

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

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Highlights

- Acoustic accelerometer biologgers enable detection of lion roars from body movement.
- Lions vocalize mainly at night with a peak just before dawn.
- Roaring is preferred when temperature and wind speed are low and humidity is high.
- Lions avoid roaring beyond their home range boundary.
- Lions are more likely to roar repeatedly when closer to rivers and water points.

Abstract

Long-distance vocalization 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 bilogger, we trained a machine-learning model to detect lion roars from long-term acceleration signals which yielded over 500 nights of data from seven individual lions. Analysis of detected roar events revealed that vocalizations occurred mainly at night with a peak just before dawn. The relative likelihood of vocalization 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 maximize 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 vocalizing beyond the home range boundary. Lions were also more likely to roar repeatedly 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 also inform new approaches for recording animal vocalizations remotely.

Keywords: biologging; *Panthera leo*; roar; vocal behaviour; vocalization

Animal vocal communication has been a topic of considerable interest over the past century with most research being dedicated to three main aspects: 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, Rodman, & Emond, 1996), foraging (Rydell, McNeill, & Eklöf, 2002), navigation (Moss & Surlykke, 2010) and deterring predators (Zuberbühler, Jenny, & Bshary, 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 vocalize 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 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 vocalizing to reduce the risk of attracting attention from territory owners (Campioni, Delgado, & Penteriani, 2010; Grinnell & McComb, 2001; Harrington & Mech, 1979). 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 vocalizing 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, Sunde, Rahbek, Dabelsteen, & Thorup, 2013; Penteriani, 2014).

In addition to spatial variation in the costs and benefits of vocalizing, 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 animal's calling area (Larom, Garstang, Payne, Raspet, & Lindeque, 1997; Wiley & Richards, 1978). Garstang, Larom, Raspet, and Lindeque (1995) found that the range of elephant vocal signals doubled in magnitude under optimum atmospheric conditions. These are generally characterized by low wind speeds and low-level vertical changes in temperature known as temperature inversions (Larom, Garstang, Payne, et al., 1997). Studies on wolf, *Canis lupus*, and coyote, *Canis latrans*, vocalizations have shown an overlap between peak periods of vocalization and the hours of best sound transmission (Harrington & Mech, 1979; Laundre, 1981).

African lions, *Panthera leo*, are well known for their impressive, long-distance vocalizations 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 (Grinnell & McComb, 2001; McComb, Packer, & Pusey, 1994). Lion vocal communication has been well studied particularly in relation to roar characteristics (Stander & Stander, 1988) individual recognition (Gilfillan, Vitale, McNutt, & McComb, 2016; McComb, Pusey, Packer, & Grinnell, 1993), information content of the signal (McComb et al., 1994; Pfefferle, West, Grinnell, Packer, & Fischer, 2007) and the limitations imposed by unwanted receivers (Gray et al., 2017; Grinnell & McComb, 2001). Playback experiments are a common methodological approach in these studies; however, some researchers have relied on various means of recording natural, spontaneous roaring events to investigate particular aspects of lion vocal

behaviour (Gray et al., 2017; Lehmann, Funston, Owen, & Slotow, 2008; Pfefferle et al., 2007; Stander & Stander, 1988). While the latter approach may be necessary, obtaining sufficient quantities of roar records can be extremely difficult especially as wild lions vocalize almost exclusively at night (Pfefferle et al., 2007; Stander & Stander, 1988). 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 500 m 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 characterized 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 vocalizing, specifically with regard 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 vocalizations with concurrent location information. To overcome this issue, we developed novel acoustic accelerometer biologgers combined with innovative machine-learning techniques to detect lion vocalizations 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 vocalization detection using the same approach (Grünewälder et al., 2012; Lush, Ellwood, Markham, Ward, & Wheeler, 2015; Wang et al., 2015). We hypothesized that lions would show a preference for vocalizing 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 hypothesized that conditions with lower temperatures and wind speeds and higher absolute humidity would be preferred given that such conditions maximize the calling range (Griffin, 1971; Harris, 1966; Larom, Garstang, Payne, et al., 1997).

Methods

Study Site

The study was conducted in the Bulya 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 km² and hosts a variety of indigenous megafauna including a large lion population (ca. 500 individuals at the time of the study; du Preez, Hart, Loveridge, & Macdonald, 2014) organized into resident female prides with associated territorial male coalitions as well as vagrant individuals. Mopane woodland savannah dominates most of the 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, Loveridge, & Macdonald, 2014). 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 5.9/100 km²). The study was conducted in the southwestern section of the Conservancy where an ongoing lion research project was established in 2009.

Biologgers

Between January and July 2014, we fitted 13 adult lions (nine males and four females, > 4 years old) with custom-designed accelerometer biologgers (Biotrack, University of Oxford, Oxford, U.K.) that recorded accelerometer data at 16 Hz in three dimensions. In November 2014, eight adult lions (five males and three females) were fitted with custom-designed acoustic accelerometer biologgers (Biotrack) that recorded audio (8 bit, 16 kHz mono) and accelerometer data (32 Hz, three dimensions) simultaneously (Wijers et al., 2018). Six of these study animals (four males and two females) were recaptures from the initial accelerometer biollogger deployment. All biologgers were manufactured to attach onto existing GPS satellite (GPS-PTT) collars (Africa Wildlife Tracking, Pretoria, South Africa) and measured ca. 50 × 20 × 30 mm with a mass of < 150 g. Collars were secured to the lions using metal brackets provided by the 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 1700 and 0700 local time and one point in the middle of the day at 1400. The mean ± SE 50% circular error probable of the collars was 9.94 ± 0.89 m (du Preez, Hart, et al., 2014). From the accelerometer biologgers we collected a total of 1069 lion days of usable data from 12 lions (no data were recorded for one male lion). Owing to the higher power requirements for recording audio, the acoustic accelerometer biologgers provided a comparatively smaller data set with a total of 60 lion days of concurrent audio and accelerometer data from all eight individuals.

Animal Capture Procedure

Each study animal was chemically immobilized using 75–100 mg Zoletil (Virbac RSA (Pty) Ltd, Halfway House, South Africa) combined with 5 mg medetomidine (Kyron Laboratories, Johannesburg, South Africa). Immobilization drugs were delivered intramuscularly by 1 cc darts (Pneudart, Williamsport, PA, U.S.A.) projected from a Dan-Inject CO₂-pressurized dartgun (Dan-Inject, Børkop, Denmark) 15–20 m from the animal. Following clear signs of immobilization and a period of approximately 15 min, 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 min after initial drug injection, ca. 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 min.

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, MA, U.S.A.). The unit was erected in an open area in the study site and set to record measurements at 5 min intervals (Trethowan et al., 2017). Because we were interested in the sound attenuation effects of humidity, we converted relative humidity (RH) to absolute humidity. The latter 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). Absolute humidity in g/m³ was calculated from RH and temperature using the following formula (Mander, 2012):

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

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

Spatial Variables

Two spatial variables were used in this study: (1) distance to closest river or water point and (2) 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 m) 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: (1) core (within the 50% isopleth), (2) peripheral (between the 50% isopleth and 90% isopleth) and (3) 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, nonvocalizing, behaviours (run, walk, feed, drink, rest) which could be recognized 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 data set for training classification algorithms. Fig. 1 illustrates the synchronized audio and accelerometer data for a single roar bout. As the training data set contained no female roars and we therefore could not validate a roar classifier for females, we chose to limit further analyses to males.

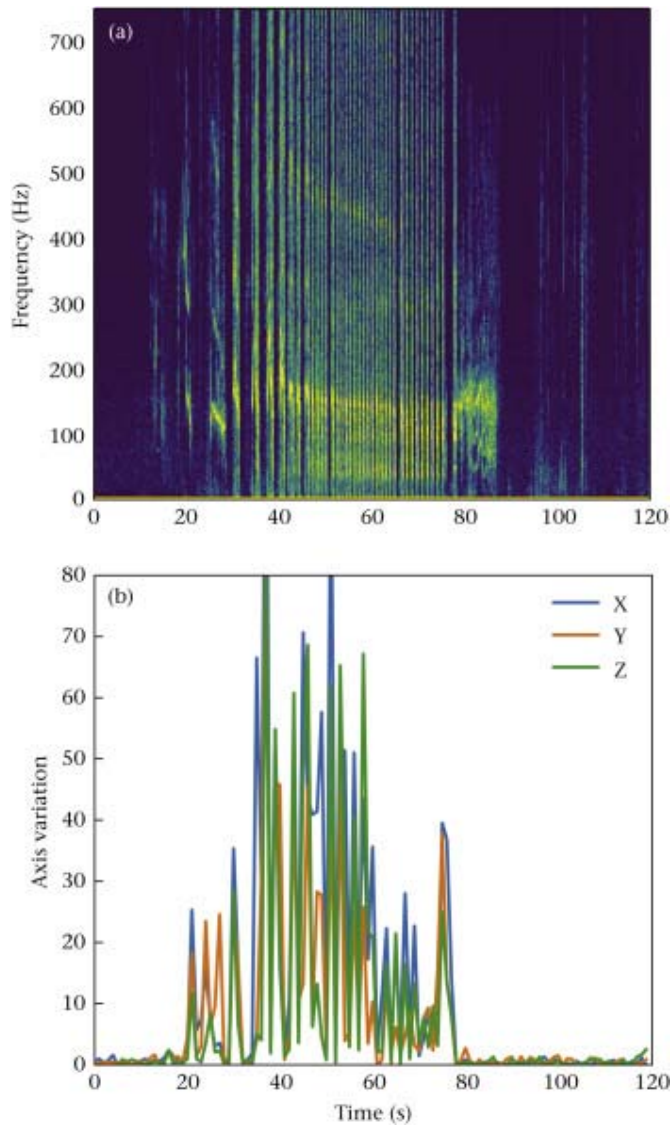


Figure 1. (a) Roar spectrogram with (b) corresponding three-axis accelerometer data. X, Y and Z refer to raw accelerometer sensor outputs and, although consistent between individuals, are not calibrated to the animal's body frame (surge, heave and sway) as this was not necessary for our analyses.

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 vocalizations occurring while the animal was stationary (a comparison between active and stationary behaviour is shown in Fig. 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 of 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 min windows centred on the hour associated with each GPS point (Fig. 2). We chose a 20 min period as a trade-off between maximizing the time available to detect roars and minimizing 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) to determine vocalization rates during daylight hours as well as at night.

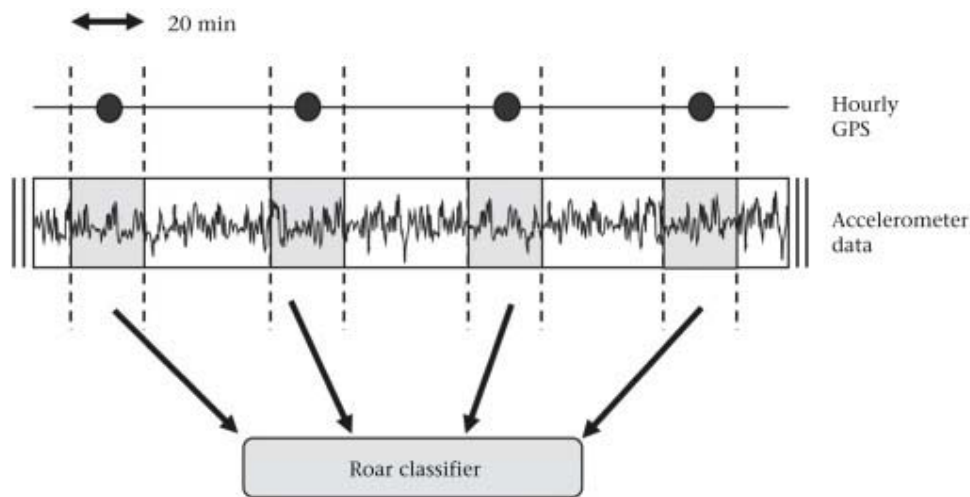


Figure 2. Schematic representation of the sampling approach used to link behaviour with location.

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 nonroars (Fig. 3). We first trained three-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, Wilson, & Shepard, 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 four-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 $\sqrt{\text{number of variables}}$ 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 five-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 nonroar. This allowed for the application of a Gaussian filter which effectively filtered out isolated 1s that were likely to be false positives (as 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.

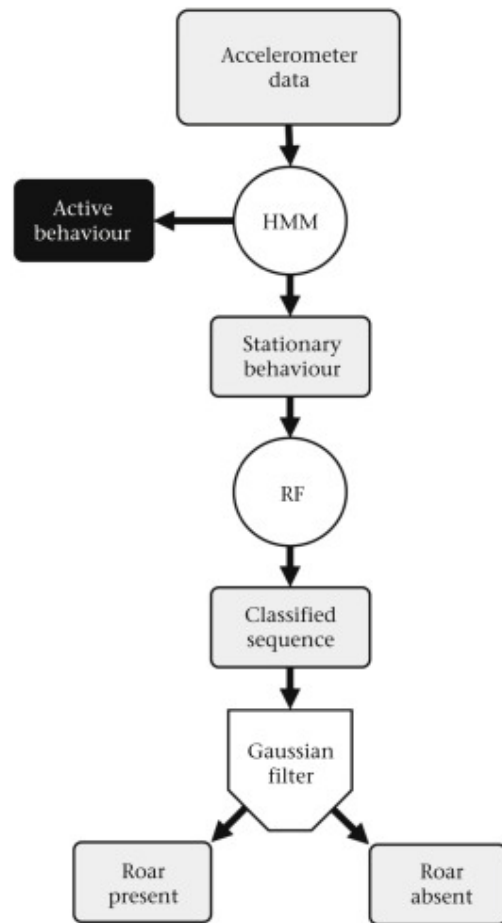


Figure 3. Flow diagram illustrating the sequence of steps in the roar classifier. HMM: hidden Markov model; RF: random forest.

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 variation in sampling effort across hours. For each individual, hourly frequencies were normalized by expressing each frequency as a fraction of the maximum frequency 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 (CIs) 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 vocalization likelihood

Lion vocalizations were analysed at two levels. First, we simply considered the presence or absence of vocalizations in each 20 min window (roar occurrence). Second, we accounted for the number of vocalizations in each window to investigate possible differences in vocalization preferences when lions chose to roar repeatedly. In the latter case, we only considered windows in which two or more roars were detected (repeated roars). Because lions primarily roar during the night, we restricted our analyses to the period between 1800 and 0600 local time.

To test whether the likelihood of roar occurrence and repeated roaring was a function of home range location and proximity to rivers and water points, we compared roar location characteristics to all nonroar stationary locations. Generalized linear mixed models (GLMM) with a binomial distribution and logit link function were used from the 'lme4' package in R (Bates, Mächler, Bolker, & Walker, 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 vocalization 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 vocalization likelihood. Specifically, we investigated whether roar likelihood was a function of temperature, wind speed and absolute humidity. All three weather variables were standardized (mean-centred and divided by the standard deviation) 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. Owing 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, Ieno, & Elphick, 2010). Model selection was carried out using the R package MuMin (Bartoń, 2019) with all potential models ranked according to the 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^2 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% CIs.

Ethical Note

This study was carried out in accordance with the recommendations of the ASAB/ABS Guidelines for the Use of Animals in Research and with the research protocol approved by the University of Oxford Animal Welfare and Ethical Review Board (AWERB). Animal handling procedures were carried out by project staff trained and certified by the Zimbabwe Veterinary Association, Wildlife Group (Certificate number: 2014/16) in accordance with Statutory Instrument 409 of 1999 (Clause 21A to 21J) amending the Regulations of 1975 to the Dangerous Drugs Act, Zimbabwe. Training was undertaken through attendance at the Chemical and Physical Restraint of Wild Animals Course (run by Zimbabwe Veterinary Association, Wildlife Group and Government Veterinary Services Wildlife Unit, see <http://wildlifecaptureafrica.com/the-course/about-the-course/>). All procedures were undertaken with the permission of the landowner. There is no evidence to suggest that the collars influenced the behavioural repertoire of the study individuals. The same collar type has been used to collect data for a number of studies (e.g. Briers-Louw, Verschueren, & Leslie, 2019; Preston, Johnson, Macdonald, & Loveridge, 2019).

Results

Home range analyses indicated that seven of the eight male lions with functioning accelerometers were territorial males with clearly defined, static home ranges (Fig. 4, 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 probably 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 seven territorial males (mean \pm SE = 1.98 ± 0.33 roars/day) with only 19 roars (0.63 roars/day) detected from the nomadic male. Owing to the low number of detected roars and to reduce possible bias as a result of social status, the nomadic male was excluded from further vocalization analyses. In total, 8701 time windows were analysed of which 641 contained roars (176 of these contained more than one roar), 4444 contained nonroar stationary behaviour and 3616 contained active behaviours and were therefore excluded (Table A4). The roar and nonroar stationary windows (Fig. A2) were used to model vocal behaviour in relation to the atmospheric and spatial variables.

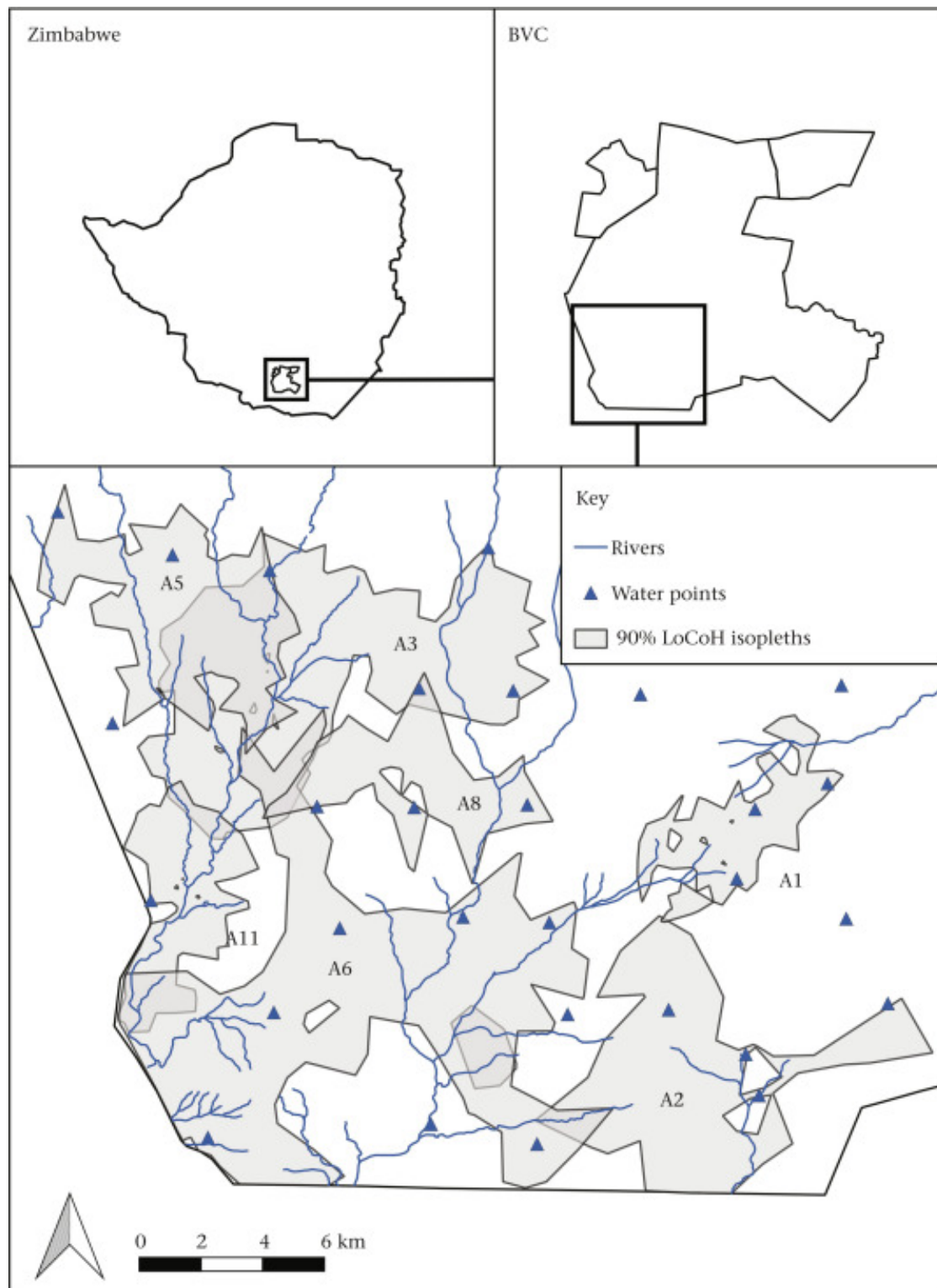


Figure 4. Map showing location of the study site in Zimbabwe and the positions of each lion home range (90% local convex hull, LoCoH, isopleths) within the study site. Note that although the home range for lion A5 appears to overlap considerably with that of lion A3, data collection for these two lions did not overlap temporally (Table A4). Lion A3 was no longer present in the area occupied by A5 at the time its biollogger was fitted.

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 1700 and 2000 and then stabilized until shortly after midnight, before peaking between 0300 and 0500. Relative frequency then steeply decreased at sunrise between 0500 and 0700 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 0300 and 0500 and further validates the accelerometer classifier.

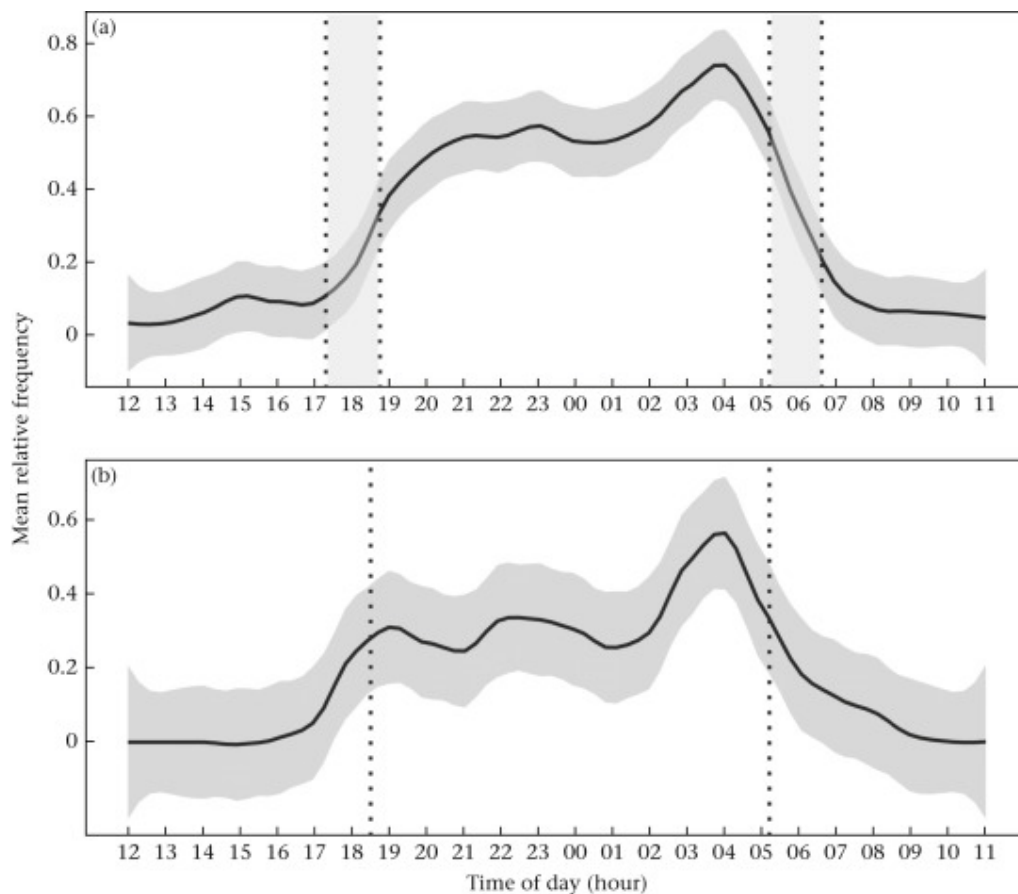


Figure 5. Diel distribution of roars obtained from (a) accelerometer biologgers and (b) acoustic biologgers. Dark grey shaded areas denote 95% confidence intervals and vertical dotted lines indicate sunset and sunrise times (with a range for each in (a) as data were collected between the summer and winter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

Effect of Atmospheric Conditions on Vocalization 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 vocalization decreasing by ca. 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 vocalization by ca. 25% (OR: 0.753; CI: 0.617–0.919) while a 1 SD (4.46 g/m³) decrease in

absolute humidity decreased the odds of vocalization by ca. 23% (OR: 0.773; CI: 0.630–0.949). When assessing the relationship between repeated vocalizations 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 repeated roars occurring decreased by ca. 44% with every 1 SD (0.733 m/s) increase in wind speed (OR: 0.559; CI: 0.416–0.751), decreased by ca. 45% for every 1 SD (4.97 °C) rise in temperature (OR: 0.551; CI: 0.389–0.781) and decreased by ca. 35% for every 1 SD (4.46 g/m³) 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 A5.

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
Vocalization Occurrence	Temp + AH + Wind	1	-1551.384	3116.8	0.00	0.789	7
	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
	Temp + AH + Wind	1	-602.188	1218.4	0.00	0.846	7
Repeated Vocalization	Temp + Wind	2	-605.246	1222.5	4.11	0.109	6
	Wind	3	-607.464	1224.9	6.54	0.032	5
	Wind + AH	4	-607.339	1226.7	8.29	0.013	6
Present (1)	Temp + AH	5	-611.921	1235.9	17.46	0.000	6
Vs	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 vocalization occurrence and repeated vocalization 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.

Effect of Location on Vocalization 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 ca. 54% lower compared to its home range core (OR: 0.459; CI: 0.289–0.730) and ca. 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 repeated vocalizations consisted of an interaction between home range location and the distance to the 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 repeated vocalizations 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 repeated roars within the periphery (OR: 1.017; CI: 0.727–1.423).

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
Vocalization Occurrence	Zone	1	-1613.795	3235.6	0.00	0.489	3
	Zone*Distance	2	-1611.234	3236.5	0.90	0.312	4
	Zone + Distance	3	-1613.696	3237.4	1.81	0.198	4
Present (1) vs Available (0)	Distance	4	-1621.445	3248.9	13.30	0.001	3
Repeated	Null	5	-1623.578	3251.2	15.56	0.000	2
Vocalization	Zone*Distance	1	-617.513	1249.1	0.00	0.987	4
	Zone + Distance	2	-624.784	1259.6	10.53	0.005	4
	Zone	3	-626.003	1260.0	10.96	0.004	3
Present (1) vs Available (0)	Distance	4	-627.418	1260.8	11.78	0.003	3
	Null	5	-629.780	1263.6	14.51	0.001	2

Response variables include vocalization occurrence and repeated vocalization occurrence and explanatory variables include location relative to home range (Zone) and proximity to closest river or water point (Distance). 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.

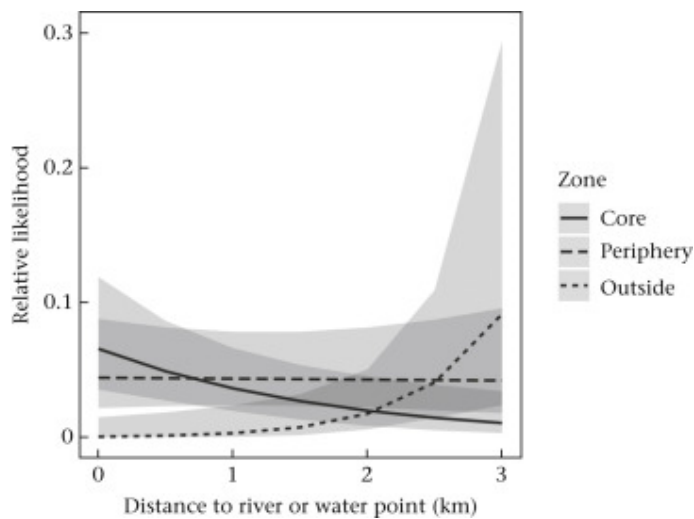


Figure 6. Relationship between relative likelihood of repeated vocalization and the interaction between location relative to home range and distance to rivers and water points. Shaded areas denote 95% confidence intervals.

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 vocalizations 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 vocalizing behaviour from accelerometry data. Although our detection method was limited to stationary behaviour and retrieved ca. 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 produced by tagged animals but the

lifetime of an acoustic biologist is considerably lower (ca. 8 days) than an accelerometer biologist (ca. 100 days) due to the higher power requirements for recording audio.

The diel distribution of roars obtained from both biologists indicated that lions vocalize 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, Garstang, Payne, et al. (1997) 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, Garstang, Lindeque, et al., 1997). Although it was not possible to determine the strength of daily temperature inversions, our results indicated that lions avoided vocalizing 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 (Larom, Garstang, Payne, et al., 1997; Wiley & Richards, 1978). As wind has multiple negative effects on signal propagation and reception, it is probable that lions actively avoid vocalizing in windy conditions as doing so would result in minimal benefit. Similar avoidance behaviour has been recorded for maned wolves, *Chrysocyon brachyurus* (Rocha, Ferreira, Venticini, Rodrigues, & Sousa-Lima, 2016) and timber wolves, *C. lupus lycaon* (Joslin, 1967). In addition to the effects of wind speed, our results also indicated significant effects of temperature and absolute humidity with lions showing an apparent preference for vocalizing in lower temperatures and higher humidity. For frequencies below 1 kHz, sound attenuation decreases with increasing humidity and increases with increasing temperature (Griffin, 1971; Harris, 1966). Low-frequency vocalizations produced in cold, humid conditions are therefore likely to travel further than those produced in warm, dry conditions. As 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 to maximize calling area.

Although atmospheric conditions are likely to be a primary factor influencing lion vocal behaviour, spatial attributes may also impact an individual's decision to vocalize. When assessing patterns of roar occurrence, we found that the primary spatial feature affecting vocalization likelihood was the animal's position relative to its home range. Despite little difference in the likelihood of roars occurring between core and peripheral areas, lions appeared to strongly avoid vocalizing outside 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 vocalizing 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 vocalized less than the territorial males (Campioni et al., 2010; Grinnell & McComb, 2001; Harrington & Mech, 1979). The locations of repeated vocalizations 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 vocalizing repeatedly while closer to rivers and water points but avoided doing so when outside their home range. Several studies have shown that rivers and water points are important features for lion prey acquisition and reproduction (Davidson et al., 2013; Mosser, Fryxell, Eberly, & Packer, 2009; Valeix et al., 2010). Lions may therefore choose to increase vocalization effort when closer to valuable territory features within their home range core to deter potential invaders. Other species such as fallow bucks, *Dama dama*, are known to increase vocalization 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 repeated vocalizations 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 vocalizations, other factors can affect an animal's decision to vocalize or remain silent. For example, some predatory animals reduce vocalization rates during foraging as prey are able to detect vocal signals and respond with antipredator behaviour (Deecke, Ford, & Slater, 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, probably 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 vocalization. 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 vocalization may reduce the risks associated with attracting potentially infanticidal males (Grinnell & McComb, 1996). We acknowledge, however, that three lionesses do 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 recognize 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 (Gilfillan et al., 2016; McComb et al., 1993). 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 vocalization behaviour is also dependent on other behavioural and social contexts, lions appear to select conditions that maximize calling area, as suggested by Larom, Garstang, Payne, et al. (1997), and also adjust vocal effort depending on their location to defend resources and minimize interpride 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 vocalizations, 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 vocalization and the influence of habitat features and environmental conditions. Furthermore, the methods employed in this study to obtain data on lion vocalizations may also be applicable to other species that are capable of carrying biologgers and that move in a unique and consistent manner while vocalizing. In future, acoustic biologgers could be improved by incorporating on-board classification of vocalizations to eliminate the requirement for continuous audio and thereby improve device lifetime.

Declaration of Interest

The authors declare no conflict of interest.

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Appendix.

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

Lion	Attributes			Roars	Data periods	
	Sex	Status	Coalition		Start	End
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 s window and a 40 s 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 s window	1
Mean maximum peak frequency	The mean maximum peak frequency from X, Y and Z axes across a 9 s window	1
Mean average peak frequency	The mean average peak frequency from X, Y and Z axes across a 9 s window	1
Mean frequency range	The mean difference between the maximum and minimum peak frequencies across a 9 s window	1

Table A3. Confusion matrix of actual behaviours (rows) versus 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. Accelerometer only data set: extracted roars for the eight male lions

Lion	Attributes			20 min time windows				Data periods	
	Sex	Status	Coalition	Roars	Stationary	Active	Total	Start	End
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

Table A5. Atmospheric conditions during the study

Condition	Mean \pm SE	Maximum	Minimum
Temperature ($^{\circ}$ C)	21.07 \pm 0.06	41.56	3.83
Absolute humidity (g/m ³)	13.23 \pm 0.05	22.05	1.00
Wind speed (m/s)	0.50 \pm 0.01	4.72	0.00

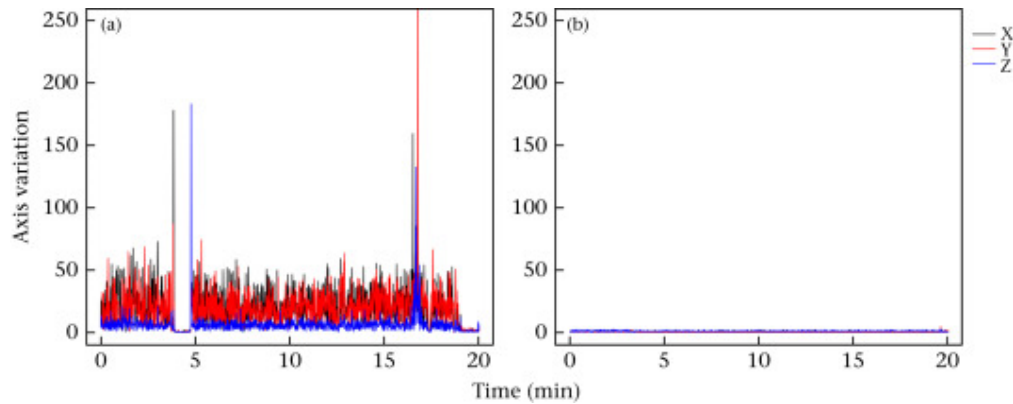


Figure A1. Three-axis accelerometer data for (a) active and (b) stationary windows. X, Y and Z refer to raw accelerometer sensor outputs and, although consistent between individuals, are not calibrated to the animal's body frame (surge, heave and sway) as this was not necessary for our analyses.

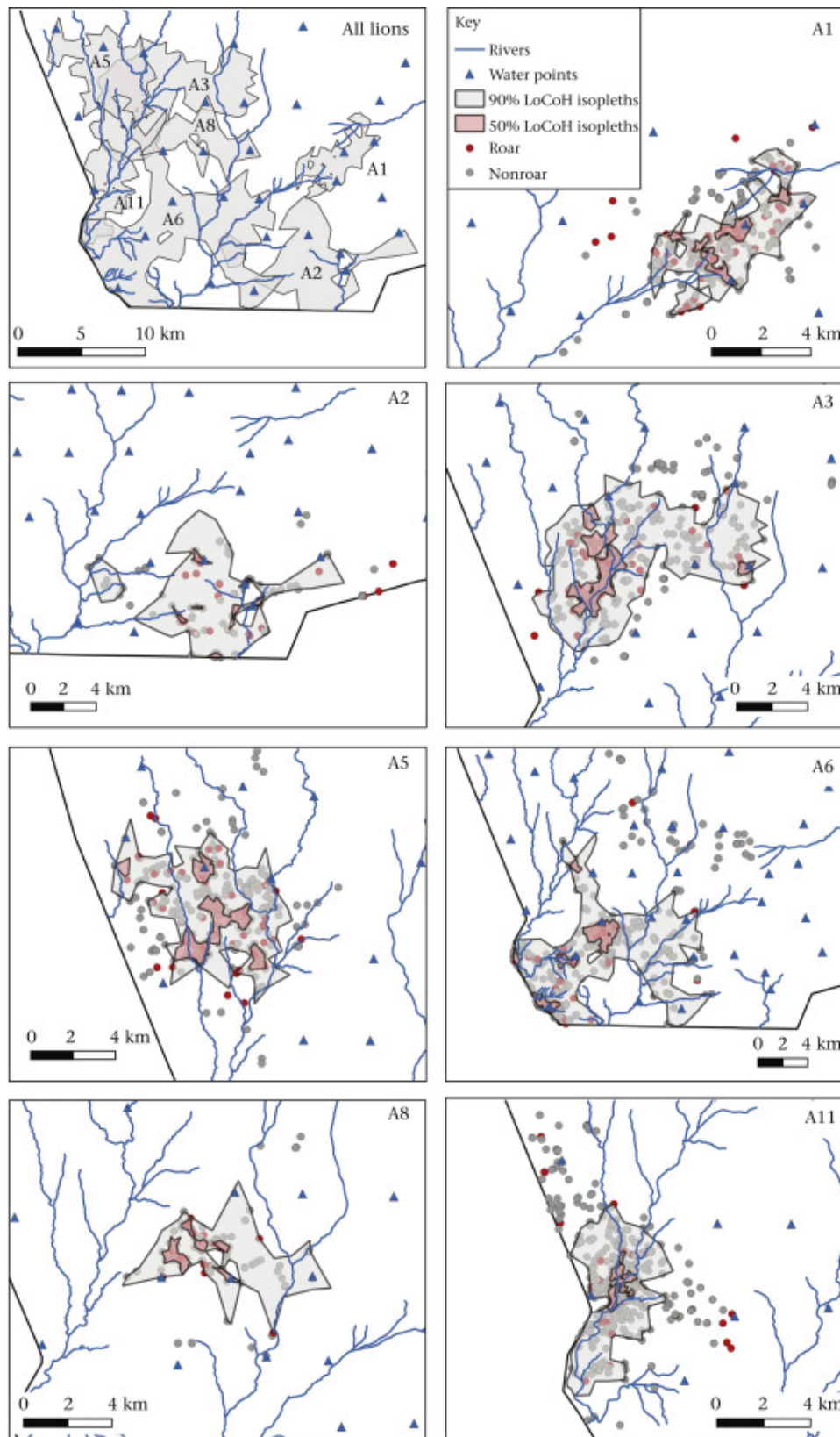


Figure A2. Maps showing 90% and 50% local convex hull, LoCoH, isopleths for each lion with stationary points (roar and nonroar).

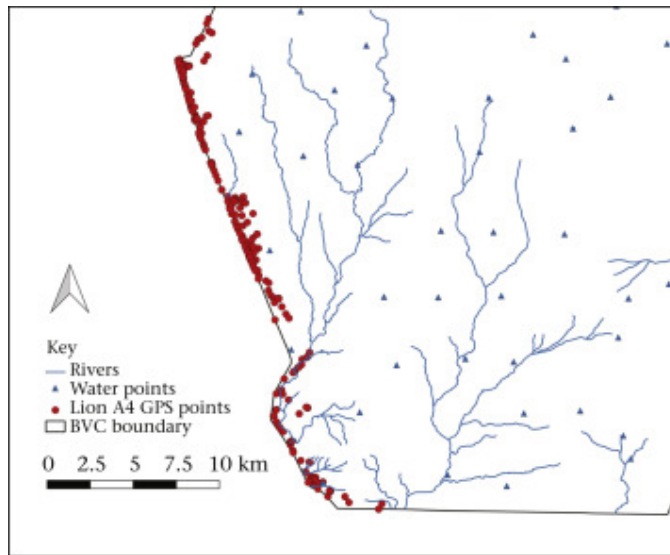


Figure A3. GPS points for lion A4 which was a vagrant during the study period and therefore not included in the analysis.