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Temporal and spatial variation of broadcasted vocalizations does not reduce lion *Panthera leo* habituation

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Estimating abundance of large carnivores is often challenging, yet important for their effective conservation. Attracting lions *Panthera leo* for visual enumeration using broadcasted vocalizations (i.e. call-ins) is commonly used to estimate their abundance. However, call-ins are typically not repeated at sites because of habituation. We evaluated lion response to repeated call-ins varying temporally (1 or 2 weeks) and spatially (1 or 2 km) in Serengeti National Park (SNP), Tanzania, during February–April 2016. We established 30 call-in sites: at 10 sites we used lion and spotted hyena *Crocuta crocuta* calls while alternating prey distress calls across five consecutive weeks; at 10 sites we alternated calls but conducted call-ins once every two weeks; and at 10 sites we alternated calls weekly for five weeks but moved among three locations separated by 1 or 2 km each week. We used *N*-mixture models to assess which sampling design would elicit greater lion detections across sessions and to estimate overall abundance. Lions habituated to broadcasted calls within each sampling design, with detectability point estimates overall declining across sessions. Estimated lion abundance at these 30 sites was 198 (95% credible interval = 186–214). Altering time interval and location of call-ins was ineffective at reducing lion habituation. However, altering calls across sessions appeared to reduce lion habituation when compared to a previous survey in SNP that used the same calls across sessions. We recommend that call-in surveys using repeated broadcasts are conducted at the same sites across sessions and use different calls to improve lion response and consequently, estimates of abundance.

Lions *Panthera leo* have reportedly declined 43% since 1993 and are currently listed as Vulnerable to extinction by the International Union for Conservation of Nature (IUCN; Bauer et al. 2015), with an estimated population of 20 000 – 35 000 individuals worldwide (Riggio et al. 2013). Dominant causes of lion population decline include land use change, illegal killing and prey depletion (Riggio et al. 2013, Bauer et al. 2015); with retaliatory killing (Woodroffe and Frank 2005, Kissui 2008), poorly-regulated harvest (Loveridge et al. 2007), and traditional medicines (Williams 2015) influencing the viability of some populations.

Accurate and precise estimates of lion abundance are critical as they have been used to assess global conservation status (Bauer et al. 2015) which in turn can influence national and international policies. Techniques used to estimate lion abundance are diverse and include mark–recapture (Ogutu et al. 2006), individual counts (Tumenta et al. 2009), distance sampling (Durant et al. 2011), remote camera (Cusack et al. 2015), track counts (Funston et al. 2010), and call-ins (Cozzi et al. 2013). Call-in surveys are among the most frequently used technique and recently have been recommended over track surveys to estimate lion abundance (Midlane et al. 2015).

Vocalizations to elicit lion approach during call-in surveys are typically broadcasted only once at each site (Kiffner et al. 2007, Cozzi et al. 2013) as lion response can decline with multiple exposures (Spong and Creel 2004). However, multiple sessions at each site are important when conducting call-in surveys to account for inherently variable detection (e.g. observer; Belant et al. 2016) and environmental (e.g. weather; Kiffner et al. 2007) processes that can influence estimates of abundance and their precision. Reduced detection of lions across sessions due to habituation or other behaviors can also reduce precision of abundance estimates (Belant et al. 2016). Modifications of existing methodologies to reduce habituation and maintain more accurate detections and constant detectability of lions over time are needed.

Our objective was to assess whether varying interval length between repeated call-ins and slight alteration of locations where call-ins were conducted would reduce habituation

of lions in Serengeti National Park (SNP). In addition, we compared lion response to varying series of broadcasted vocalizations across call-in sessions used in this survey to an earlier survey conducted in a different area within SNP (Belant et al. 2016) that used a single series of vocalizations across five sessions.

Material and methods

Study area

We conducted this in the western corridor and northern Serengeti National Park (Fig. 1). Annual rainfall varies along a southeast (500 mm) to northwest (1100 mm) gradient (Mduma et al. 1999), with rains typically occurring from November to May (Sinclair 1995). The study area contains a sparse woodland-grassland mosaic interspersed with patches of dense woodland (McNaughton 1983). In contrast to the plains of southern SNP, the study area includes populations of resident ungulates (McNaughton 1983). Lions are not subject to legal harvest within SNP.

Methods

We established 30 call-in sites with spacing of about 8 km to minimize the effects of double counting among sites (Ogutu and Dublin 1998, Cozzi et al. 2013; Fig. 1). Lions in our study area on average moved about 450 m every two hours at night during dry season (Kittle et al. 2016); thus, we considered our sites independent. We used a digital recording comprised of a single female lion roar; warthog *Phacochoerus africanus*, zebra *Equus quagga*, or wildebeest *Connochaetes taurinus* in distress; and spotted hyena *Crocuta crocuta* whoop call; vocalizations previously demonstrated successful in attracting lions (Cozzi et al. 2013) or prey of lions in SNP (Schaller 1972). At 10 sites we alternated prey distress calls among warthog, zebra and wildebeest each week for five sessions. At another 10 sites we again alternated prey vocalizations but conducted call-ins once every two weeks for five sessions. At the remaining 10 sites we alternated calls weekly for five weeks but moved among three locations separated by 1 or 2 km each week. Prey species vocalizations used were warthog, zebra, wildebeest, warthog and zebra during sessions 1–5, respectively. We used the same warthog and zebra vocalizations between sessions. Different lion and hyena vocalizations were used during each of the first three sessions but were then repeated (i.e. the same lion and hyena calls were used in sessions 1 and 4 and sessions 2 and 5, respectively). Using two observers, we conducted the survey during February–April 2016, with each observer typically broadcasting at three sites each night. We began broadcasts at 19:00 h when lions increase movements (Cozzi et al. 2012).

Call-in procedures generally followed Belant et al. (2016). We broadcasted vocalizations at each site for 70 min, playing calls for 10 min, followed by a 5-min pause, and then repeated this pattern five times. Each 10-min broadcast started with 40–60 s of a single female lion, followed by 80–100 s of prey, and 40 s of a spotted hyena; this sequence was repeated three times. We broadcasted calls with maximum intensity of 110 dB using a commercial game calling system (Foxpro Inc., Lewistown, Pennsylvania, USA). We

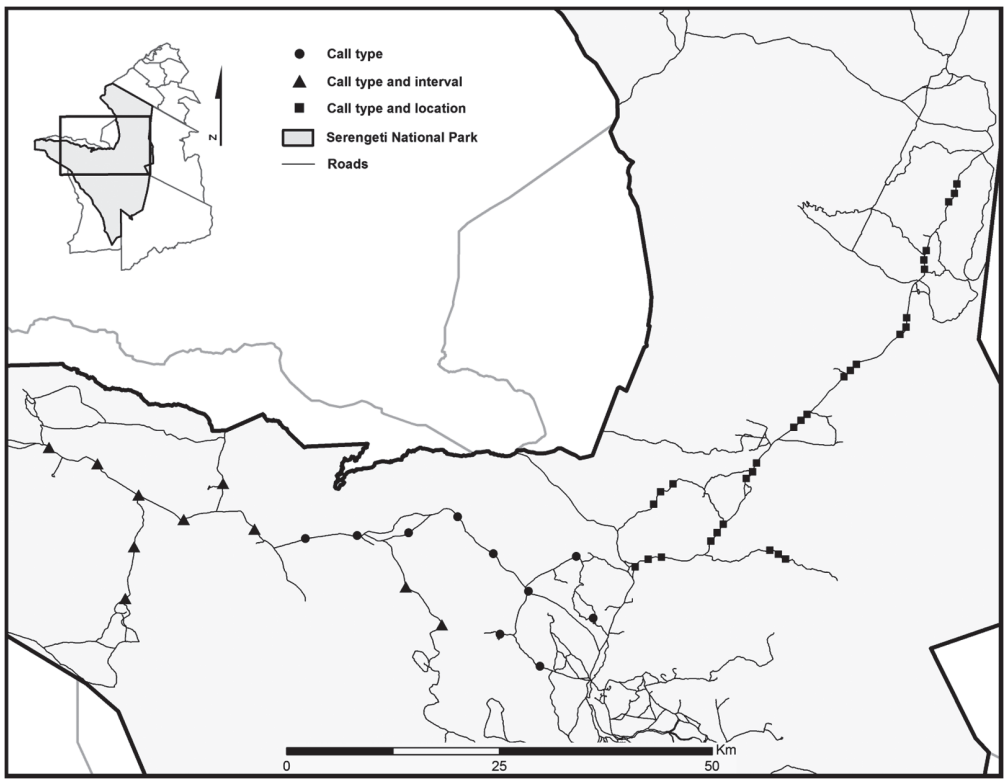

Figure 1. Sites used to elicit lion approach using broadcasted vocalizations, Serengeti National Park, Tanzania, February–April 2016.

used four speakers mounted at 90° intervals on the roof of the vehicles (about 2.4 m above ground) and alternated broadcasts between opposing pairs of speakers midway through each 10-min broadcast. We alternated call-in sites surveyed by each observer each session and included observer as a covariate in the detection process of our models to account for variation in their ability to detect lions.

We recorded the number of lions observed during the broadcast through a vehicle roof hatch using a spotlight with red filter (model EF170CC; Lightforce USA, Inc., Orofino, ID) and forward-looking infrared monocular (FLIR Scout TS24; Tactical Night Vision Company, Redlands, CA). We used a red filter to minimize disturbance to lions (Omoya et al. 2013, Belant et al. 2016). We used the maximum number of lions detected at each site during each 70-min broadcast to estimate abundance.

We modeled detected abundance at call-in sites using *N*-mixture models (Royle 2004, Chandler et al. 2011) in a hierarchical Bayesian framework and compared estimated detection probabilities for our three sampling designs. *N*-mixture models commonly assume closure in the studied population. We considered the population size to be stable during the survey based on month-to-month stability of lion population size in a nearby area within SNP (Packer et al. 2005). The 'true' ecological state N_i describing abundance (i.e. number of individuals in the area of influence of our call-in sites) in site i was defined as a Poisson random variable, with an expected value λ_i. A site corresponded to the area of assumed influence of a call-in. We modeled the expected value of the Poisson distribution as a linear combination of an intercept a, and a random site effect ε_i on the log-scale as:

$$N_i \sim Poisson(\lambda_i)$$

$$\log(\lambda_i) = a + \varepsilon_i$$

To account for imperfect detection, we modeled the count process y_{it} in cell i during session t conditionally on the true abundance as:

$$y_{it} \sim Binomial(N_i, p_{it})$$

where p_{it} is the individual detection probability in cell i during week t.

We allowed detection probability p_{it} to vary among sites and sessions, following a non-informative uniform prior as:

$$p_{it} \sim \text{Uniform}(0,1)$$

Next, we derived the mean session detection probability for each sampling design, averaged over the relevant sites, to compare the effects of our three designs. We then estimated the population size over the 30 call-in sites by first accounting for potential sampling biases among our three designs before adding site-specific abundance estimates (Supplementary material Appendix 1).

N-mixture models typically rely on several assumptions including population closure, absence of false positives, and independence and homogeneity of detection (Royle 2004). While some of these assumptions might not be fully met in our system, we suggest our sampling approaches mitigated any departures. For example, the short duration of the survey; distance between call-in sites; and reducing the potential of double-counting through knowledge of direction of lion approach and departure, recording of individuals by sex and age classes, and using individual identification when possible. Moreover, we expected that if some model assumptions were not fully met, the violations that occurred during the study were likely consistent and therefore should not affect conclusions regarding our comparison among sampling methods.

We developed models for call-in counts using the program WinBUGS, with non-informative priors for each parameter. We ran three chains of 100 000 iterations after a 100 000 burn-in with a thinning of 10, and monitored convergence by visual inspection of the MCMC chains and using the Gelman–Rubin convergence statistic $\hat{R}$ (Gelman et al. 2014). We assessed goodness-of-fit of our model based on its derived Bayesian p-value. We present average estimated abundance at call-in sites, as well as corresponding detection probabilities with 95% credible intervals.

Results

Goodness-of-fit of the model for the call-in survey was good (Bayesian p-value = 0.36). The detection probability of lions responding to broadcasted calls varied within and among sampling designs and generally declined across sessions (Fig. 2). Detection probabilities during sessions 1 and 5 for call type were 0.62 (0.52–0.71) and 0.25 (0.17–0.35), respectively; for call type and interval were 0.38 (0.27–0.48) and 0.28 (0.18–0.38), and for call type and location were 0.54 (0.39 –0.69) and 0.39 (0.24–0.53). Point estimates of the number of lions detected with each sampling design were similarly variable and also declined generally across sessions; however overlapping 95% confidence intervals suggested no difference overall within each design across sessions (Fig. 3). We estimated the total lion abundance for sites with call type, call type and interval, and call type and location designs to be 76 (70–86), 24 (20–31), and 97 (90–108), respectively. We estimated an overall abundance of 198 lions (186–214) at the 30 sites.

Discussion

Learned behavior by lions was suggested by an overall decline in probability of detection across sessions to broadcasted vocalizations. Numerous authors conducting call-in surveys to estimate lion abundance have suggested lions habituate to broadcasted calls (Kiffner et al. 2007, Cozzi et al. 2013); however, few have modeled this behavioral response (Spong and Creel 2004, Belant et al. 2016) and none have explicitly evaluated the effects of temporal and spatial variation in broadcasted calls to elicit lion approach for abundance estimation. We observed similar habituation to consecutive broadcasted calls separated by one or two weeks. Spong and Creel (2004) noted that lions were less likely to approach and took longer to approach broadcasted vocalizations (separated by >7 days) as number of exposures increased. Ogutu and Dublin (1998) used 60 days to separate repeated call-ins at the same site for lions, but provided no data to

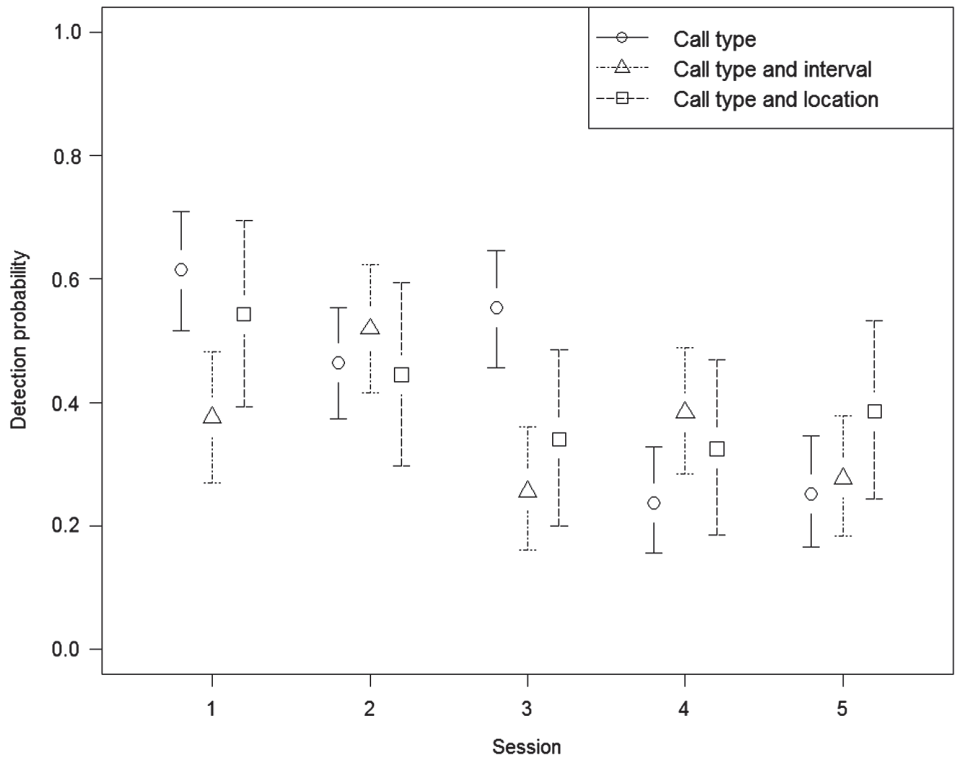

Figure 2. Mean (95% credible intervals) probability of individual lion detection during repeated call-ins at sites with varying call type, call type and time interval, and call type and location, Serengeti National Park, Tanzania, February–April 2016.

support their use of this interval. Increasing time intervals between call-ins >2 weeks may reduce lion habituation, but demographic closure assumptions for abundance estimates would need to be evaluated. Nevertheless, additional studies to determine optimal interval length between call-ins would be beneficial.

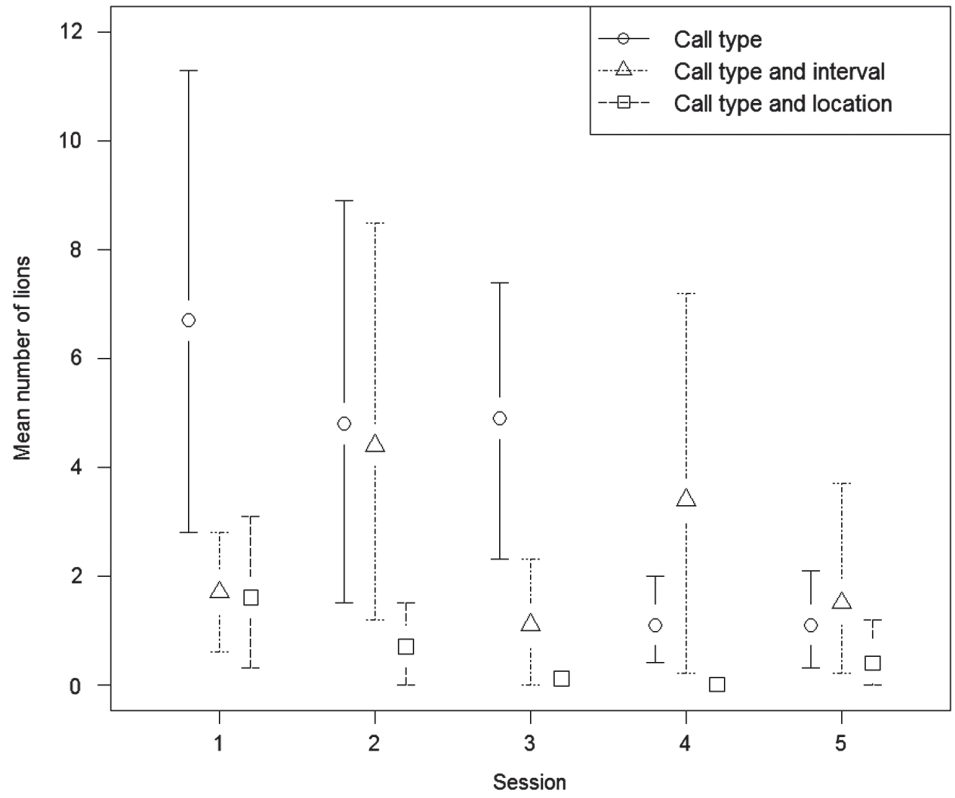

Figure 3. Mean (95% confidence intervals) number of lions detected during repeated call-ins at sites with varying call type, call type and time interval, and call type and location, Serengeti National Park, Tanzania, February–April 2016.

The slight variation (1 or 2 km) we used to separate consecutive call-ins in one of our sampling designs also appeared ineffective in reducing habituation by lions. We are unaware of previous studies evaluating lion habituation to spatial variation in call-ins. Increasing distance of call-in sites during multiple sessions >1 km from a fixed point to reduce lion habituation would likely be impractical due to difficulties maintaining independence among sites. Further, sessions could not be considered replicated counts as the sampling areas would differ. Thus, we do not recommend altering locations for repeated call-in surveys.

Mills et al. (2001) recommended varying the sequence that calls are played to reduce spotted hyena habituation and Belant et al. (2016) suggested using different call sequences to reduce lion habituation. In this latter study, using the same call sequences across the first five sessions, probability of lion detection decreased 82% (Belant et al. 2016). In our study, using call sequences with different lions, prey species, and spotted hyenas during the first three sessions before repeating call sequences resulted in a decline of 20–60% in probability of lion detection between sessions 1 and 5. Further, in contrast to Belant et al. (2016), we did not observe a decline in point estimates of lion detection probability in any of our sampling designs until session 3. We suggest that using different calls across sessions will have a greater positive effect for reducing habituation by lions than would altering time interval or location of call-ins. Altering the sequence that calls are broadcast or using different calls during each session might further reduce habituation.

The habituation to call-ins we observed was likely a consequence of lions receiving no positive stimuli to reinforce the desired approach behavior. Mills et al. (2001) suggested using a small food reward to reduce habituation of spotted hyenas to call-ins and increase response rates. Though food rewards would likely enhance approach by lions and other large carnivores, feeding wildlife is prohibited in many protected areas. Use of food rewards also would need to be accounted for in models to facilitate comparison of estimates within and across study areas.

Greater detection rates across sessions in this study appeared to markedly improve precision of the estimated number of lions (95% CrI = 186–214). A previous survey of 39 call-in sites in the savanna of southeastern SNP using primarily the same broadcasted vocalizations across seven sessions estimated 270 lions with a 95% CrI of 170–551 (Belant et al. 2016). Probability of individual detection declined in that study, from 0.93 in session 1 to 0.11 in session 5 (Belant et al. 2016). We suggest the improved precision in the present study was a consequence of increased probability of detection, with fewer sites having no lions observed which reduced the effects of zero-inflation in our model. Lion detections did not significantly decline until sessions 3 or 4 in this study whereas Belant et al. (2016) noted a significant decline in detections in the second session.

Call-in surveys employing multiple sessions can account for variation in detection and environmental processes which can improve abundance estimates relative to single session call-in surveys (Belant et al. 2016). However, the disadvantage of using multiple sessions has been habituation by target species, resulting in poor estimates of precision (Belant et al. 2016). We have demonstrated that using different call sequences across sessions reduces lion habituation such that estimates with high precision are attainable. Accurate and precise estimates of lion and other large carnivore abundances are essential for evaluating their conservation status and population trends. We encourage additional evaluations of call-ins to estimate lion abundance, including areas where lions are hunted, as lions response may differ. Further, refinement of optimal timing between repeated call-ins and evaluating lion response to varying order in which calls are broadcast are recommended.

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Supplementary material (Appendix wlb.00287 at <www.wildlifebiology.org/appendix/wlb.00287>). Appendix 1.

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