheses being different combinations of explanatory factors for: the probability of a station being visited; 1) by any lions, 2) by adult males, 3) by adult females, 4) by adult females with cubs, and 5) by hyena, and for each station the mean number of; 6) lions in the total group, 7) adult male lions, 8) adult female lions, and 9) lion cubs. For each response variable we calculated generalised additive models for: 1) 2005 2) 2006 3) 2008, 4) all years combined, and 5) 2005/2006 combined.

For each candidate model we calculated the Akaike's information criterion corrected for small sample size (AICc) (Burnham and Anderson 2002) and stepwise selected the model with the lowest AICc value as the most likely model to represent the data (Burnham and Anderson 2002). We also calculated AICc differences (AICc (Δ_i)) to assess support for each model where for the best model AICc (Δ_i) = 0; values from 0 to 2 indicate substantial support; values of 4–7 less support and values > 10 no support (Burnham and Anderson 2002). Next we calculated AICc weights (AIC(wi)) to indicate the probability that each model was the most likely model of all candidate models to represent the dataset. Where the difference between best fit models and next fit model(s) according to AIC(wi) was negligible and mostly involved the removal of one explanatory factor with limited reduction in evidential support for the model fit to the data i.e. AICc (Δ_i) < 2, we also report the respective variable.

We used logistic regressions for response variables 1) to 5) (probability models), and the Poisson family of models for response variables 6) to 9) (explanation of variance). For our logistic regressions, we calculated the discriminative ability of models as the area under the curve (AUC) of the receiver operating characteristic (AUC-ROC). The ROC curve is calculated as the curve of true positives versus false positives and therefore varies from 0.5 (discriminating power no better than chance) to 1.0 (perfect discriminating power). Accordingly the AUC-ROC represents the percentage of all possible pairs of cases in which the model assigns a higher probability to a correct case than to an incorrect case. Accordingly AUC-ROC values below 0.7 are considered to have poor discriminatory ability (Hosmer and Lemeshow 2000) and we categorised models with AUC-ROC values > 0.7 as

useful or plausible (Hastie et al. 2001, Boyce et al. 2002). For our Poisson models, we calculated the deviance explained from the predicted means of the models (D^2) where $D^2 = (\text{null deviance} - \text{residual deviance}) / \text{null deviance}$. We also calculated the correlation between observed and predicted values (COR) as a measure of model accuracy.

For both our logistic regressions and Poisson models we calculated model stability, being the performance of the model to predict correct values from subsets of the data, using five-fold cross validation (Hastie et al. 2001). Where cross validation values were < 0.6 and or departed considerably from respective ROC or COR values, we considered models unstable in their ability to accurately predict correct values from new data.

For each response variable, we evaluated differences in its relationship with explanatory factors among sampling occasions together and independently by comparing model statistics (D^2 and AUC-ROC values), performance under cross validation, included explanatory factors, relative importance of these and associated shape of relationships.

All models were calculated using generalised regression and spatial prediction (GRASP, Lehmann et al. 2002) in the R statistical environment ver. 1.12.3.

To distinguish between behavioural responses and real declines, we simulated the likely effect on the lion population estimator developed before (Ferreira and Funston 2010) if females made behavioural choices resulting in pseudo-observations of females without cubs (i.e. these are observations of females which do have cubs but did not show up with them at calling stations). We simulated a fixed number of females changing progressively from nearly all turning up with cubs to nearly all turning up without cubs. By fitting a linear relationship between predicted population estimates (estimated by applying Ferreira and Funston's 2010 estimator) and percentage of females visiting call-up stations with cubs, we could estimate the likely effect of such behavioural changes on a population estimates when all else stays equal.

We then collated survey data for 2005/2006 (Ferreira and Funston 2010) and 2008 (SANParks, unpubl. data) and calculated the observed percentage of females visiting call-up stations with cubs for each of the two surveys. Using the derived linear relationship, we then predicted the population estimate as well as the estimated number of adult females for 2008 if the population did not change, but behavioural responses did as indicated by the change in percentage of females with cubs visiting stations. We reasoned that if this predicted estimate differs from observed estimates during 2008 we have reason to believe there were changes other than, or in addition to female behavioural changes.

Results

Lion responses

Among 2005, 2006 and 2008 sampling years

The proportions of stations that were visited by any lions, adult females, adult females with cubs, cubs and hyena were lower in 2008 relative to 2005, 2006 (Fig. 1A). However, in

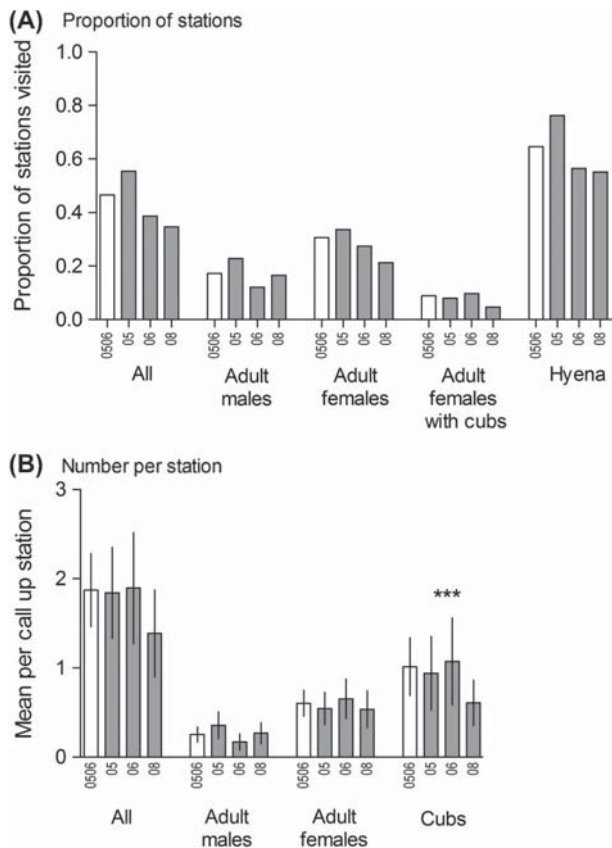


Figure 1. Proportion of stations visited by lions and mean number of lions per station according to several age and sex classes of interest in 2005/2006 combined (clear bars, $n = 225$), 2005 ($n = 101$), 2006 ($n = 124$) and 2008 ($n = 127$). In (A) we also show proportion of stations visited by hyenas for the same year combinations. Error bars in (B) are the 95% confidence intervals of the means and *** denote significance difference ($p < 0.0001$) between means for 2005/2006 and 2008.

2006, the proportion of stations visited by all lions, adult females and hyena were higher than for 2008, but lower than for 2005. The proportion of stations visited by adult males was lowest in 2006 relative to 2005 and 2008, and lower in 2008 relative to 2005 (Fig. 1A).

The total number of lions and the number of cubs visiting call-up stations was lower in 2008 than in 2005 or 2006, however these differences were not statistically significant (ANOVA: $p = 0.35$ and $p = 0.21$ respectively). The number of adult males and the number of adult females were similar among the three sampling years (ANOVA: $p = 0.09$ and $p = 0.69$ respectively), despite the mean number of adult males being lower and mean number of adult females being higher in 2006, than in 2005 and 2008 (Fig. 1B).

Between the 2005/2006 and 2008 sampling periods

The mean group size and mean number of cubs were lower in 2008 than during the 2005/2006 sampling period, although for the former this difference fell just below statistical significance (one tailed t-test: $p = 0.07$, $p < 0.0001$ respectively). The mean number of adult males and adult females did not differ between the two sampling periods combined (one tailed t-test: $p = 0.42$, $p = 0.29$ respectively).

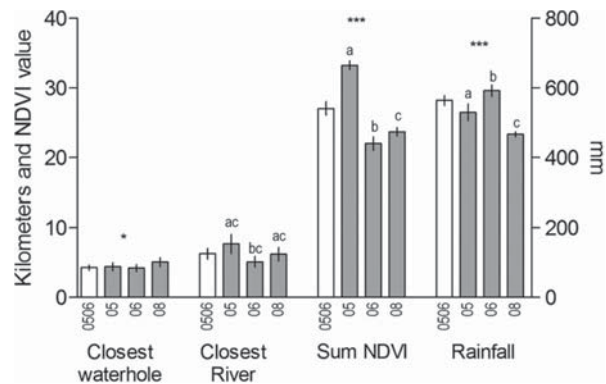


Figure 2. Summary of structural and functional landscape factors associated with call-up stations in 2005/2006 combined (clear bars, $n = 225$), 2005 ($n = 101$), 2006 ($n = 124$) and 2008 ($n = 127$). Mean distance in kilometres is shown for closest waterhole and closest river, and the mean values are shown for the sum of NDVI and rainfall associated with each call-up station (Methods). a, b and c denote statistically significant differences among years from one way ANOVA and Tukey's post hoc tests. * are for significant differences between 2005/2006 combined and 2008 (where $p < 0.05$ *, $p < 0.001$ **, $p < 0.0001$ ***). Error bars are the 95% confidence intervals of the means.

Distance to water, NDVI and rainfall

Among 2005, 2006 and 2008 sampling years

The distance to closest river, sum of NDVI and rainfall in the preceding 12 months differed among the 2005, 2006 and 2008 sampling years (Fig. 2). In 2006, call-up stations were distributed nearer to the closest river than in 2005 and 2008 (ANOVA $p = 0.0029$), but distance to closest river did not differ between 2005 and 2008. Sum of NDVI was highest for call-up stations in 2005, lowest for 2006 call-up stations and slightly higher for stations in 2008 than for those in 2006 (ANOVA: $p < 0.0001$). Rainfall at call-up stations was highest in 2006, lower in 2005, and lowest in 2008 (ANOVA: $p < 0.0001$). The difference in distribution of sampling sites in relation to the closest waterhole was not quite significant among sampling occasions (ANOVA: $p = 0.07$) even though mean distance for 2008 was greater than for that in 2005 and in 2006 (Fig. 2).

Between the 2005/2006 and 2008 sampling periods

In 2008, call-up stations were distributed further from the closest waterhole than in the 2005/2006 sampling period (one way t-test: $p < 0.0001$). Sum of NDVI was smaller in 2008 than 2005/2006 (one way t-test: $p < 0.0001$), and rainfall in the 12 months preceding sampling was lower for 2008 than for 2005/2006 (one way t-test: $p < 0.0001$). The distribution of sampling sites in relation to the closest river did not differ between sampling occasions (one way t-test, $p = 0.46$).

Probability of visits to call-up stations

Our best fit models differed among sampling years and sampling periods in their ability to plausibly explain the probability of a station being visited by our lion groups (any lions, adult males, adult females, adult females with cubs) and hyenas. Note that the suite of explanatory factors included in selected models were relatively consistent among years for explaining adult male lion visits, but in contrast changed

considerably for adult females and adult females with cubs among sampling years (Table 1). In the wetter years of 2005 and 2006, the likelihood of visits by adult females with cubs was explained predominantly by rainfall and the presence of hyenas. By contrast in the dry year of 2008, distance to rivers was the most important explanatory variable followed by sumNDVI and distance to closest water (Table 1). Other notable distinctions include a strong and consistent ability for latitude to explain adult male visits to stations, but this was not the case for explaining the visits of adult females and females with cubs to call-up stations (Table 1). Finally, the visits of adult female lions to call up stations could only plausibly be explained during the driest sampling year (2008).

Discriminatory ability among sampling years

Our best fit models plausibly explained the probability of adult males and females with cubs visiting a station in each

sampling year. However, for the probability of a station being visited by any lions or by hyenas, our best fit models were only plausible for the 2005 and 2008 sampling years (Table 1). For the likelihood of adult females visiting a station, our best fit model was only plausible for the 2008 sampling year. For all of our models, except those for the likelihood of a station being visited in 2008, and male lions visiting a station in 2008, the difference between ROC and cvCOR values suggested some degree of instability, particularly for hyenas visiting stations in 2005 and 2008 where cvCOR values are less than 0.6. The difference between best fit models and next fit model(s) for which there was support according to AICc (Δ_i) and AIC(wi) for most response variables was often negligible and mostly involved the removal of one explanatory factor with limited reduction in evidential support for the model fit to the data as per AICc (Δ_i) and AIC(wi) (Table 1, Supplementary material Appendix 1–3).

Table 1. Summaries of best fit generalised additive models selected according to AIC for four visitation response variables where AUC-ROC is the discriminatory ability of the model (Methods) and cvROC represent the models performance under fivefold cross validation (Methods). Explanatory factors are those included in the selected model and relative importance is their respective percentage of the model's total discriminatory ability. Note that values in bold are for plausible models where AUC-ROC > 0.7 and we show models with AUC-ROC < 0.7 in grey. Lower case 'x' denotes an explanatory factor not included in the best fit model but included in a next best fit model where only limited loss of evidence of for model support was noted (Methods).

Response	Dataset	AUC-ROC	cvROC	Explanatory factors and relative importance (proportion)							
				Year	Waterhole	River	Prey biomass	NDVI	Rain	Latitude	Hyena
Probability of a station being visited											
	2005	0.82	0.69			x		0.32	0.43	0.25	
	2006	0.67	0.50		0.17		x	0.38		0.45	
	2008	0.74	0.67		0.12	0.30		x	0.21	0.16	0.22
	2005/2006	0.70	0.56		0.09	x		0.31	0.27	0.33	
	all years	0.70	0.61	0.17	0.13			0.13	0.23	0.33	
Probability of adult males visiting a station											
	2005	0.86	0.66		0.15	x	0.14	0.15	0.17	0.39	
	2006	0.87	0.69			0.17	0.10	0.28	x	0.30	0.16
	2008	0.73	0.70		0.21	x		0.28	0.29	0.23	
	2005/2006	0.72	0.63		x	x	x	0.40	0.35		0.25
	all years	0.73	0.64	x	0.12	0.11		0.17	0.11	0.49	
Probability of adult females visiting a station											
	2005	0.66	0.53		0.41					0.59	
	2006	0.67	0.61		0.28		x	0.72			x
	2008	0.80	0.68		0.18	0.14	0.41				0.28
	2005/2006	0.64	0.59		0.45			0.55			x
	all years	0.67	0.63		0.44			0.23	x	0.11	0.22
Probability of female visiting with cubs											
	2005	0.91	0.63		0.25			0.28	0.46	x	
	2006	0.81	0.66				x	X	0.76		0.24
	2008	0.94	0.67		0.22	0.39		0.27	0.12	x	XX
	2005/2006	0.69	0.55		x		0.42			0.39	0.19
	all years	0.71	0.65	0.27	0.19					0.33	0.21
Probability hyena visiting a station											
	2005	0.77	0.59			0.39		0.16	0.12	0.33	
	2006	0.67	0.46			x		0.43		0.57	
	2008	0.71	0.39		x	0.34		0.27	0.19	0.20	
	2005/2006	0.73	0.63		x	0.26		0.21	0.17	0.36	
	All years	0.69	0.57		x	0.36		0.16	0.17	0.31	

2005/2006 sampling period

Our models for the 2006/2006 sampling period plausibly explained the probability of a station being visited, of adult males visiting a station and of hyenas visiting a station, but did not plausibly explain the probability of adult females or adult females with cubs visiting stations. The stability of the plausible models was low for probability of visiting a station and the difference between ROC and cvROC values for adult male lions and hyenas suggested some instability in these models. Best fit models were negligibly better fits than next fit model(s) with one to two variables removed with limited loss of evidence in support of the model fitting the data (Table 1, Supplementary material Appendix 4).

All years

Our models for data from when all years were combined plausibly explained the probability of visiting a station, and adult males and adult females with cubs visiting stations but did not explain the visits of adult females or hyenas. Differences between ROC and cvROC values for visiting a station and for adult males suggested some model instability, but the model for explaining the likelihood of a female with cubs visiting a station was stable (Table 1). Best fit models were negligibly better fits to the data than next fit model(s), but differed mostly in terms of degrees of freedom for each variable and not in explanatory factors themselves (Table 1, Supplementary material Appendix 5).

Explanatory factors

Among sampling years and response factors

SumNDVI rainfall and latitude consistently explained whether a station was visited, was visited by adult male lions and was visited by hyenas. In general latitude was the most important factor for these response variables among all years. Secondary importance wavered between rainfall and NDVI among years. In contrast, latitude did not explain the visits of females with cubs to stations (although it was indicated as important in the next best fit models, Supplementary material Appendix 4) but rainfall and sumNDVI did (Table 1). Of note none of these factors explained adult female visits to call-up stations in the only plausible model (2008).

The relationships between lion responses and sumNDVI and rainfall were complex in most models for all response variables (Supplementary material Appendix 6 Fig. A1–A5) but in general likelihood of visits decreased with increasing latitude (Supplementary material Appendix 6 Fig. A1–A5).

Closest river explained the likelihood of a station being visited, of females with cubs visiting stations and of adult females visiting stations only in the 2008 models. For the likelihood of adult females visiting, it was the most important explanatory factor in 2008. Closest river patchily explained the likelihood of adult males and hyenas visiting stations among sampling years. The relationships between lion responses and closest river were inconsistent. For adult males, adult females and hyenas the likelihood of a visit decreased with increasing distance to river (Supplementary material Appendix 6, Fig. A2, A3, A5). For visits by any lions or by adult females with cubs the relationship was complex (Supplementary material Appendix 6 Fig. A1, A4).

Closest waterhole had a patchy ability to explain response variables among years with limited pattern apparent except an absence from most 2006 models when rainfall was highest (Table 1). Of note, in all plausible models closest water was the least important explanatory variable. In contrast, where closest water hole explained lion responses, the likelihood of a station being visited decreased with increasing distance from the closest waterhole (Supplementary material Appendix 6 Fig. A1–A4).

Prey biomass was selected or indicated as important in next best fit model in only four plausible models among years and response variables. Prey biomass explained the likelihood of a station being visited by an adult male in 2005 and 2006 and by an adult female in 2008. For adult males the relative importance of prey biomass was low, however for adult females in 2008 prey biomass was the most important explanatory variable (Table 1). For both response variables, a station was more likely to be visited where prey biomass was low (Supplementary material Appendix 6 Fig. A2, A3).

Finally, the presence of hyena was also variably important in explaining lion responses with no clear pattern apparent among years or response variables. However the presence of hyena did explain whether a call-up station was visited in at least one of the sampling years for each response variable (Table 1). Of note, where hyenas were present a call up station was considerably less likely to be visited (Supplementary material Appendix 6 Fig. A1–A5).

2005/2006 sampling period

In this sampling period, no plausible models explained the likelihood of stations being visited by adult females or females with cubs. Similar to models for 2005, 2006 and 2008 above, sum NDVI, rainfall and latitude together explained the likelihood of a station being visited, or visited by hyenas in the combined 2005/2006 dataset. For the likelihood of a station being visited, closest waterhole was also an explanatory factor, but of considerably less relative importance (Table 1) and for the likelihood of a station being visited by hyena, distance to closest river was important. SumNDVI and rainfall together with the presence of hyenas explained the likelihood of a station being visited by adult male lions. The relationships between lion responses and sumNDVI, rainfall, latitude and closest rivers were complex in respective models for response variables (Supplementary material Appendix 6 Fig. A1, A2, A5), however the likelihood of a station being visited by any lions decreased with increasing distance from closest waterhole.

All years

Of most interest to our evaluation, year explained likelihood of a station being visited and being visited by females with cubs, but not whether a station was visited by adult males. Note that the best fit model for adult females and hyenas were not plausible. Where year was selected the likelihood of a station being visited was lower in 2008 (Supplementary material Appendix 6 Fig. A1, A2, A4). SumNDVI, rainfall and latitude explained likelihood of a station being visited by any lions, by adult male lions, by hyenas, but did not additionally explain the likelihood of a station being visited by adult females with cubs. This was rather explained by latitude, distance to closest waterhole and the presence

of hyena. The relationships between lion responses and sumNDVI and rainfall were complex in respective models for response variables, but probability of a visit consistently declined with increasing latitude (Supplementary material Appendix 6 Fig. A1, A2, A4). The likelihood of a station being visited by any lions decreased with increasing distance from closest waterhole and was lower where hyenas were present (Supplementary material Appendix 6 Fig. A1, A2, A4).

Variation in numbers among stations

Our models for explaining variation in the number of lions (number in group, number of males, number of females and number of cubs) were weak (low D^2 values) and unstable under cross validation (very low cvCOR values) (Table 2). This held for all sampling years combined, as well as for the 2005/2006 sampling period and for when all years were combined. Hence while our structural and functional landscape factors were plausibly able to predict probability of lion occurrence, they were unable to explain variation in numbers among call-up stations.

Consequences for population estimates

Our simulations showed that population estimates (N) increased with the relative proportion of females with cubs (P_{fc}) following the equation: $N = 3.72P_{fc} + 261.55$. During 2005/2006, the percentage of females with cubs was 29.57% which decreased to 22.22% during 2008. Given the 2005/2006 estimate of 1684 (95% CI: 1617–1751) lions (Ferreira and Funston 2010), our regression predicted 1408

Table 2. Summaries of best fit generalised additive models selected according to AIC for explaining variation in lion group size, number of adult males lions, number of adult female lions and number of lion cubs. D^2 represents the proportion of deviance explained, COR is the correlation of observed versus predicted values and cvCOR represent the models performance under fivefold cross-validation (Methods).

Response	D^2	COR	cvCOR
Total number in a group			
2005	0.26	0.50	0.24
2006	0.22	0.47	0.13
2008	0.26	0.43	0.04
2005/2006	0.11	0.30	-0.03
all years	0.11	0.28	0.05
Number of adult males			
2005	0.38	0.63	0.31
2006	0.41	0.66	0.47
2008	0.15	0.31	0.15
2005/2006	0.22	0.45	0.26
all years	0.15	0.35	0.14
Number of adult females			
2005	0.12	0.37	-0.05
2006	0.24	0.54	0.10
2008	0.29	0.48	0.11
2005/2006	0.09	0.31	0.16
all years	0.09	0.28	0.15
Number of cubs			
2005	0.26	0.46	0.02
2006	0.22	0.53	0.42
2008	0.23	0.35	0.00
2005/2006	0.12	0.32	-0.13
all years	0.11	0.27	-0.07

(95% CI: 1288–1515) lions from the percentage of females with cubs in 2008, if only a behavioural response occurred. This was higher than the observed estimate of 1016 (95% CI: 862–1180) during 2008 (SANParks unpubl. data). In contrast, when we considered estimates of adult females only (2005/2006: 415, 95% CI: 380–450, Ferreira and Funston 2010), the response by females predicts 381 (95% CI: 349–413) substantially lower than the observed estimate of 612 (95% CI: 556–669).

Discussion

Reliable estimates of population size are needed to inform sound conservation management decisions (Krebs 2003). This is especially relevant when interpreting trends in populations of threatened carnivore species subject to multiple stressors including human induced habitat changes and mortality (Ogutu and Dublin 2002, Ogutu et al. 2005, Woodroffe and Frank 2005, Loveridge et al. 2007, Kiffner et al. 2009, Packer et al. 2011). Our assessment of the influence of structural and functional landscape factors on lion responses to call-up stations strongly supports our concern that quantifying real trends in lion population size between two sampling periods (2005/2006 and 2008) in Kruger National Park, South Africa, was complicated by variation in rainfall among sampling years and its flow on effects on the spatial configuration of resources on lion behaviour.

Call-up sampling relies on behavioural responses to an attractant stimulus (Ogutu and Dublin 1998, Ferreira and Funston 2010). Behavioural responses are flexible (Snell-Rood 2013) and therefore subject to influences of several intrinsic and extrinsic factors. In our assessment, the mean number of adult males as well as adult females per station did not differ between the two sampling periods, or among the three sampling years. However, the proportion of stations visited by adult females and visited by adult females with cubs was lower in 2008 relative to 2005 and 2006 independently and combined, and the mean number of cubs was lower between the 2005/2006 and 2008 sampling periods. Put simply, while the number of adult females visiting stations did not differ between sampling periods, the presence of cubs with them did. Our result that year explained the likelihood of a call-up station being visited by adult females with cubs when all years were combined is consistent with this interpretation.

The reduction of cubs appearing at call-up stations may result from lower fecundity of females and/or higher mortality of cubs, thus resulting in fewer cubs in the population to respond to call-up stations. Alternatively, females may make behavioural choices hiding young cubs when perceiving dangers such as presence of hyenas or large male lions when taking part in feeding events.

Rainfall is a primary driver of heterogeneity at the landscape scale in savannah systems and drives surface water and prey food availability for lions (Hopcroft et al. 2005, De Boer et al. 2010, Valeix et al. 2010). We knew that rainfall differed between the two sampling periods and our results confirmed it also differed among the three sampling years. We had predicted that because lions take advantage of their prey being limited to the configuration of available water sources and

prey food availability, particularly in dry years (Hopcroft et al. 2005, Mosser et al. 2009, De Boer et al. 2010, Valeix et al. 2010), lions would be patchily distributed in association with water sources during the drier sampling period of 2008. In addition, females with cubs may be less likely to respond to call up stations given that prey may be more concentrated and readily available at such water sources, but with increased chances of encountering fear agents such as other male lions and hyenas. Hence, we predicted that the relationships between structural and functional factors and lion responses should be stronger in 2008 when we noted lower rainfall.

Consistent with our predictions, landscape factors influenced lion responses to call up stations and more so in 2008 for the response of adult females and adult females with cubs. In fact, only the 2008 model was plausible amongst those explaining adult female visits to call-up stations. This suggests that the influence of landscape factors on the response of this demographic group could only be confirmed when conditions were dry. Moreover, distance to rivers only explained the likelihood of a station being visited by adult females and adult females with cubs during the driest sampling year (2008). Given the complete absence of this explanatory factor in best fit or even next best fit models for all other years for these two demographic groups, the relationships between the distribution of surface water – in this case rivers for adult females with cubs, and closest waterholes and rivers for adult females, and lion responses only became relevant when we noted low rainfall.

The strong ability for models to explain adult male visits to call-up stations for all sampling years and the inclusion of surface water features either in best models or next best models in all sampling years suggests that adult male responses may not be as sensitive to differences in conditions among years as adult females and adult females with cubs. Indeed for adult males, the relative importance and inclusion of factors explaining call-up station visits remained generally similar among sampling years and combinations of sampling years when factors from next best fit models were also considered. Hence, the behavioural response of adult females and of those with cubs may be more strongly influenced by variation in rainfall than adult males and adult females alone. The lack of year as an explanatory factor for adult male visits when all years were combined, together with the lack of change in number of males attending stations and proportion of stations attended by males among sampling years and between 2005/2006 and 2008 sampling periods, supports this notion.

Changes in the relative importance of explanatory factors among sampling years, changes in the shapes of relationships between landscape factors and the response of adult females with cubs was also consistent with expected flow-on effects of varying rainfall among years, particularly on the response of adult females with cubs. Certainly, in the higher rainfall years of 2006 and 2005, variation in rainfall among stations was the most important landscape factor determining the probability of adult females with cubs attending call-up stations and this relationship was complex. In contrast, in the drier year of 2008, rainfall was the least important explanatory factor and the probability of adult females with cubs visiting a call-up station linearly declined with increasing

rainfall. Indeed in this dry year, distance to closest river was the most important explanatory factor most likely because lionesses prefer to hunt in riverine areas where there is cover (Mosser et al. 2009, Loarie et al. 2013) and refuge to hide their cubs and where prey is more likely to be concentrated (Smit et al. 2007, Mosser et al. 2009) especially during dry years (Valeix et al. 2010). Hence, the difference in the influence of explanatory variables in relation to rainfall and rivers on the probability of station being visited by adult females with cubs may reflect on our prediction that lions were more concentrated around water sources during the dryer 2008 years and that this altered their responses.

The effect of distance from water (rivers and waterholes) between years may also have been amplified by call-up stations being further from rivers in 2008 than in 2006 independently, and further from waterholes in 2008 than in 2005/2006 combined. We could not isolate this effect from that of the other landscape factors. Given the importance of these variables in explaining adult female and adult females with cubs visiting call up stations, and the decline in likelihood with increasing distance from waterholes, it is important to ensure that sample designs for different surveys keep distances to water sources from call-up stations constant. Furthermore, given that prey is concentrated about water (rivers and water sources) during dryer years (Smit et al. 2007, Valeix et al. 2010), the higher likelihood of adult females visiting stations where prey biomass is low as noted during 2008, makes sense. A lioness using areas where prey are tethered to water sources, may not respond to a prey distress calls as readily as those located where prey biomass is low. Consistent with this notion, in 2008 prey food availability was the most important landscape factor for the probability of females attending stations in 2008, noting that models were not plausible for female visits to stations in 2005 or 2006. Hence, in the dryer sampling period of 2008, when prey food availability was lower, the probability of females attending stations appears more strongly driven by this landscape factor. Notably however, prey food availability was not selected as a landscape factor for whether females with cubs visited stations in any of the sampling years.

The inclusion of latitude into our analyses allowed us to infer differences between the influence of spatial variation and inter-annual variability in rainfall on lion responses. In Kruger National Park increasing rainfall from the north to the south of the park (Gertenbach 1980) creates an increasing north to south gradient in surface water availability. Hence the decreasing probability of adult males visiting stations with increasing latitude seems consistent with male lions attending call-up stations in association with the spatial distribution of surface water. Indeed the similarity in the inclusion and relative importance of latitude among years and combinations of years for adult males is consistent with inter-annual variability in rainfall having limited influence on male lion responses to call-up stations. In contrast, the complete lack of latitude as an explanatory variable for adult females and for adult females with cubs (except for inclusion in next best fit models), but high relative importance of rainfall in wetter years and low relative important of rainfall in dry years, is consistent with the response of adult females with cubs being more sensitive to inter-annual variability rather than spatial variability in rainfall. The importance

of latitude as explanatory factor in the model for all years combined is not inconsistent with this suggestion. When total variation in rainfall is only considered spatially and not specific to a set of conditions temporally, then spatial variation in rainfall reflected best by latitude is relevant.

The lack of ability of landscape factors to plausibly explain variation in lion numbers for any of our demographic groups in any year is not surprising. Like most carnivores lion distribution is non-uniform and associated with the patchy distribution and dynamics of their prey species (Valeix et al. 2011). Hence, the large prevalence of non-visited stations makes predicting variation in numbers for such species difficult. Nevertheless, this patchiness combined with lower visitation rates most likely amplified the flow-on effects for estimating population size. Lionesses operate and make decisions as a pride (Mosser and Packer 2009). The lack of a visit by adult females with cubs, or failure to bring cubs to the station could mean that a whole pride of individuals of adult females and cubs may not be counted with large flow-on effects for calculating population estimates.

The explanatory factors and their relative importance among years for explaining hyena visits to stations were similar to those of adult male lions and thus consistent with the notion that the distribution of hyenas and lions overlap according to the distribution of surface water and other landscape factors. Indeed, we had expected that hyenas would modulate the behaviour of lions and in particular adult lionesses with cubs given that hyenas are a competitor of lions (Owen-Smith and Mills 2008). Certainly, we found that the probability of a station being visited by adult female lions with cubs and adult male lions was markedly higher when hyenas did not visit stations in the higher rainfall year of 2006. Perhaps in periods of high rainfall, when prey concentrates less around water sources, competition between lions and hyenas weakens. Alternatively, when surface water is more restricted and prey more concentrated, lions may be able to exercise more discretion over their behavioural responses to a prey distress call and choose not to attend stations where hyena are present. Either reason, hyenas influenced lion responses to call-up stations and this relationship differed among sampling years with stronger influence occurring during higher rainfall years.

Our inability to definitively conclude that population estimates for 2008 were the result of landscape factors on the behaviour of lions is a limitation of this study. This is because the one-off surveys that we employed, do not provide the ability to estimate detection error (Ferreira and Funston 2010), thus it is difficult to empirically separate non-detection and behavioural responses from real absence. We had anticipated that reduction in the number of cubs was unlikely because lion cub survival is typically higher during relatively dry years compared to relatively wet years (Eloff 1980) when lionesses may take advantage of prey clustering and concentrations associated with reduced surface water availability (Smit et al. 2007, Valeix et al. 2010). We had thus reasoned that lion cub survival was most likely higher during 2008 when rainfall was markedly lower compared to that recorded during 2005/2006 and 2005 and 2006 independently. By contrast, however, our simulation outcomes compensated for potential female behavioural responses

when their choice to not bring cubs along to call-up stations introduced pseudo-frequencies of females without cubs. The lower than predicted estimate for total population size in 2008, combined with the higher than predicted estimate for adult females in 2008 suggest that the total number of adult females may actually have increased from 2005/2006 to 2008, but that substantially fewer cubs were present during 2008 compared to 2005/2006. Hence, lion attendance to call-up stations differed between sampling periods, and some of these differences may be a result of real population changes.

Quantifying real differences, however, was constrained by flow-on effects of inter-annual variability in rainfall among sampling years that determined the importance of proximity to rivers and spatial variation in rainfall to whether adult females and adult females with cubs responded to call-up stations. The reduction in relative importance of rainfall in 2008 from 2006 and replacement by rivers and waterholes as explanatory variables strongly support this notion. Adult females effectively make decisions for their cubs and their reduced probability of visiting stations and bringing cubs to stations impacted on the ability to calculate comparable population estimates between surveys. As a matter for further attention, we note that the estimated number of adult females did not change between surveys, but that their visitation of stations and decisions to bring cubs with them did. Because variability in fecundity and cub survival is a feature that results from lion's resilient population demographic capabilities (Whitman et al. 2007), there may be a good argument to consider trends in lion abundances according to stable reproductive units – being number of adult females, as opposed to total population size.

In summary, our results suggest the need for caution when interpreting results from population estimates for lions that rely on behavioural responses that may be modified by variability in structural and functional landscape factors among sampling occasions. This is especially the case for population estimators that are sensitive to changes in demographic components of the population most likely to be affected by variable conditions. Our analyses demonstrate that the flow-on effects of variation in landscape factors on lion behavioural responses to the configuration of resources are difficult to unravel from real changes in population size. This was especially the case for adult females with cubs, an important demographic component in calculating population estimates. Hence, further to the above suggestion, we advocate the exploration of methods to evaluate trends in lion populations according to the number of adult females and the complementary use of other non-invasive sampling methods that do not rely on behavioural responses to estimate population size. Furthermore, we suggest that behavioural responses to prey distress calling, particularly the decision/ability to bring cubs by females, could be more directly tested by conducting experimental, repeated, calling targeting prides of known composition (including numbers of young), among contrasted areas and years.

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Supplementary material (available online as Appendix wlb.00015 at <www.wildlifebiology.org/readers/appendix>). Appendix 1–6.