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The influence of spatial features and atmospheric conditions on African lion vocal behaviour

Matthew Wijers[1], Paul Trethowan[1], Byron du Preez[1], Simon Chamaillé-Jammes[3,4], Andrew J. Loveridge[1], David W. Macdonald[1] and Andrew Markham[2]

[1] Wildlife Conservation Research Unit, Recanati-Kaplan Centre, Department of Zoology, University of Oxford, United Kingdom.

[2] Department of Computer Science, University of Oxford, United Kingdom

[3] CEFE, CNRS, University Montpellier, University Paul Valéry Montpellier, EPHE, IRD, Montpellier, France

[4] Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria, Pretoria, South Africa

Corresponding author:

Matthew Wijers

matthew.wijers@gmail.com

Wildlife Conservation Research Unit
Recanati-Kaplan Centre, Tubney House
Abingdon Rd
Tubney
OX13 5QL
United Kingdom

Abstract

Long-distance vocalisation is a characteristic of African lion (*Panthera leo*) behaviour and is important for maintaining territorial boundaries as well as locating distant group members. Vocal signalling is, however, a flexible behaviour that involves varying costs and benefits depending on environmental, social and spatial factors. Motivated by previous data collection limitations, we developed a novel approach to investigate the influence of atmospheric conditions and animal home range geography on lion vocal behaviour using acoustic and accelerometer biologgers. To compensate for the short lifetime of the acoustic biologger, we trained a machine learning model to detect lion roars from long term acceleration signals which yielded over 500 nights of data from 7 individual lions. Analysis of detected roar events revealed that vocalisations occurred mainly at night with a peak just before dawn. The relative likelihood of vocalisation was negatively related to wind speed and temperature and positively related to absolute humidity suggesting that lions preferred to roar under conditions that reduce sound attenuation and thereby maximise calling area. Roar occurrence was found to be dependent on an animal's location relative to its home range with lions demonstrating an apparent avoidance for vocalising beyond the home range boundary. Lions were also more likely to roar repetitively while closer to rivers and water points within their home range. This study is the first of its kind and not only improves the understanding of lion vocal behaviour but can inform new approaches for recording animal vocalisations remotely.

Keywords

Biologging, *Panthera leo*, Roar, Vocal behaviour, Vocalisation.

Introduction

Animal vocal communication has been a topic of considerable interest over the past century with the majority of research being dedicated to three main aspects which include function, structure and production (Garcia & Favaro, 2017). Vocal signalling is known to fulfil a variety of biological functions including territorial defence (Darden & Dabelsteen, 2008) contacting members in a social group (Rendall et al., 1996), foraging (Rydell et al., 2002), navigation (Moss & Surlykke, 2010) and deterring predators (Zuberbühler et al., 1999). Long distance vocal communication functions, in general, as a spacing mechanism between territorial individuals and allows distantly separated group members to locate each other (Marler, 1967; Mitani & Nishida, 1993). Like other behaviours, an animal's decision to vocalise or remain silent is likely to be based on a trade-off between the relative costs and benefits of calling under certain conditions (Mcfarland, 1977).

Vocal signalling can be costly for the emitter as it may reveal information about identity, fitness, behaviour and location to potentially hostile listeners. Studies on territorial species have shown that nomadic individuals avoid vocalising in order to reduce the risk of attracting attention from territory owners (Harrington & Mech, 1979; Grinnell & McComb, 2001; Campioni et al., 2010). Dominant individuals may also show varying degrees of preference and avoidance behaviour depending on their location within their home range. For example, territorial swift foxes (*Vulpes velox*; Darden & Dabelsteen, 2008) and eagle owls (*Bubo bubo*; Delgado & Penteriani, 2007) have been reported to increase vocal effort in the core of their home ranges while tawny owls (*Strix aluco*; Sunde & Bolstad, 2004) appear to prefer vocalising in peripheral areas. Variation in vocal intensity may also be influenced by the distribution of important resources within a territory such as nests, access to mates, or areas of highest food availability (Jacobsen et al., 2013; Penteriani, 2014).

In addition to spatial variation in the costs and benefits of vocalising, the efficacy of long-distance acoustic communication is subject to changes in atmospheric conditions which result in varying degrees of signal degradation. Factors such as wind speed, temperature and humidity can significantly increase or reduce an animals' calling area (Wiley & Richards, 1978; Larom et al., 1997b). Garstang et al. (1995) found that the range of elephant vocal signals doubled in magnitude under optimum atmospheric conditions. Such optimum conditions are generally characterised by low wind speeds and low-level vertical changes in temperature known as temperature inversions (Larom et al., 1997b). Studies on wolf and coyote vocalisations have shown an overlap between peak periods of vocalisation and the hours of best sound transmission (Harrington & Mech, 1979; Laundre, 1981).

African lions are well known for their impressive, long-distance vocalisations commonly referred to as 'roars'. These signals typically consist of a series of moans leading to several full-throated roars and end with a sequence of short grunts (McComb et al., 1994; Grinnell & McComb, 2001). Lion vocal communication has been well studied particularly in relation to roar characteristics (Stander & Stander, 1988) individual recognition (McComb et al., 1993; Gilfillan et al., 2016), information content of the signal (McComb et al., 1994; Pfefferle et al., 2007) and the limitations imposed by unwanted receivers (Grinnell & McComb, 2001). The majority of these studies have used playback experiments to test hypotheses and thus there are few cases where researchers have relied on records of natural, spontaneous roaring events to investigate aspects of lion vocal behaviour (Stander & Stander, 1988; Pfefferle et al., 2007; Lehmann et al., 2008). This preference may be partly related to the difficulty in obtaining sufficient quantities of roar records especially as wild lions vocalise almost exclusively at night (Stander & Stander, 1988; Pfefferle et al., 2007). Apart from the observations of Schaller (1972) and Stander and Stander (1988) little is known about the temporal or spatial patterns of

lion vocal behaviour that may arise as a result of spatial and temporal variations in the costs and benefits of communication. Lehmann et al. (2008) documented an apparent preference for roaring along drainage lines and within 500m of water but were limited by sample size and therefore encouraged further research on this topic. At a home range scale, lions are known to positively select areas closer to water which are characterised by high prey abundances (Davidson et al., 2012). Such areas within a territory are high value resources and are therefore likely to be more intensely protected with increased territorial behaviour such as scent marking and roaring (Darden & Dabelsteen, 2008).

In this study, we aimed to investigate whether lions exhibit spatial preferences for vocalising, specifically with regards to proximity to rivers and water points and an individual's location within its home-range. Previously, it has been impossible to manually obtain sufficient data on spontaneous lion vocalisations with concurrent location information. To overcome this issue, we developed novel acoustic-accelerometer biologgers combined with innovative machine learning techniques to detect lion vocalisations from accelerometer data alone. Generally, animal activity recognition from accelerometers has been limited to locomotion and feeding and therefore, this work presents the first example of vocalisation detection using the same approach (Grünewälder et al., 2012; Lush et al., 2015; Wang et al., 2015). We hypothesised that lions would show a preference for vocalising nearer rivers and water points as an attempt to retain and protect these valuable territory features and avoid roaring outside their home ranges due to the risks of provoking conflict with neighbouring individuals. We also aimed to test how lion vocal behaviour is influenced by atmospheric conditions. In this case we hypothesised that conditions with lower temperatures and wind speed and higher absolute humidity would be preferred given that such conditions maximise the calling range (Harris, 1966; Griffin, 1971; Larom et al., 1997b).

Methods

Study Site

The study was conducted in the Bubye Valley Conservancy (BVC), a privately-owned wildlife area in southern Zimbabwe located between latitudes 21.209 and 21.851° S and between longitudes 29.798 and 30.521° E. The BVC measures approximately 3400 km^2 in area and hosts a variety of indigenous megafauna including a large lion population (~ 500 individuals at the time of the study; du Preez et al., 2014a) organised into resident female prides with associated territorial male coalitions as well as vagrant individuals. Mopane woodland savannah dominates the majority of habitat within the conservancy with some riparian woodland occurring along seasonal river lines. Annual rainfall is low, averaging 351 mm, and falling mostly during the summer months from November to March (du Preez et al., 2014b). Daytime temperatures are generally high in summer, regularly exceeding 40 °C, with mild conditions in winter. Permanent surface water is artificially provided at a relatively high density (approximately 5.9 / 100km^2). The study was conducted in the south-western section of the Conservancy where an ongoing lion research project was established in 2009.

Biologgers

Between January and July 2014, we fitted thirteen adult lions (9 males and 4 females, > 4 years old) with custom designed accelerometer biologgers (Biotrack / University of Oxford) that recorded accelerometer data at 16 Hz in 3 dimensions. In November 2014, eight adult lions (5

males and 3 females) were fitted with custom designed acoustic-accelerometer biologgers (Biotrack / University of Oxford) that recorded audio (8 bit, 16 kHz mono) and accelerometer data (32 Hz, 3 dimensions) simultaneously (Wijers et al., 2018). Six (4 males and 2 females) of these study animals were recaptures from the initial accelerometer biologger deployment. All biologgers were manufactured to attach onto existing GPS satellite (GPS-PTT) collars (Africa Wildlife Tracking, Pretoria, South Africa) and measured ~ 50 x 20 x 30 mm with a mass of < 150 g. Collars were secured to the lions using metal brackets provided by manufacturer that were designed to prevent abrasion. Biologgers were retrieved by recapturing each study animal which could be easily relocated as the BVC perimeter is fenced and thus prevents movement of lions beyond the Conservancy boundary. The GPS collars recorded 16 geographical locations per day at an hourly interval between 17:00 and 07:00 local time and one point in the middle of the day at 14:00. The mean $\pm$ SE 50% circular error probable of the collars was 9.94 $\pm$ 0.89 m (du Preez et al., 2014a). From the accelerometer biologgers we collected a total of 1069 lion days of useable data from 12 lions (no data was recorded for one male lion). Due to the higher power requirements for recording audio, the acoustic-accelerometer biologgers provided a comparatively smaller dataset with a total of 60 lion days of concurrent audio and accelerometer data from all 8 individuals.

Animal Capture Procedure

Each study animal was chemically immobilised using 75-100 mg Zoletil (Virbac RSA (Pty) Ltd, Halfway House, South Africa) combined with 5 mg medetomidine (Kyron Laboratories, Johannesburg, South Africa). Immobilisation drugs were delivered intramuscularly by 1 cc darts (Pneudart, Williamsport, Pennsylvania, USA) projected from a Dan-Inject CO_2-pressurised dartgun (Dan-Inject, Børkop, Denmark) at a distance of 15-20 m from the animal. Following

clear signs of immobilisation and a time period of approximately 15 minutes, the animal was carefully approached and blindfolded. The front legs were then secured together with a rope and earplugs inserted to reduce auditory stimuli. At approximately 60 minutes after initial drug injection, ~ 25 mg atipamazol (Antisedan, Pfizer Animal Health, Johannesburg, South Africa) was administered to reverse the effects of medetomidine allowing the animal to recover within 15 – 90 mins.

Weather data

Weather data which included air temperature, relative humidity and wind speed were obtained using a portable weather station (HOBO® Weather Station Data Logger H21-001, Onset Computer Corporation, Massachusetts, USA). The unit was erected in an open area in the study site and set to record measurements at 5-minute intervals (Trethowan et al., 2017). Because we were interested in the sound attenuation effects of humidity, we converted relative humidity (RH) to absolute humidity (AH). AH is a more appropriate measure than RH as the interaction of water molecules with oxygen contributes towards the largest proportion of molecular attenuation (Griffin, 1971). AH in g/m^3 was calculated from relative humidity and temperature using the following formula (Mander, 2012):

$$AH = \frac{6.112 \times e^{\left[\frac{17.67 \times T}{T+243.5}\right]} \times RH \times 2.1674}{273.15 + T}$$

where RH is relative humidity in % and T is temperature in °C. Data were then summarised into hourly means for each variable.

Spatial variables

Two spatial variables were used in this study: i) distance to closest river or water point and ii) position relative to home range. Using GIS layers of rivers and water points within the study site, we generated a raster proximity surface (cell size = 50 meters) in Quantum GIS 2.14 (QGIS Development Team, 2016) indicating the distance of each cell to the closest river or water point. Home range zones were estimated from GPS collar data using the local convex hull (LoCoH) method (Getz et al., 2007) with heuristic value $k = \sqrt{n}$ (n = number of locations). Three home range zones were defined: i) core (within 50% isopleth), ii) peripheral (between the 50% isopleth and 90% isopleth) and iii) outside (beyond the 90% isopleth).

Roar Classifier

From the raw audio recordings recovered from the acoustic-accelerometer biologgers we manually labelled the start and end times of roar events in Audacity 2.1.1 (Audacity Team, 2015). A total of 296 roars were found for the five male lions (Table A1). The three females did not roar and could only be heard uttering soft moans. We further labelled random segments of audio according to other identified, non-vocalising, behaviours (run, walk, feed, drink, rest) which could be recognised from characteristic acoustic cues (e.g. footfalls) as described in Wijers et al. (2018). All behaviour labels were then matched with concurrent accelerometer data to obtain a labelled dataset for training classification algorithms. Figure 1 illustrates the synchronised audio and accelerometer data for a single roar bout. Considering that the training dataset contained no female roars, we chose to limit further analyses to males as it was impossible to validate a roar classifier for females.

Since roar events can overlap with active behaviours such as walking we noticed distinct differences in the roar acceleration signal when an animal was stationary compared to when it was active. Active behaviours appeared to override the roar acceleration signal making it more difficult to determine the presence or absence of a roar. Given that our objective was to investigate patterns of lion vocal behaviour, it was essential that the classifier functioned with high precision (no false positives). Initial attempts to build a classifier that could identify roars in both active and stationary behavioural states produced a high number of false positives. We therefore decided to exclude periods of active behaviour from our analysis and focus on vocalisations occurring while the animal was stationary (a comparison between active and stationary behaviour is shown in Figure A1). We reasoned that this approach was valid as the majority (68%) of roars heard in the audio data occurred when animals were stationary. This finding was also consistent with the observations of Stander and Stander (1988) who found that 70% of roars emitted by lions from Etosha National Park occurred while animals were sitting, lying or standing.

A second important consideration in our analysis was being able to link location with a roar event. Given that the GPS satellite collars only recorded location on the hour at an hourly interval we systematically sampled the accelerometer data by extracting 20-minute windows centred on the hour associated with each GPS point (Fig. 2). We chose a 20-minute period as a trade-off between maximising the time available to detect roars and minimising the probability of detecting active behaviour which would result in the window being excluded from further analyses. Although lions are stationary for most of the day, rest periods are frequently interrupted by brief periods of activity. We used the same sampling method to investigate the diel distribution of roars but used all hours of the day (instead of the GPS point hours) in order to determine vocalisation rates during daylight hours as well as at night.

To extract roar events from accelerometer data we built a hierarchical classifier consisting of hidden Markov models (HMM) to distinguish between active and stationary behaviour, and a random forest (RF) to differentiate between roars and non-roars (Fig. 3). We first trained 3-state HMMs for active and stationary behaviour (a time window containing both active and stationary periods was classified as active) based on overall dynamic body acceleration (ODBA) which is a single, integrated measure of body motion (Gleiss et al., 2011). ODBA sequences could then be tested against each HMM to determine which model (active or stationary) was most likely to produce the given sequence (based on log-likelihood). A 4-fold cross-validation procedure resulted in 100% recall and precision indicating perfect classification of active and stationary sequences. Accelerometer windows that were classified as stationary in the first step were then passed to the RF (1000 trees and $\sqrt{}$(number of variables) considered at each split) which was trained to classify each second of the 20 min window as 'roar', 'rest' or 'other' (features used for RF classification are described in Table A2). The RF classification performance was tested using 5-fold cross validation where each fold represented data from only one of the five individual lions. Roars were classified with 93.3% recall and 86.1% precision (Table A3). We used this approach to simulate the scenario where the classifier would be required to predict behaviour on individual animals not included in the training set. The predicted series of behaviours generated by the RF were then converted into 1s and 0s where a '1' indicated a roar and a '0' indicated a non-roar. This allowed for the application of a gaussian filter which effectively filtered out isolated 1s that were likely to be false positives (considering that a single lion roar lasts for approximately 40 s). We selected a classification threshold of 0.82 which was found to yield high roar precision (100%) and satisfactory recall (68.9%). All stages of roar classification were carried out in Python using the hmmlearn 0.2.2 (hmmlearn Development Team, 2019) and Scikit-learn (Pedregosa et al., 2011) libraries.

Statistical Analyses

Diel distribution of roars

To determine the diel distribution of roars from the accelerometer data, we first calculated the total number of roars (frequency) in each hour for each individual. The hourly frequencies were then divided by the total number of stationary windows in each hour to account for potential variations in sampling effort across hours. For each individual, hourly frequencies were normalised by expressing each frequency as a fraction of the maximum frequency in order to compare distribution patterns across individuals. The resulting relative hourly frequencies were averaged across each individual and plotted with a loess smoothing function and 95% confidence intervals to remove high-frequency variability (Cleveland, 1988). We used the same method to plot the diel distribution of roars obtained from the raw audio recordings on the acoustic-accelerometer biologgers. However, because all data were used, it was not necessary to account for any variation in sampling effort.

Effect of location and atmospheric conditions on vocalisation likelihood

Lion vocalisations were analysed at two levels. Firstly, we simply considered the presence or absence of vocalisations in each 20-min window (roar occurrence). Secondly, we accounted for the number of vocalisations in each window in order to investigate possible differences in vocalisation preferences when lions choose to roar repetitively. In the latter case, we only considered windows in which two or more roars were detected (repetitive roars). Because

lions primarily roar during the night, we restricted our analyses to the period between 18:00 and 06:00 local time.

To test whether the likelihood of roar occurrence and repetitive roaring was a function of home range location and proximity to rivers and water points, we compared roar location characteristics to all non-roar stationary locations. Generalised linear mixed models (GLMM) with a binomial distribution and logit link function were used from the 'lme4' package in R (Bates et al., 2015). The response variable was coded as 1 (roar) and 0 (no roar). In each model lion identity was included as a random intercept, which accounted for individual-level variation in vocalisation behaviour and allowed for inference to the population level. This use-availability design allowed for robust comparison of locations chosen by lions for roaring to those available to them. We considered five candidate models consisting of each of the explanatory variables alone, combined and in interaction. Using the same GLMM approach, we also tested for effects of atmospheric conditions on vocalisation likelihood. Specifically, we investigated whether roar likelihood was a function of temperature, wind speed and absolute humidity. All three weather variables were standardised (mean-centred and divided by the standard deviation (SD)) to allow comparison of results within the model. Eight potential models were considered that consisted of the explanatory variables alone and in all possible combinations. Due to gradual changes in atmospheric conditions through the night and through the year we included random intercepts for hour and for month. A random intercept was also included for individual identity. All variables were checked for collinearity using variance inflation factors which were found to be < 3 and could therefore be included in the models (Zuur et al., 2010). Model selection was carried out using the R package MuMin (Bartoń, 2019) with all potential models ranked according to Akaike Information Criterion corrected for small sample sizes (AICc). The model with the lowest AICc was considered the

most plausible following the recommendations of Arnold et al. (2010) for small sets (< 10) of a priori models. Model fit was assessed using Nagelkerke's R^2, which is a pseudo R-squared test that provides an estimate (between 0 and 1) of the amount of variation that can be explained by the model and is defined as one minus the ratio of the likelihood under the null model to the likelihood of the fitted model (Nagelkerke, 1991; Xu, 2014). Predictor effects were interpreted in terms of odds ratios (OR) and their 95% confidence intervals (CI).

Results

Home range analyses indicated that 7 out of the 8 male lions with functioning accelerometers were territorial males with clearly defined, static home ranges (Fig. 4 and Fig. A2). One of the study males (A4) was not resident in any one area and appeared to only move along the boundary fence (Fig. A3). Of the seven territorial males, all belonged to separate coalitions except for lion A6 which was a singleton. All males were associated with at least one pride of females with which they would have likely sired cubs, however, specific details pertaining to this are not available. Small overlaps were evident between the 90% LoCoH isopleths (< 16%), while areas within the 50% LoCoH isopleths appeared to be used exclusively by each tagged individual and their associated pride members (although, realistically, nomadic males would also pass through these areas). A total of 990 roars were detected from the 7 territorial males (mean $\pm$ SE = 1.98 $\pm$ 0.33 roars/day) with only 19 roars (0.63 roars/day) detected from the nomadic male. Due to the low number of detected roars and in order to reduce possible bias as a result of social status, the nomadic male was excluded from further vocalisation analyses. In total, 8701 time windows were analysed of which 641 contained roars (176 of these contained > 1 roar), 4444 contained non-roar stationary behaviour and 3616 contained active behaviours and were therefore excluded (Table A5). The roar and non-roar stationary windows

(Figure A2) were used to model vocal behaviour in relation to the atmospheric and spatial variables.

Diel distribution of roars

The diel distribution of classified roars derived from the accelerometer data indicated that the territorial male lions roared predominantly during the night (Fig. 5). Relative frequency of roars increased steeply between 5pm and 8pm and then stabilised until shortly after midnight, before peaking between 3am and 5am. Relative frequency then steeply decreased at sunrise between 5am and 7am with relatively few roars detected during daylight hours. The hourly distribution of roars obtained from the acoustic biologgers shows an almost identical pattern with an obvious peak just before dawn between 3am and 5am and further validates the accelerometer classifier.

Effect of atmospheric conditions on vocalisation likelihood

The likelihood of roar occurrence in relation to atmospheric conditions was best explained by a model consisting of temperature, wind speed and absolute humidity which had a Nagelkerke R^2 of 0.022 (Table 1). Wind speed had the greatest effect with the odds of vocalisation decreasing by ~ 32 % for every 1 SD (0.733 m/s) increase in speed (OR: 0.677, CI: 0.590 – 0.778). Comparatively, a 1 SD (4.97 °C) rise in temperature decreased the odds of vocalisation by ~ 25 % (OR: 0.753, CI: 0.617 – 0.919) while a 1 SD (4.46 g/m^3) decrease in absolute humidity decreased the odds of vocalisation by ~ 23 % (OR: 0.773, CI: 0.630 – 0.949). When assessing the relationship between repetitive vocalisations and atmospheric conditions, the best model consisted of all three atmospheric predictor variables, as was the case for roar occurrence, and

had a Nagelkerke R^2 of 0.030 (Table 1). The odds of repetitive roars occurring decreased by ~ 44 % with every 1 SD (0.733 m/s) increase in wind speed (OR: 0.559, CI: 0.416 – 0.751), decreased by ~ 45 % for every 1 SD (4.97 °C) rise in temperature (OR: 0.551, CI: 0.389 – 0.781) and decreased by ~ 35 % for every 1 SD (4.46 g/m^3) decrease in absolute humidity (OR: 0.645, CI: 0.457 – 0.909). Further details on the atmospheric conditions during the study can be found in Table A4.

Effect of location on vocalisation likelihood

The best model explaining the likelihood of roar occurrence in relation to spatial variables consisted of home range location as the only explanatory variable and had a Nagelkerke R^2 of 0.009 (Table 2). A Tukey post-hoc analysis revealed that the odds of a lion roaring outside its home range was ~ 54% lower compared to its home range core (OR: 0.459, CI: 0.289 – 0.730) and ~ 43% lower compared to the periphery (OR: 0.571, CI: 0.353 – 0.919). No significant difference was found between the likelihood of roar occurrence in the home range periphery and the core (OR: 0.805, CI: 0.644 – 1.001). The best model explaining the likelihood of repetitive vocalisations consisted of an interaction between home range location and the distance to nearest river or water point and had a Nagelkerke R^2 of 0.023 (Table 2). The effect of distance to rivers and water points therefore depended on home range location (Fig. 6) with the odds of repetitive vocalisations increasing by 86% for every 1 km decrease in distance to rivers and water points in the home range core (OR: 1.863, CI: 2.835 – 1.224) and decreasing by 82% for every 1 km decrease to rivers and water points outside the home range boundary (OR: 0.179, CI: 0.045 – 0.703). No significant effect was detected for the influence of distance to rivers and water points on the likelihood of repetitive roars within the periphery (OR: 1.017, CI: 0.727 – 1.423)

Discussion

Recording animal vocal behaviour with simultaneous location information is challenging, particularly for species such as lions which are mostly active at night and therefore difficult to identify. The use of biologgers provides a unique opportunity to monitor animal movement continuously and thereby overcomes many of the challenges associated with direct observation. Lion vocalisations involve consistent movements of the animal's head and neck which can be captured by three-dimensional accelerometer loggers. To our knowledge, this study is the first to retrieve animal vocalising behaviour from accelerometery data. Although our detection method was limited to stationary behaviour and retrieved ~69% of roar events, it still provided more than three times the number of roars as the raw audio recorded by the acoustic-accelerometer biologgers. On-animal audio recordings may be preferable for detecting all roars emitted by tagged animals but the lifetime of an acoustic biologger is considerably lower (~ 8 days) than an accelerometer biologger (~ 100 days) due to the higher power requirements for recording audio.

The diel distribution of roars obtained from both biologgers indicated that lions vocalise mainly at night with a distinct peak just before dawn. This pattern corresponds closely with the observations reported by Schaller (1972) and Stander and Stander (1988) who also noted a consistent peak in the hours before sunrise. Larom et al. (1997b) suggested that lion calling behaviour is likely to be driven by predictable atmospheric fluctuations that enhance the range of vocal signal propagation. Optimal conditions occur when there is a strong surface temperature inversion and no wind as acoustic energy is refracted downwards and thereby increases sound levels near the ground (Larom et al., 1997a). Although it was not possible to

determine the strength of daily temperature inversions, our results indicated that lions avoided vocalising with increasing wind speed. Strong winds cause vertical and horizontal mixing of air and thus prevent the development of a surface temperature inversion. Furthermore, wind has the added effect of causing fluctuations in the received signal and introduces considerable low frequency noise that overlaps with low frequency vocal signals, such as lion roars, resulting in acoustic masking (Wiley & Richards, 1978; Larom et al., 1997b). Considering the multiple negative effects of wind on signal propagation and reception it is probable that lions actively avoid vocalising during these periods as doing so would result in minimal benefit. Similar avoidance behaviour has been recorded for maned wolves (Rocha et al., 2016) and timber wolves (Joslin, 1967). In addition to the effects of wind speed, our results also indicated significant effects for temperature and absolute humidity with lions showing an apparent preference for vocalising in lower temperatures and higher humidity. For frequencies below 1 kHz, sound attenuation decreases with increasing humidity and increases with increasing temperature (Harris, 1966; Griffin, 1971). Low frequency vocalisations emitted in cold, humid conditions are therefore likely to travel further compared to signals emitted in warm, dry conditions. Considering that the fundamental frequency of a roar typically ranges between 40 Hz and 250 Hz, it is likely that lions also choose to exploit these conditions by roaring more frequently when temperatures are low and humidity is high in order to maximise calling area.

Although atmospheric conditions are likely to be a primary factor influencing lion vocal behaviour, spatial attributes may also impact an individuals' decision to vocalise. When assessing patterns of roar occurrence, the primary spatial feature affecting vocalisation likelihood was the animal's position relative to its home range. Despite little difference in the likelihood of roar occurrence between core and peripheral areas, lions appeared to strongly

avoid vocalising outside of their home range. This result is consistent with the findings of Grinnell and McComb (2001) who reported, from anecdotal observations, that resident male lions in the Serengeti and Ngorongoro crater refrain from roaring beyond their territory boundaries. This avoidance behaviour can be attributed to the increased costs of engaging in conflict with other territorial males and the reduced benefits of vocalising away from owned resources. Similar 'low profile' behaviour is commonly displayed by nomadic individuals that do not possess a territory as was evident in this study where the nomadic male vocalised less than the territorial males (Harrington & Mech, 1979; Grinnell & McComb, 2001; Campioni et al., 2010). The locations of repetitive vocalisations appeared to be influenced by proximity to the nearest river or water point with the effect being dependent on the animal's position relative to its home range. Within the home range core, lions showed a preference for vocalising repetitively while closer to rivers and water points but avoided doing so when outside of their home range. Several studies have shown that rivers and water points are important features for lion prey acquisition and reproduction (Mosser et al., 2009; Valeix et al., 2010; Davidson et al., 2013). Lions may therefore choose to increase vocalisation effort when closer to valuable territory features within their home range core in order to deter potential invaders. Other species such as fallow bucks (*Dama dama*) are known to increase vocalisation rates as a threat display directed at rival males particularly in contexts requiring protection of a resource such as access to females (Mcelligott & Hayden, 1999). The apparent avoidance of repetitive vocalisations closer to rivers and water points beyond an individual's home range boundary reflects the increased risks of inviting attacks from aggressive resident males that may be more willing to engage in conflict when access to a valuable resource is challenged.

While the objective of this work was to investigate the influence of spatial features and atmospheric conditions on lion vocalisations, it is important to note that there are other

factors that can affect an animal's decision to vocalise or remain silent. For example, some predatory animals reduce vocalisation rates during foraging as prey are able detect vocal signals and respond with antipredator behaviour (Deecke et al., 2004). Social factors may also play a role; in this study the three lionesses did not produce full throated roars and could only be heard uttering soft moans, likely as a means of short distance communication between other members of the pride. Although this was unexpected, the presence of small cubs in the prides may have contributed to a temporary cessation of long-distance vocalisation. Similar behaviour has been reported for wolves where adults appeared to stop howling until pups had reached an age of 6-9 weeks; a strategy that is thought to be employed to protect pups from predators (Joslin, 1967). In the case of lions, avoiding long-distance vocalisation may reduce the risks associated with attracting potentially infanticidal males (Grinnell & Mccomb, 1996). We acknowledge, however, that 3 lionesses does not constitute an adequate sample size and therefore further work would be required to support this assumption. Another social factor that can influence the frequency and timing of roars is an individual's proximity to its coalition or pride members. Lions are known to roar frequently in chorus with other members of the pride which conveys information relating to pride size and thus deters potential competitors (McComb et al., 1994). Roaring close to and in chorus with companions is likely to be advantageous and potentially preferred to roaring alone. However, given that lions are able to recognise the roars of familiar conspecifics and rely on vocalizations and scent to locate each other, individuals may also vocalize frequently while searching for distant companions (McComb et al., 1993; Gilfillan et al., 2016). Although the vocal behaviour of pride females in response to spatial features and atmospheric conditions is likely to be similar to that of pride males, we acknowledge that the findings presented in this research are based entirely on territorial males. We would therefore encourage additional studies on this topic to explore female vocal behaviour in similar detail.

In this study we have shown that lion vocal behaviour is influenced by both spatial and atmospheric variables. Although vocalisation behaviour is also dependent on other behavioural and social contexts, lions appear to select conditions that maximise calling area, as suggested by Larom et al. (1997b), and also adjust vocal effort depending on their location in order to defend resources and minimise inter-pride conflict. Understanding how environmental factors influence animal vocal behaviour is not only important for interpreting patterns relating to species ecology but can also directly benefit species conservation through passive acoustic monitoring (PAM; Marques et al., 2013). To our knowledge, no study has attempted to monitor lions from their vocalisations, but with rapidly advancing technology, PAM could provide an alternative, cost effective option for future lion research and conservation initiatives. This work has highlighted some important considerations for PAM system design such as the time of peak vocalisation and the influence of habitat features and environmental conditions. Furthermore, the methods employed in this study to obtain data on lion vocalisations may also be applicable to other species that are capable of carrying biologgers and that move in a unique and consistent manner while vocalising. In future, acoustic biologgers could be improved by incorporating on-board classification of vocalisations to eliminate the requirement for continuous audio and thereby improve device lifetime.

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Tables

Table 1. Model selection statistics for mixed effects logistic regression analysis of the relationship between lion vocal behaviour and atmospheric conditions.

Response	Model	Rank	LLH	AICc	Δi	w_i	K
Vocalisation	**Temp + AH + Wind**	**1**	**-1551.384**	**3116.8**	**0.00**	**0.789**	**7**
occurence	Temp + Wind	2	-1554.286	3120.6	3.80	0.118	6
	Wind	3	-1556.101	3122.2	5.42	0.052	5
Present (1)	Wind + AH	4	-1555.354	3122.7	5.93	0.041	6
vs	Temp	5	-1569.985	3150.0	33.19	0.000	5
Available (0)	Temp + AH	6	-1569.076	3150.2	33.38	0.000	6
	Null	7	-1575.453	3158.9	42.12	0.000	4
	AH	8	-1575.381	3160.8	43.98	0.000	5
Repetitive	**Temp + AH + Wind**	**1**	**-602.188**	**1218.4**	**0.00**	**0.846**	**7**
vocalisation	Temp + Wind	2	-605.246	1222.5	4.11	0.109	6
	Wind	3	-607.464	1224.9	6.54	0.032	5
Present (1)	Wind + AH	4	-607.339	1226.7	8.29	0.013	6
vs	Temp + AH	5	-611.921	1235.9	17.46	0.000	6
Available (0)	Temp	6	-613.937	1237.9	19.48	0.000	5
	Null	7	-618.108	1244.2	25.82	0.000	4
	AH	8	-618.074	1246.2	27.76	0.000	5

Response variables include vocalisation occurrence and repetitive vocalisation occurrence and explanatory variables include wind speed (Wind) absolute humidity (AH) and temperature (Temp). A random intercept was included in each model for individual animal, month and hour of the night. Selection statistics include log-likelihood (LLH), Akaike Information Criterion corrected for small sample sizes (AICc), AICc difference from the most plausible model (Δi), Akaike weight (w_i) and number of parameters (K). Models highlighted in bold indicate the most plausible models.

Table 2. Model selection statistics for mixed effects logistic regression analysis of the relationship between lion vocal behaviour and spatial features.

Response	Model	Rank	LLH	AICc	Δi	w_i	K
Vocalisation	**Zone**	**1**	**-1613.795**	**3235.6**	**0.00**	**0.489**	**3**
occurence	Zone*Dist	2	-1611.234	3236.5	0.90	0.312	4
	Zone + Dist	3	-1613.696	3237.4	1.81	0.198	4
Present (1) vs	Dist	4	-1621.445	3248.9	13.30	0.001	3
Available (0)	Null	5	-1623.578	3251.2	15.56	0.000	2
Repetitive	**Zone*Dist**	**1**	**-617.513**	**1249.1**	**0.00**	**0.987**	**4**
vocalisation	Zone + Dist	2	-624.784	1259.6	10.53	0.005	4
	Zone	3	-626.003	1260.0	10.96	0.004	3
Present (1) vs	Dist	4	-627.418	1260.8	11.78	0.003	3
Available (0)	Null	5	-629.780	1263.6	14.51	0.001	2

response variables include vocalisation occurrence and repetitive vocalisation occurrence and explanatory variables include location relative to home range (Zone) and proximity to closest river or water point (Dist). A random intercept was included in each model for individual animals. Selection statistics include log-likelihood (LLH), Akaike Information Criterion corrected for small sample sizes (AICc), AICc difference from the most plausible model (Δi), Akaike weight (w_i) and number of parameters (K). Models highlighted in bold indicate the most plausible models.

Figures

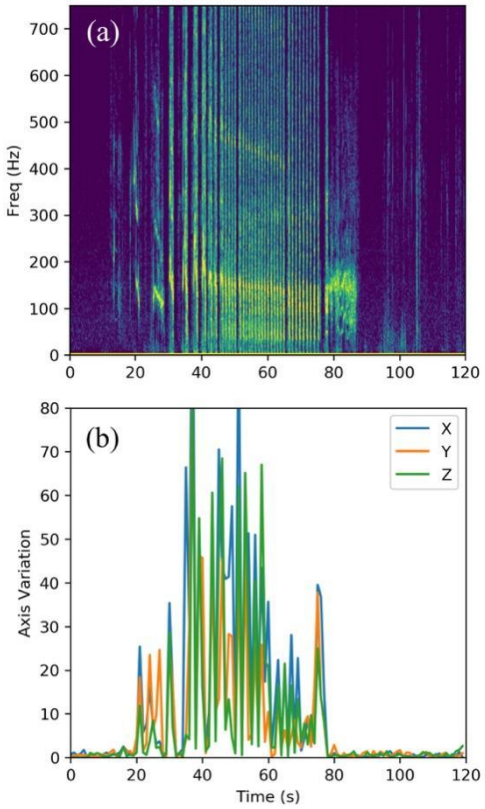


Figure 1. Roar spectrogram (a) with corresponding 3-axis accelerometer data (b). X, Y and Z refer to raw accelerometer sensor outputs and although consistent between individuals, are not calibrated to the animal's body frame (surge, heave and sway) as this was not necessary for our analyses.

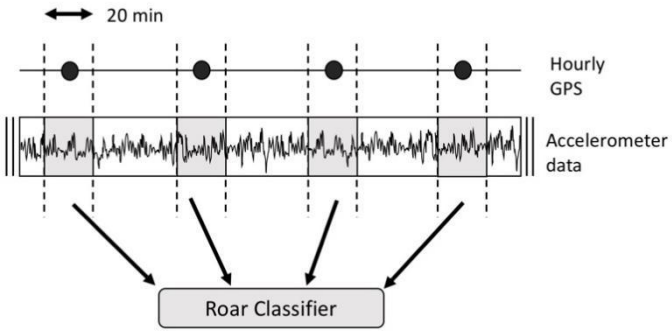


Figure 2. Schematic representation of the sampling approach used to link behaviour with location.

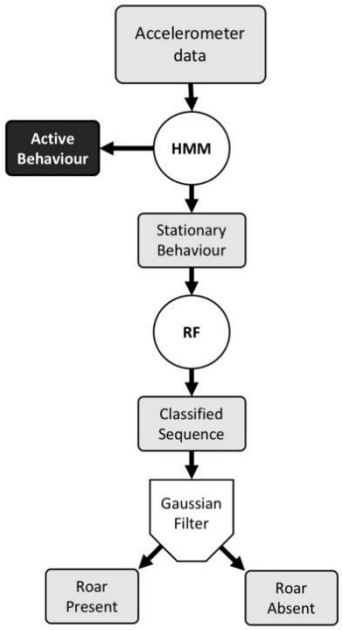


Figure 3. Flow diagram illustrating the sequence of steps in the roar classifier.

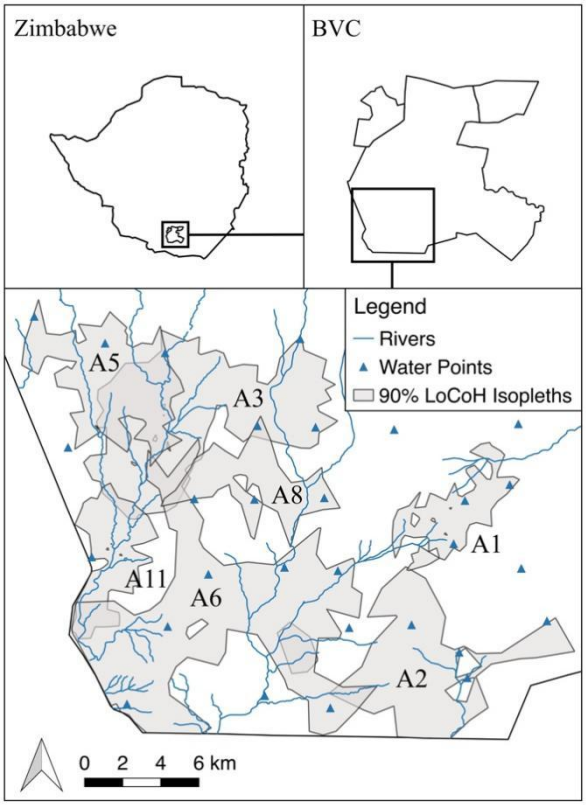


Figure 4. Map showing location of the study site in Zimbabwe and the positions of each lion home range (90% LoCoH isopleths) within the study site. Note that although the home range for lion A5 appears to overlap considerably with that of lion A3, data collection for these two lions did not overlap temporally (Table A5). Lion A3 was no longer present in the area occupied by A5 at the time it's biologger was fitted.

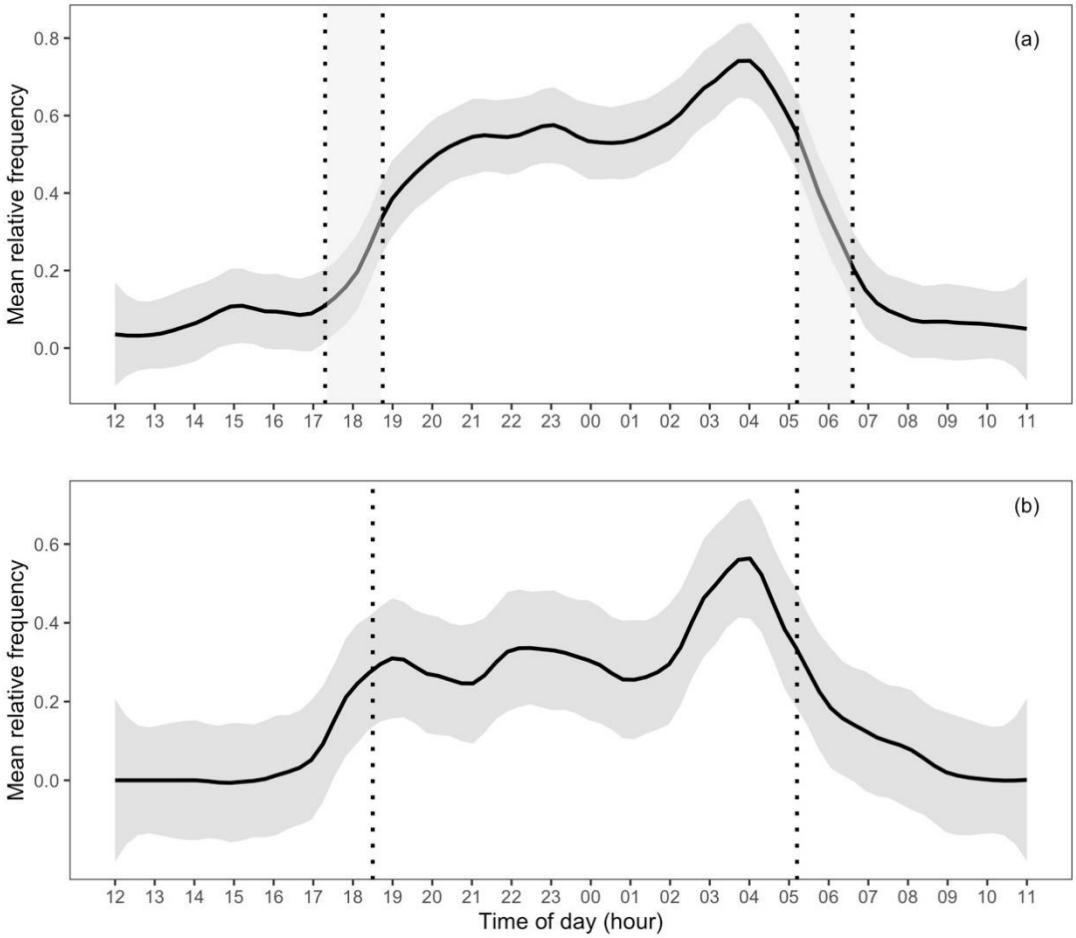


Figure 5. Diel distribution of roars obtained from accelerometer biologgers (a) and from acoustic biologgers (b). Dark grey shaded areas denote 95% confidence intervals and vertical dotted lines indicate sunset and sunrise times (with a range for each in (a) as data were collected between the summer and winter solstice).

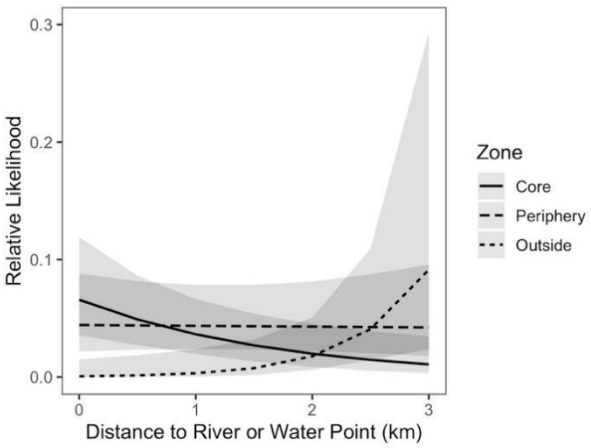


Figure 6. Relationship between relative likelihood of repetitive vocalisation and the interaction between location relative to home range and distance to rivers and water points. Shaded areas denote 95% confidence intervals.

Appendix

Table A1. Accelerometer and audio dataset (used to train roar classifier).

Lion	Attributes			Roars	Data Periods	
	Sex	Status	Coalition		Start (dd/mm)	End (dd/mm)
A4	Male	Pride	2	51	28 Nov	01 Dec
A8	Male	Pride	2	83	21 Nov	30 Nov
A9	Male	Pride	2	35	25 Nov	30 Nov
A10	Male	Pride	2	39	23 Nov	30 Nov
A11	Male	Pride	2	88	23 Nov	04 Dec

Table A2. Features used for RF classification.

Feature	**Definition**	**Number of variables**
Variance in each axis	Variance for X,Y and Z axes	3
Pitch	Ratio between X,Y and Z axes	1
ODBA filter	The difference between median filters of the sum of the dynamic acceleration values for X,Y and Z axes taken from a 200 second window and a 40 second window	1
Relative Frequency	The difference between Gaussian filters of average peak frequency (frequency bin with the maximum energy level) with sigma level 70 and 10.	1
Roll Variation	The variation in the angle between the Y and Z axes across a 9 second window	1
Mean Maximum Peak Frequency	The mean maximum peak frequency from X, Y and Z axes across a 9 second window	1
Mean Average Peak Frequency	The mean average peak frequency from X,Y and Z axes across a 9 second window	1
Mean Frequency Range	The mean difference between the maximum and minimum peak frequencies across a 9 second window	1

Table A3. Confusion matrix of actual behaviours (rows) vs predicted behaviours (columns) for random forest roar classifier.

Activity	**Roar**	**Rest**	**Active**	**Recall %**	**Precision %**
Roar	3522	82	171	93.3	86.1
Rest	24	4807	54	98.4	96.7
Active	545	81	4445	87.7	95.2

Table A4. Atmospheric conditions during the study.

Condition	**Mean $\pm$ SE**	**Max**	**Min**
Temperature (°C)	21.07 ± 0.06	41.56	3.83
Absolute Humidity (g/m^3)	13.23 ± 0.05	22.05	1.00
Wind Speed (m/s)	0.50 ± 0.01	4.72	0.00

Table A5. Accelerometer only dataset – extracted roars for the 8 male lions.

Lion	Attributes			20-min Time Windows				Data Periods	
	Sex	Status	Coalition	Roars	Stationary	Active	Total	Start (dd/mm)	End (dd/mm)
A1	Male	Pride	2	188	713	480	1381	28 Jan	27 Apr
A2	Male	Pride	2	41	178	166	385	28 Jan	20 Feb
A3	Male	Pride	2	123	993	898	2014	29 Jan	06 Jun
A4	Male	Nomad	Singleton	7	249	211	467	29 Jan	28 Feb
A5	Male	Pride	2	94	500	440	1034	16 Jul	16 Sep
A6	Male	Pride	Singleton	84	989	813	1886	19 Jan	21 May
A8	Male	Pride	2	35	148	128	311	28 Jan	16 Feb
A11	Male	Pride	2	76	923	691	1690	29 Jan	17 May

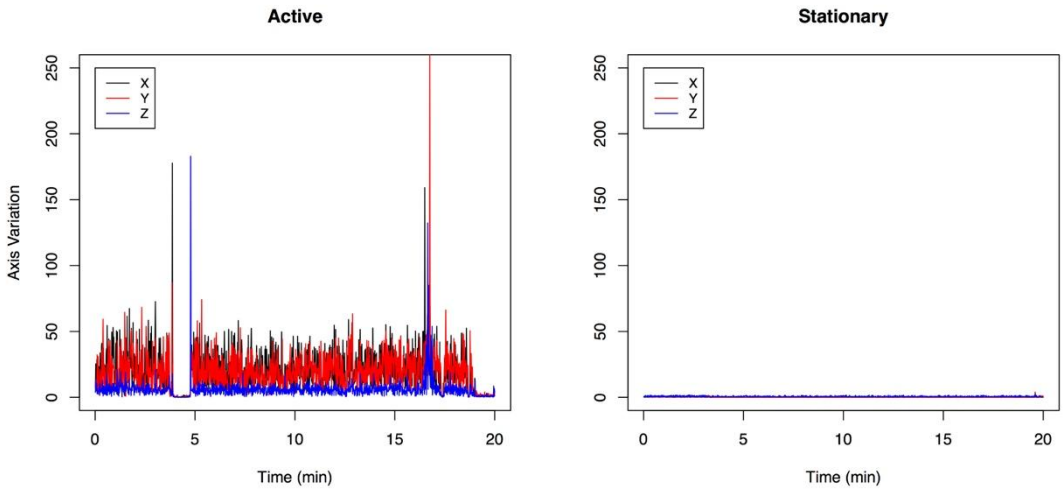


Figure A1. Three-axis accelerometer data for active and stationary windows.

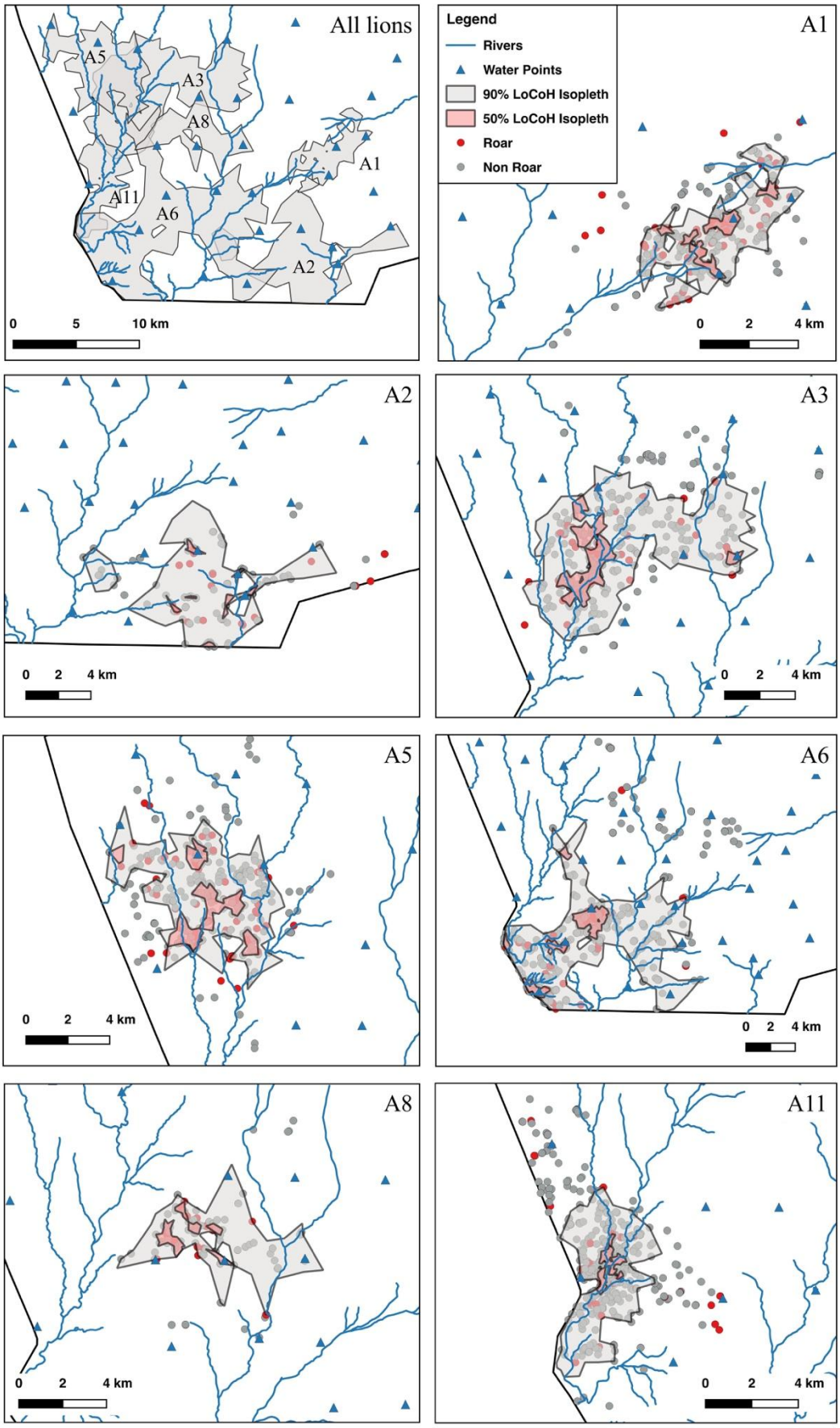

All lions
A5
A3
A8
A1
A11
A6
A2
0 5 10 km
Legend
Rivers
Water Points
90% LoCoH Isopleth
50% LoCoH Isopleth
Roar
Non Roar
A1
0 2 4 km
A2
0 2 4 km
A3
0 2 4 km
A5
0 2 4 km
A6
0 2 4 km
A8
0 2 4 km
A11
0 2 4 km

Figure A2. Maps showing 90% and 50% LoCoH isopleths for each lion with stationary points (roar and non-roar).

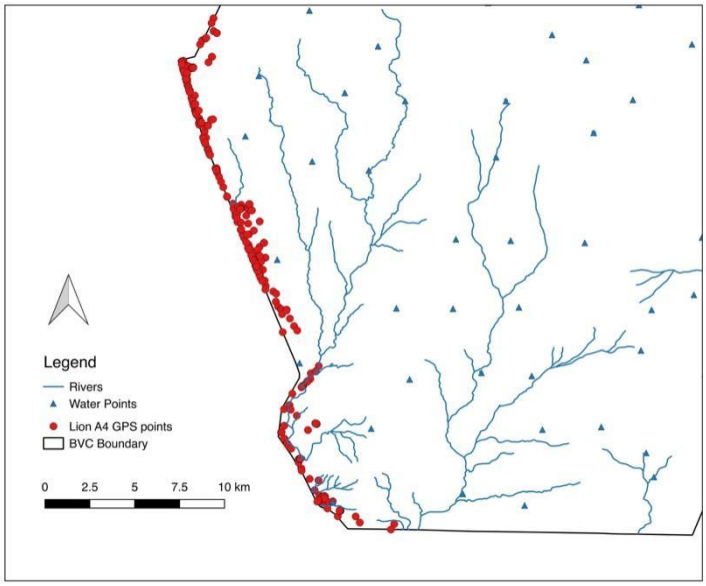


Figure A3. GPS points for lion A4 which was a vagrant during the study period and therefore not included in the analysis.