



Mastozoología Neotropical

ISSN: 0327-9383

ISSN: 1666-0536

kittlein@gmail.com

Sociedad Argentina para el Estudio de los Mamíferos
Argentina

Ferreira, Luane S; Rocha, Luciana H. S; Duarte, Danielly; Neto, Edvaldo;
Baumgarten, Júlio E; Rodrigues, Flávio H. G; Sousa-Lima, Renata S
TEMPORAL AND SPATIAL PATTERNS OF THE LONG-
RANGE CALLS OF MANED WOLVES (*Chrysocyon brachyurus*)
Mastozoología Neotropical, vol. 27, núm. 1, 2020, -Julio, pp. 81-95
Sociedad Argentina para el Estudio de los Mamíferos
Tucumán, Argentina

Disponible en: <https://www.redalyc.org/articulo.oa?id=45768065010>

- ▶ Cómo citar el artículo
- ▶ Número completo
- ▶ Más información del artículo
- ▶ Página de la revista en redalyc.org

redalyc.org

Sistema de Información Científica Redalyc

Red de Revistas Científicas de América Latina y el Caribe, España y Portugal
Proyecto académico sin fines de lucro, desarrollado bajo la iniciativa de acceso
abierto

TEMPORAL AND SPATIAL PATTERNS OF THE LONG-RANGE CALLS OF MANED WOLVES (*Chrysocyon brachyurus*)

Luane S. Ferreira¹, Luciana H. S. Rocha¹, Danielly Duarte¹, Edvaldo Neto¹, Júlio E. Baumgarten², Flávio H. G. Rodrigues³ and Renata S. Sousa-Lima¹

¹Laboratory of Bioacoustics, Universidade Federal do Rio Grande do Norte, Departamento de Fisiologia e Comportamento, Natal, Rio Grande do Norte, Brasil. [Correspondence: Luane S. Ferreira - fsluane@gmail.com]

²Applied Ecology and Conservation Lab, Departamento de Ciências Biológicas, Universidade Estadual de Santa Cruz, Ilhéus, Bahia, Brasil.

³Departamento de Biologia Geral, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brasil.

ABSTRACT. Passive acoustic monitoring can aid conservation efforts and elucidate the behavior and ecology of nocturnal/crepuscular secretive species, like the maned wolf. Here we characterize the seasonal, lunar, and nightly patterns in the long-range vocalizations (roar-barks) of free ranging maned wolves at Serra da Canastra National Park (Brazil) throughout eight months of recordings over two years with a grid of 12/13 autonomous recorders. We found an increase in vocal activity coinciding with the mating and the circa-parturition period of the species. Those peaks indicate a role of roar-barks in partner attraction and mate guarding, and in intra-familiar-group communication. Vocal activity happened throughout all recorded periods and was much higher at some sites than at others, suggesting that roar-barks also function to announce territorial ownership and defense. Maned wolves vocalize more around the waxing gibbous lunar phase, and after dusk until mid-night. Moonlight likely reduces foraging time, resulting in more time available to communicate acoustically, while vocalizations early on the onset of activity suggest a territorial announcement function. Group vocalizations did not always follow the general vocal activity pattern, which suggests that social events may require: immediate response, as territorial contests; and/or simultaneous location of animals, as mate guarding, and joint territorial defense. Based on spatial patterns, we estimate between 6 and 11 individuals contributed to the recordings.

RESUMO. Padrões espaciais e temporais dos chamados de longa distância de lobos-guará (*Chrysocyon brachyurus*). O monitoramento acústico passivo pode ajudar nos esforços para conservação e elucidar o comportamento e ecologia de espécies evasivas noturno-crepusculares, como o lobo-guará. Aqui nós caracterizamos os padrões sazonais, lunares e nictemerais nas vocalizações de longo alcance (aulidos) de lobos-guará de vida livre no Parque Nacional da Serra da Canastra (Brasil) através de oito meses de gravações ao longo de dois anos com uma rede de 12/13 gravadores autônomos. Nós descobrimos um aumento na atividade vocal coincidindo com a estação de acasalamento e o período em torno do parto. Esses picos indicam que os aulidos têm um papel na atração e guarda de parceiros e na comunicação intra grupo familiar. Houve atividade vocal durante todo o período amostral e mais em alguns locais do que em outros, sugerindo que aulidos também funcionam para anúncio e defesa territorial. Lobos-guará vocalizam mais na Lua crescente gibosa e depois do anoitecer até meia-noite. A luz da Lua provavelmente reduz o tempo de forrageio, resultando em mais tempo disponível para comunicação acústica, enquanto vocalizações logo no início da atividade sugerem uma função de anúncio territorial. Vocalizações de grupo nem sempre seguiram o padrão geral de atividade vocal, sugerindo que eventos sociais requerem: resposta imediata, como disputas territoriais; e/ou localização simultânea dos animais, como para guarda de parceiro e defesa territorial conjunta. Baseado nos padrões espaciais, nós estimamos que entre 6 e 11 animais contribuíram para as gravações.

Key words: Canidae, moon, passive acoustic, seasonal, vocal.

Palavras-chaves: acústica passiva, Canidae, lua, sazonal, vocal.

INTRODUCTION

The majority of mammals are nocturnal, crepuscular or cathemeral (Jones et al. 2009), with nocturnality assumed to be the ancestral condition (Gerkema et al. 2013). Nocturnality favors communication modalities other than vision, such as chemical and acoustic (Fox 1975). Most mammals are also solitary (Lukas & Clutton-Brock 2013), which implies that an important part of their social interaction is mediated by long-distance signals to maintain spacing among individuals (Kleiman 1972; Morton 1977).

For those reasons, passive acoustic monitoring of terrestrial mammals has great potential in aiding conservation efforts and in elucidating their behavior and ecology (Blumstein et al. 2011). In fact, many mammals are more easily heard than seen at distance (Marques et al. 2013). Besides allowing monitoring of species hard to visually follow, passive acoustic monitoring has the advantage of enabling behavioral sampling over large temporal and spatial scales (Van Parijs et al. 2009; Blumstein et al. 2011). This feature is crucial for investigating patterns in animal behavior. For instance, some species can have the breeding season tracked by increased number of vocalizations, as most cervids, e.g. the red deer (Clutton-Brock & Albon 1979; Bocci et al. 2013). Other temporal cues, such as sun and moon light are important drivers for regulating the activity of nocturnal animals (Kronfeld-Schor et al. 2013). A meta-analysis found that the majority of terrestrial mammals reduce their overall activity around full moon nights, probably as a predator avoidance strategy, for prey animals, and as an energy conserving response to lower prey availability, in predators (Prugh & Golden 2014). In solitary nocturnal/crepuscular mammals, these temporal activity patterns should be acoustically perceptible. For instance, coyotes emit more group vocalizations on new moon nights, when territorial pressure is higher and/or pack coordination for hunting large prey is required (Bender et al. 1996).

Dawn and dusk choruses are other examples of temporal animal patterns. One explanation for this increased acoustic activity is that during twilight sound propagation is more efficient (Brown & Handford 2003). This phenomenon may be particularly influential for mammals that live in open habitats and vocalize at relatively low frequencies, as elephants, lions, and wolves (Larom et al. 1997).

Diel vocalization patterns may denounce the function of the vocalizations used. For instance, dusk loud calling by nocturnal primates is normally associated with territorial/resource announcement/defense, while their dawn calling is normally associated with coordination of group reassembly to sleep (Bearder 2003).

The South American maned wolf (*Chrysocyon brachyurus*, Illiger 1815) is a good model species for acoustic monitoring. They are large (70-90 cm shoulder height, 20-30 kg weight; Silveira 1999), but very shy and cryptic, crepuscular/nocturnal canids (Melo et al. 2007). All of which, combined with the fact they are solitary and occur in low densities (1–8/100 km²; Paula et al. 2008), makes them hard to observe and visually follow in the wild (LSF personal observation; Emmons 2012).

In captivity maned wolves communicate acoustically using at least 10 types of vocalizations, mainly to maintain spacing between individuals (Brady 1981; Sábato 2011). Of those the roar-bark (Kleiman 1972) is ideal for passive acoustic monitoring, as it is the most frequent vocalization and one of the only two long-ranged types (Sábato 2011). Roar-barks are explosive, low frequency (250-1200 Hz bandwidth), generally noisy vocalizations emitted in sequences (bouts) of 5-15 roar-barks separated by 2-4 seconds (Rocha et al. 2016). Both male and female maned wolves roar-bark, although in captivity males may vocalize more (Sábato 2011). The species is hardly sexually dimorphic (males are slightly larger, Jácomo et al. 2009). Roar-barks recorded at close range have been shown to be individually and sexually discriminable (Sábato 2011). However, the acoustic features that allow for identity and for sex discrimination degrade over long distances (Ferreira 2019).

Maned wolves home ranges can be very large (mean 80 km², Jácomo et al. 2009). Individuals are thought to defend at least their core home range area as territories (Azevedo 2008) using a combination of urine, scats and roar-barks to advertise it (Rodden et al. 2004). Both sexes have been observed in agonistic encounters in the wild (Azevedo 2008; Rodrigues et al. 2013) and in captivity (Brady 1981; Sábato 2011; Balieiro & Monticelli 2019). Maned wolves from adjacent ranges have been observed exchanging roar-barks in the wild (Dietz 1984) and in captivity roar-barks of one individual often induce vocalizations

of other maned wolves, especially same-sex animals (Brady 1981; Sábato 2011).

Monogamous breeding pairs share the same home range, yet rarely meet outside the mating season (Dietz 1984; Jácomo et al. 2009). Matings can occur from March to June, being more common in April (Carvalho & Vasconcellos 1995; Rodden et al. 2004). Reports from captivity describe the rate of vocalizations increase weeks prior to estrous up to the end of the mating season (Brady 1981; Dietz 1984; Sábato 2011) as for other canids (Sillero-Zubiri et al. 2004). Female maned wolves are monoestral and stay fertile for only 5 days (Rodden et al. 2004). A report from the wild described during this period a pair stayed together, copulating often, and foraging close to each other (Rodden et al. 2004). This report showed that animals emitted roar-barks whenever the partner was out of sight (Rodden et al. 2004). During and outside the mating season researchers report that between roar-barks maned wolves may search visually for the partner (Bestelmeyer 2000), that often the partner appears after the vocalization or move towards it (Bestelmeyer 2000; Emmons 2012), and pairs have been heard roar-barking together many times (Dietz 1984; Sábato 2011; Emmons 2012; Balieiro & Monticelli 2019).

The gestation period is 65 days (Carvalho & Vasconcellos 1995) and births peak in June (Rodden et al. 2004), with a mean litter size of 3 pups in captivity (Maia & Gouveia 2002). Some males reduce their activity and stay closer to females on the days around parturition (Melo et al. 2007; Emmons 2012) and all participate in parental care (Dietz 1984; Bestelmeyer 2000; Rodrigues 2002; Jácomo et al. 2009; Emmons 2012). Pups start eating regurgitated food around 4-5 weeks (Brady & Ditton 1979), when they start leaving the den (Bestelmeyer 2000). Pups are weaned at around 15 weeks of age (Rodden et al. 2004) but might stay in their natal range as non-reproductive juveniles (Melo et al. 2007; Emmons 2012). Emmons (2012) describes high emission rates of roar-barks in the presence of pups, and vocal exchanges between all family members were common.

The diel pattern of roar-bark emission in captivity is reported to peak at dusk and dawn (Brady 1981; Balieiro & Monticelli 2019) and a previous study in the wild (4 months, 8 nights each) suggests maned wolves roar-bark more around full moon (Rocha et al. 2016). The influence of the lunar cycle on maned wolf activity is controversial. There is evidence that 2 individuals decrease movement around bright nights (Sábato et al. 2006), although a more recent study found that maned wolves' pattern of periodic space

use was not associated with it (Péron et al. 2016; N = 13). Terrestrial predators theoretically should be less active in bright moon nights (Prugh & Golden 2014), but maned wolves consume as much fruit as they prey upon small vertebrates (Rodden et al. 2004). Hence, maned wolves' activity pattern in relation to the moon cycle is not as predictable. Investigation of maned wolves' calling activity in the wild might shed light on this issue.

Our main goal was to characterize the maned wolf seasonal, lunar, and nightly long-range acoustic communication patterns in the wild. Additionally to detecting these temporal patterns of roar-bark usage, we aimed to estimate the number of animals recorded by also identifying spatial patterns in long-distance calling activity. We hypothesize that roar-barks' function include: i) mate attraction/defense (Sábato 2011); ii) territorial announcement (Kleiman 1972; Dietz 1984); and iii) maintenance of contact among family members (Emmons 2012). We also hypothesize that iv) the moon cycle influences maned wolf long-distance communication. We predict that roar-barks will be detected throughout the year with a peak in long-distance calling recorded during the mating season. We predict high vocal activity during twilight hours, peaking at dusk and an uneven spatial distribution of roar-bark detection. We predict that the number of roar-barks detected will increase near the full moon. We also hypothesize that group vocalizations (any roar-bark sequence involving more than one animal) have a distinct function than solo vocalizations and, thus, we predict that their seasonal, lunar, and nightly patterns will differ from those of solo roar-bark sequences.

MATERIAL AND METHODS

Study area

The study was conducted at Serra da Canastra National Park, Minas Gerais state, Brazil (Fig. 1). The park is mainly composed of Cerrado open savannas with a cold, dry season (April-September) and a hot, rainy season (October-March; Queirolo & Motta-Junior 2007). Maned wolf density at the park is considered high (0.08 individuals/km²; Paula et al. 2013).

Recordings

Recordings were made with autonomous recorders (SongMeter SM2+; Wildlife Acoustics, Inc., Concord, Massachusetts) coupled with a single SMX-II weatherproof microphone each (Wildlife Acoustics, Inc.). Autonomous recorders were programmed to record continuously for 12 hours each night, partitioning samples in 30 minutes files, with an +36dB gain, 8 kHz sample rate, and 16-bit wav coding. Recorders were attached to 1.4m high wooden stakes and distributed in areas where tracks, scats, and reported

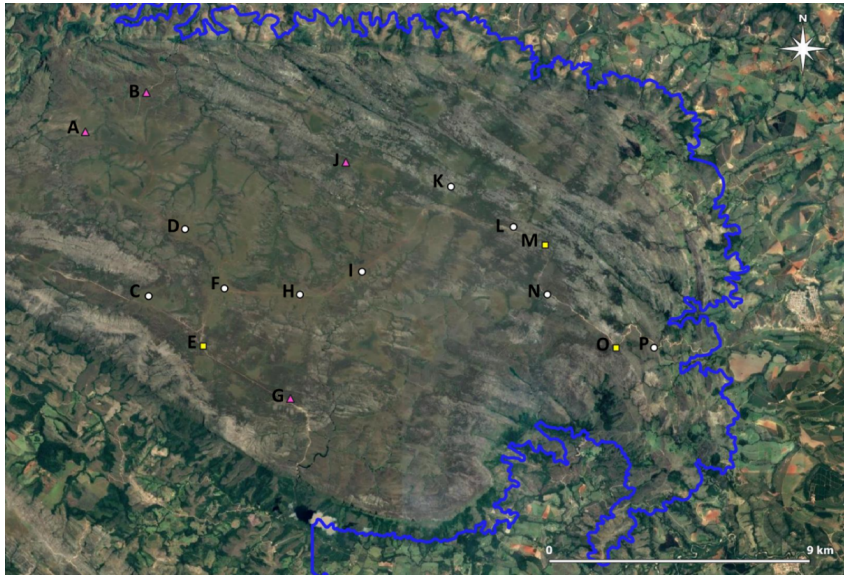


Fig. 1. Study region at the Serra da Canastra National Park, MG/Brazil. Yellow squares indicate autonomous recorder (SongMeter SM2+) sites used only in 2014, pink triangles sites used only in 2016, and white circles sites used in both years.

observations of maned wolves had been made. We aimed to sample high elevation sites (1.373 ± 56.65 m; all measures are reported in mean \pm SD, unless noted otherwise) and the broadest distribution possible, but accessibility was a major constraint.

In 2014 we deployed 12 autonomous recorders, with the linear distance between them of 2.27 km (± 0.72 km). Recorders remained active between April 05 to August 08, recording from 18h to 06h. With this time window we expected to record from the mating period to the first month of parental care. Longer deployment time was not possible due to financial constraints and the start of the wildfire risk period followed by the rainy season. The daily recording schedule was planned to maximize battery and thus deployment time. Although maned wolves may be active during the day (Paula 2016), our pilot study in the area showed an almost exclusive vocal activity during the night (UFRN Laboratory of Bioacoustics unpublished data).

In 2016, we deployed 13 autonomous recorders (8 were the same from 2014), with the linear distance between them of 3.03 km (± 0.78 km). Recorders remained active between March 09 to July 01, recording from 17h to 05h. Due to a technical problem the equipment failed to record between March 29 and April 03 2016. In 2016 we scheduled the recordings to start earlier because 2014 data suggested an increase in the amount of roar-barks before April. We also anticipated the start of the daily recording schedule because 2014 data suggested an earlier daily start in the vocal activity and very low vocal activity at the end of the night.

Audio processing and measures

During our previous study using the same recorders (Rocha et al. 2015) we manually searched the audio files for any maned wolf vocalization from those described by

Sábato (2011) and the only type found was the roar-bark. Therefore, the present study was focused on this vocalization type.

Roar-barks were detected automatically using XBAT (Extensible Bioacoustic Tool; Figueroa 2007) extension for Matlab (R2010a version, MathWorks, Inc., Natick, MA, USA. <https://www.mathworks.com>) following the methodology detailed by Rocha et al. (2015). In summary, spectrograms are scanned with a mobile cross correlation using 4 roar-barks templates. Matches above a threshold (0.21) are then manually verified for false positives and undetected roar-barks within 24 seconds of the detected ones (Fig. 2a). We used 4 different templates, including different frequency portions, and a very low threshold to guarantee that even very faint, partially masked, or uncommon frequency shaped roar-barks were detected, at the cost of increasing the number of false positives. In our test data, this methodology resulted in 100% of roar-bark sequences being detected in half the processing time. This method yielded even more detections than found by manually scanning spectrograms (93%; Rocha et al. 2015).

We defined a sequence as one or more roar-barks that were not separated by more than 10 seconds of the previous roar-bark (based in Bender et al. 1996, and preliminary observation of the roar-barks we recorded here). Intervals greater than 10 seconds ended the previous sequence and the next roar-bark was considered the start of another sequence. Sequences with a single roar-bark are possible. We verified single roar-barks' spectral characteristics to ensure they were not miss identified "single barks", the other long-range maned wolf vocalization type (Sábato 2011). For each roar-bark sequence we noted the recording site (A-P), date, absolute start time (17h to 06h), start time in relation to sunset ($\pm 0-12$ h), number of roar-barks, and

the number of animals vocalizing at the same moment (solo x group sequences, detailed below).

Sunset times used to calculate the start time in relation to sunset were extracted from <https://www.sunearthtools.com/pt/solar/sunrise-sunset-calendar.php>, which allows for GPS location specification.

The number of vocalizing animals was detected inspecting Raven's pro 1.5 spectrograms (Bioacoustics Research Program, 2014. Ithaca, NY: The Cornell Lab of Ornithology. <http://www.birds.cornell.edu/raven>. Configurations: grayscale, 50% brightness and contrast, 50% overlap, 512 points Hann window, smoothing active; Fig. 2). The presence of a second, and very rarely a third, animal could be verified by differences in the spectral shape of roar-barks, cadence, intensity, and eventual overlaps. We termed sequences as "solo vocalizations" when only one animal could be detected on the sequence (Fig. 2a). We termed sequences as "group vocalizations" when two or more animals alternated roar-barks on the same sequence (Fig. 2b). General vocal activity refers to both number of sequences and roar-barks, with no separation between solo and group vocalizations.

In some cases, the same sequence was recorded on more than one Song Meter. This was verified by temporal proximity and comparison of inter roar-bark intervals, guaranteeing that it was in fact the same sequence in two different sensors and not two animals vocalizing at the same moment. Only the most intense sequence (measured with Raven's peak power function) was counted for the analysis. The autonomous recorders' clocks were not exactly synchronized, therefore triangulation of the emitter position based on the time difference in the signal arrival at different sensors was not possible.

The total area recorded by Song Meters – in the sense of roar-bark detectability – was estimated in two ways: first a 'minimum estimate' by using half the mean distance between recorders as the radius for each recorder (we used 2014 mean recorders' distance for both year so values would be comparable); and second a 'maximum estimate' by using half the distance between the most distant recorders that ever registered the same sequence as the radius for each recorder (overlapping areas were discounted).

We mapped the vocal activity distribution over the months according to recorder sites, identifying regions with concentrated activity. This was done to verify if space and roar-bark use were associated, which would indicate a territorial or resource defense function for this vocalization. We also wanted to see if the vocal activity during the mating season occurred at the same sites as during other periods.

We also used the spatial information to estimate the number of animals recorded. We calculated the radius (5.36 km) of the mean home range (90.29 km²) from a recent study in the area (Paula 2016) and looked for roar-bark sequences on sites farther away than this value within 1-3 consecutive nights. Those sequences were considered having been emitted by different animals, or group of animals (in the cases of group vocalizations). We estimated the number of animals in two other ways: by dividing the mean number of roar-bark sequences per night by the mean number of sequences emitted per individual per night in captivity, which was obtained in another work (0.28-0.68 sequences/wolf/night; Sábado 2011); and by multiplying our estimate of total area recorded by the maned wolf density in the studied park (0.08/km²; Paula et al. 2013).

Statistical analyses

The monthly vocal activity was compared with ANOVAs followed by Tukey contrasts on R software (R Core Team 2018). For the circular data, moon phases and hours of the day, we used Rayleigh's test on Oriana software (version 4; Kovach Computing Services, Anglesey, Wales; <https://www.kovcomp.co.uk/oriana/>). In an effort to eliminate the seasonal variation as a confounding effect on the lunar variation, we standardized the vocal activity of each lunar cycle and then compared moon phases with ANOVAs.

RESULTS

Roar-bark calling general characterization

We detected a total of 13180 roar-barks distributed in 1220 sequences over the 233 nights of recording (2014 and 2016). There were fewer sequences and roar-barks in 2014 than in 2016 (503 x 717 sequences, supplementary Table S1). Few sequences were emitted by more than one animal (12%), and there were more group vocalizations in 2014 than 2016 (17% x 9%; Table S1). On five occasions the group vocalization involved three animals (3.3% of group vocalizations). All other group vocalizations involved only two animals (96.7%, 151 sequences).

Overall the mean number of roar-barks per sequence was 10.89 (\pm 8.07 SD). The sequences were shorter in 2014 than in 2016 ($t=-7.0333$, $df=912.02$, $p=0.0001$; Fig. 3). Sequences with a single roar-bark in general preceded or followed other sequences (60% within 1 minute). The longest sequence (highest number of roar-barks) of 2014 involved two animals and had 91 roar-barks, followed 10 seconds later by a 56 roar-bark sequence and right after that 6 more sequences summing 31 roar-barks. In 2016 the longest sequence had 50 roar-barks uttered by a single animal.

In 2014, 23.1% of roar-bark sequences were detected by more than one autonomous recorder, with 8% of those being detected by three or more (up to five) recorders. In 2016 we obtained the same percentage of sequences detected by more than one recorder (23.9%), but only 3.2% of those were detected by three recorders and none in four or more.

In 32 cases, group sequences were registered in more than two recorders. In all but two of those events, the time difference between the same vocalization of each individual differed by 0.5-8.8 seconds between sensors. Therefore, the relative position of each emitter suggests animals were between 86 m and 1517 m away from each other (considering a sound speed of 343 m/s). Those were the only

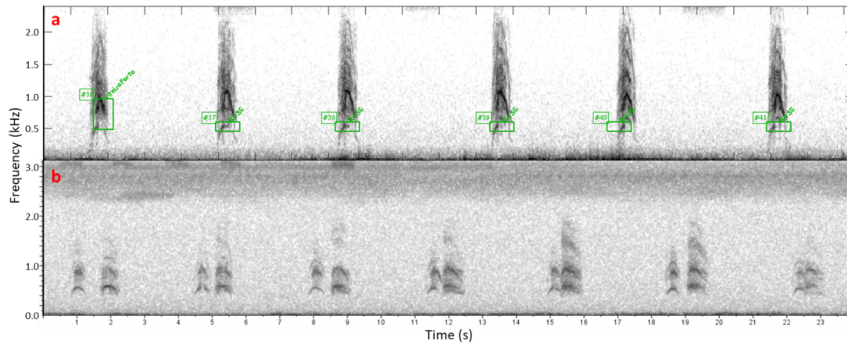


Fig. 2. Wild maned wolf roar-bark sequences recorded passively with a grid of 12/13 autonomous recorders (Song Meter SM2+) at Serra da Canastra National Park, MG/Brazil. a) solo roar-bark sequence with detection boxes from XBAT (Figueroa 2007) extension for Matlab (MathWorks, Inc.). Spectrogram parameters: 512 window size, Hann window, 100% brightness, 43% contrast, 50% overlap on an 8 kHz sampling rate wav file. b) group vocalization consisting of two animals alternating roar-barks. Spectrogram made on Raven pro 1.5 (Cornell Bioacoustics Lab, Ithaca, NY, USA), Hann window, 512 window size, 50% brightness and contrast, 50% overlap, smoothing active, on an 8 kHz sampling rate wav file.

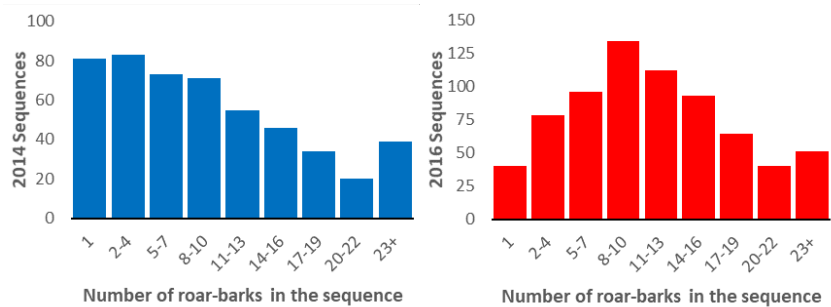


Fig. 3. Histogram of the number of roar-barks on each sequence of maned wolves’ vocalizations recorded passively with a grid of 12/13 autonomous recorders (Song Meter SM2+) at Serra da Canastra National Park, MG/Brazil. One sequence was defined by one or a bout of roar-barks not separated by more than 10 seconds.

situations in which we could estimate distances (and not from the recorder).

Seasonal variation

The seasonal fluctuation in maned wolf vocal activity was very similar in both years (Fig. 4). During March and April the vocal activity reached the maximum, dropping in mid-April and remaining low until the beginning of June. There was a second smaller increase in vocal activity in June, dropping to the previous levels again at the end of the month. There was no visible seasonal pattern on the number of roar-barks by sequence (the sequence size), neither on the percentage of group vocalizations. The number of group vocalization in general followed the vocal activity, except for a marked peak in the middle of June on 2014 (Fig. 4, bottom right).

In 2014 there was a significant monthly variation on the mean number of sequences by night ($F=4.4978$,

$df=3$, $p=0.005$; **Table 1**). There were more sequences by night in April than in other months ($p<0.05$), except for June ($p=0.0954$). The result was the same for the monthly mean number of roar-barks by night ($F=7.5311$, $df=3$, $p=0.0001$), except that there were also more roar-barks by night in April than June ($p=0.0317$). No significant differences were found for the size of the sequences ($F=0.9681$, $df=3$, $p=0.4115$), number of group vocalizations ($F=1.0522$, $df=3$, $p=0.3724$), and percentage of group vocalizations ($F=0.2698$, $df=3$, $p=0.847$) by night.

In 2016 there was also a significant monthly variation on the mean number of sequences by night ($F=5.4306$, $df=3$, $p=0.0016$; **Table 1**). There were more sequences by night in March than in other months ($p<0.05$), except for April ($p=0.0953$). The results were the same for the monthly number of roar-barks ($F=4.9486$, $df=3$, $p=0.003$). There was a

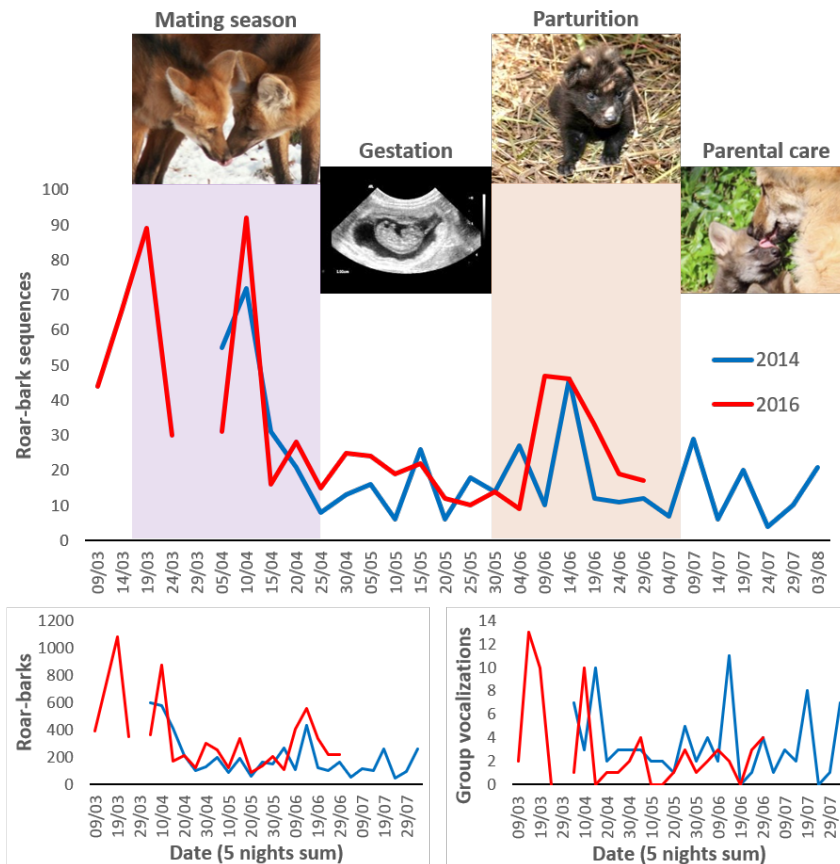


Fig. 4. Seasonal variation in the maned wolf vocal activity recorded passively with a grid of 12/13 autonomous recorders (Song Meter SM2+) at Serra da Canastra National Park, MG/Brazil. Each point is a sum of 5 nights. Photos: Daniela L. Ratzen Berger and Adriano Gambarini.

marginal trend in the monthly number of group vocalizations by night ($F=2.6757$, $df=3$, $p=0.051$), mean values were higher for March than for May ($p=0.0461$). No significant difference was found in the size of the sequences ($F=0.8459$, $df=3$, $p=0.4725$), and percentage of group vocalizations ($F=0.2068$, $df=3$, $p=0.8915$) by night.

Lunar pattern

Overall (2014 and 2016) vocal activity was concentrated on the waxing gibbous phase (Fig. 5). This was true for the number of sequences ($122.9 \pm 98.4^\circ$ [mean angle \pm Circular Standard Deviation]; $Z=63.125$, $p<0.0001$, $N=1206$), for total number of roar-barks ($124.7 \pm 99.3^\circ$; $Z=623.101$, $p<0.0001$, $N=12556$), and also for the number of group vocalizations ($114.2 \pm 111.8^\circ$; $Z=3.325$, $p=0.036$, $N=150$).

In 2014 the roar-bark sequences were significantly concentrated in the waxing gibbous phase (Fig. 5; $Z=31.225$, $p<0.0001$, $N=501$), with a mean angle of $158.9^\circ (\pm 95.5^\circ)$. The total number of roar-barks followed the same pattern ($152.6 \pm 101.1^\circ$ [waxing gibbous]; $Z=221.87$, $p<0.0001$, $N=4989$). The number of group vocalization was not significantly concentrated in any moon phase ($Z=2.336$, $p=0.097$, $N=87$).

In 2016 there were significantly more roar-bark sequences during the waxing crescent and waxing gibbous phases (Fig. 5), with a mean angle of $95.3^\circ (\pm 90.9^\circ$ [1st quarter]; $Z=57.097$, $p<0.0001$, $N=707$). The total number of roar-barks followed a similar pattern, with a slightly greater angle (mean $104.6 \pm 93.4^\circ$ [waxing gibbous]; $Z=530.156$, $p<0.0001$, $N=7578$). The number of group vocalizations was concentrated during the waxing crescent phase (mean $74.4 \pm 92.6^\circ$; $Z=530.156$, $p=0.01$, $N=63$).

Table 1

Maned wolf vocal activity recorded passively with a grid of 12/13 autonomous recorders (Song Meter SM2+) at Serra da Canastra National Park, MG/Brazil. Values reported are mean by night ± SD.

	Year	Total	March	April	May	June	July
Sequences of roar-barks	2014	4.0±5.7	-	7.4±8.7	2.8±3.9	4.0±4.0	2.6±4.6
	2016	6.6±7.1	11.5±8.6	6.8±8.9	3.8±4.0	5.9±5.0	-
Number of roar-barks	2014	39.9±49.0	-	75.0±71.3	26.1±29.5	41.3±39.6	23.6±34.0
	2016	73.8±83.4	127.6±100.5	80.0±111.2	42.0±39.1	65.0±56.5	-
Roar-barks / sequences	2014	10.8±5.7	-	12.7±5.6	10.1±5.4	10.9±4.4	10.1±7.1
	2016	11.9±4.7	11.5±3.6	12.0±4.8	13.0±5.9	10.9±3.9	-
Group vocalizations	2014	0.7±1.3	-	1.0±1.3	0.5±0.8	0.7±1.6	0.5±1.0
	2016	0.6±1.2	1.3±1.9	0.5±1.1	0.4±0.8	0.5±0.9	-
% of group vocalizations	2014	18.5±26.8	-	15.0±18.4	20.9±27.3	17.5±27.0	21.1±3.7
	2016	9.4±20.5	8.9±13.1	7.2±15.1	11.9±28.1	9.5±21.6	-

Higher vocal activity during March and April could have biased the moon concentration results, therefore we tested each moon cycle separately (supplementary **Table S2**). Of eight cycles recorded in both years, for three the number of roar-bark sequences was concentrated during the waxing gibbous phase, two during the waxing crescent, one during the waning gibbous, and two were not concentrated on any moon phase. Results were similar for the number of roar-barks, and only in March and April 2016 the number of group vocalizations was concentrated on the waxing gibbous and waxing crescent phases, respectively (**Table S2**).

After standardizing vocal activity of each lunar month, the mean values seemed to decrease from the waxing crescent (e.g. number of roar-barks: 0.732) to the new moon phase (e.g. number of roar-barks: -0.512). However, the difference was not significant for any variable (ANOVAs; number of sequences: $p=0.3714$; number of roar-barks: $p=0.0809$; group vocalizations: $p=0.4055$).

Nightly pattern

Vocal activity during the first two recording hours (17-19h) revealed a seasonal variation correlated with sunset (supplementary **Fig. S1**). During March and April, when sunset was after or close to 18h, the vocal activity was lower between 17-18h and higher between 18-19h. The inverse pattern is seen when sunset was before 18h, in May and June. In July

the sunset starts to get later again and the vocal activity between 18-19h starts to increase again. Because of this variation we decided to report the nightly vocalization pattern as time relative to sunset (**Fig. 6**).

In both years the vocal activity was concentrated in the first half of the night (**Fig. 6**). In 2014 the first hour after sunset alone comprised 18% of roar-barks, and the first 3 hours 44%. In 2016 there was a moderate vocal activity already during the hour preceding sunset, and this level doubled during the hour after. Although there was a tendency for vocal activity to decrease throughout the night, in 2016 it continued relatively high until 5-6h after sunset.

Group vocalizations did not always follow vocal activity (number of sequences and roar-barks). In 2014 there was an increase in group vocalizations after 7 hours after sunset despite the overall low vocal activity in this period. That resulted in a higher percentage of group vocalization between 7 and 12 hours after sunset in 2014 (**Fig. 6**). In 2016, while the vocal activity was high between 2 and 4 hours after sunset, the number of group vocalizations decreased markedly during this period (**Fig. 6**). On 3 occasions a peak in the vocal activity was followed by a peak in group vocalizations in the next hour (**Fig. 6**): in 2014 6-7 hours (sequences) and 7-8 hours (group vocalizations), in 2016 0-1 hours and 1-2 hours, and on 2016 3-4 hours and 4-5 hours.

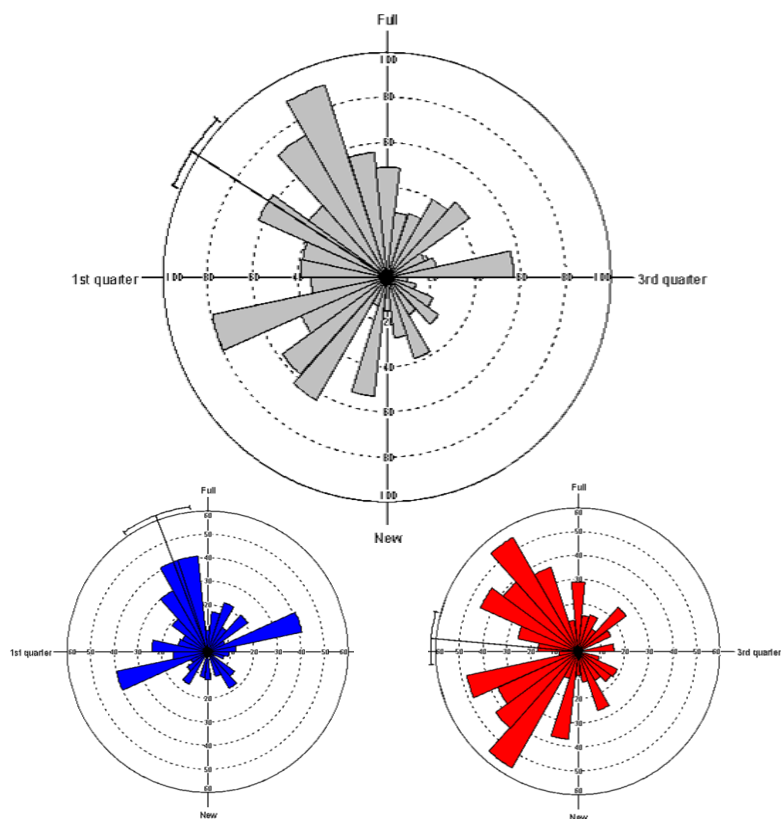


Fig. 5. Maned wolf roar-bark sequences distribution over the lunar phases (gray = total). Records were made from April to July in 2014 (blue) and from March to June in 2016 (red) with a grid of 12/13 autonomous recorders (Song Meter SM2+) at Serra da Canastra National Park, MG/Brazil. The radial line represents the mean angle and the concentric bar at the end of the line the 95% confidence interval.

The mean hour of roar bark sequence start for the two combined years was 22:02 ($\pm 03:16$ [mean hour \pm Circular Standard Deviation]). In 2014 the mean hour of sequence emission was 22:14 ($\pm 03:27$; $Z=220.97$, $p<0.0001$, $N=503$), and in 2016 21:51 ($\pm 03:05$; $Z=317.911$, $p<0.0001$, $N=614$). Some caution with the Rayleigh test is needed in this case, as the recording period of the two years differed in one hour and in both years half of the 24h cycle was not sampled (only night records). Despite this bias, the result showing a concentration of vocal activity in the first half of the night is consistent.

Spatial patterns and number of recorded animals

The mean distance between Song Meters in 2014 was 2.27 km, giving a 1.14 km radius for the total area recorded “minimum estimate”. The most distant

recorders to register the same sequence were 4.86 km away (K and N), giving a radius for the total area recorded ‘maximum estimate’ of 2.43 km. That resulted in an estimated area covered of 48.97 to 139.90 km² (minimum to maximum) for 2014 and of 53.05 to 195.25 km² for 2016.

The spatial distribution of vocal activity revealed 4 main regions with concentrated activity in 2014: C/D sites, H/J sites, K/L/M sites, and O/P sites (Fig. 7 and supplementary Fig. S2). There was high vocal activity at the sites between C/D and H/I, making it unclear if this larger area was the home range of two animals that moved around, three animals with one moving between the two areas, or four or more different animals. There were many group vocalizations in all those sites (Fig. 7).

In April 2014 there was high and widespread vocal activity. In May vocal activity is reduced and

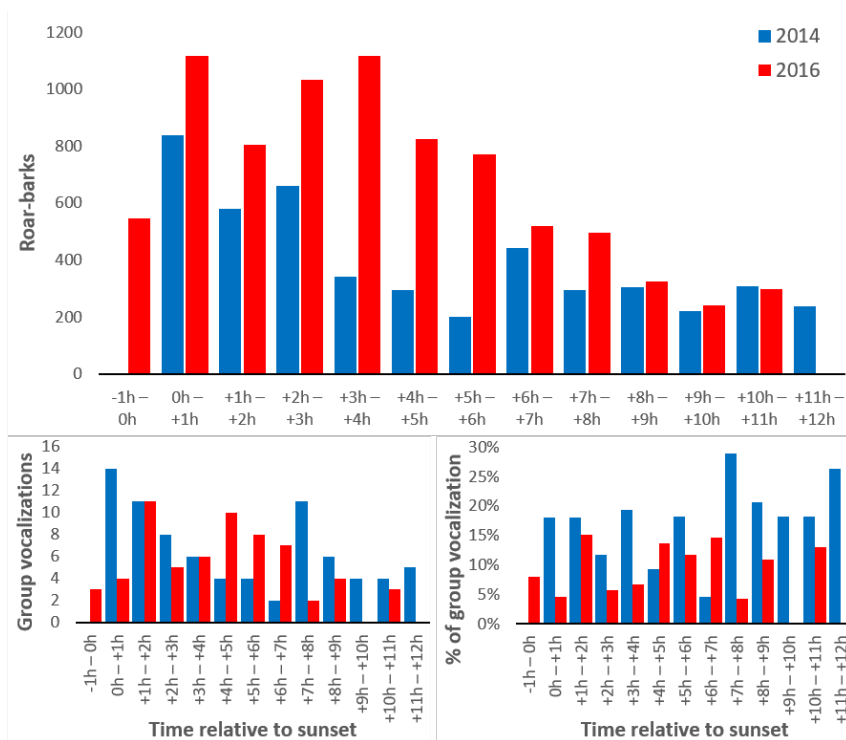


Fig. 6. Maned wolf nightly vocal activity relative to sunset. Recordings were made with a grid of 12/13 autonomous recorders (Song Meter SM2+) at Serra da Canastra National Park, MG/Brazil.

becomes more concentrated at the eastern portion of the park. In June 2014 the vocal activity increased again and was concentrated at 3 points (C, H, and O). Finally, in July 2014 the vocal activity was low and concentrated on the western and eastern sides.

Based on the vocal activity of distant (> 5.36 km) sites in consecutive 1-3 nights, we estimate between 6 and 9 different animals were recorded during 2014 (example in Fig. S2 top). Based on Sabato (2011) captivity report of mean number of sequences by animal by night (0.68 in the mating season, 0.28 outside the mating season) and our mean number of sequences by night (Table 1), our estimate would be 10.88 (April: mating) and 11.17 (May-July: non-mating) recorded animals in 2014. Based on our estimates of recorded area and the reported maned wolf density in this park (0.08/km², Paula et al. 2013) the number of animals would range from 3.92 to 11.19 individuals (minimum and maximum area estimate).

The spatial distribution of vocal activity revealed 5 not well separated regions of concentrated activity in 2016: A/B sites, C/D/F sites, H/I sites, J site, and M/N sites (Fig. 8 and supplementary Fig. S2). Compared

to 2014, the K/L/M focus seems to have shifted south and the O/P focus seems to have become much less active (only recorder P is present in 2016). It was not clear if the activity on sites J and G were from animals of nearby sites (I, K and E, H), or from different animals. Although this year had fewer group vocalizations than 2014, there were still group vocalizations in most regions (Fig. 8).

In 2016 the vocal activity on sites C, F, H, and J was high during all recorded months. This included a single night (from 17:06 to 00:24) in April with 41 sequences, totaling 510 roar-barks, involving at least two animals. From the vocal activity on this night, it seems there was an individual near site C and one or two near site J. After some hours of the J animal/s vocalizing the animal from C comes between H and J and they utter group vocalizations (only after 23:45).

Based on the vocal activity of distant sites in consecutive 1-3 nights, we estimate that between 7 and 11 different animals were recorded during 2016 (example in Fig. S2 bottom). Based on the captivity report of mean sequences by animal by night and our mean sequences by night (Table 1), our estimate would be 13.20 (March-April: mating)

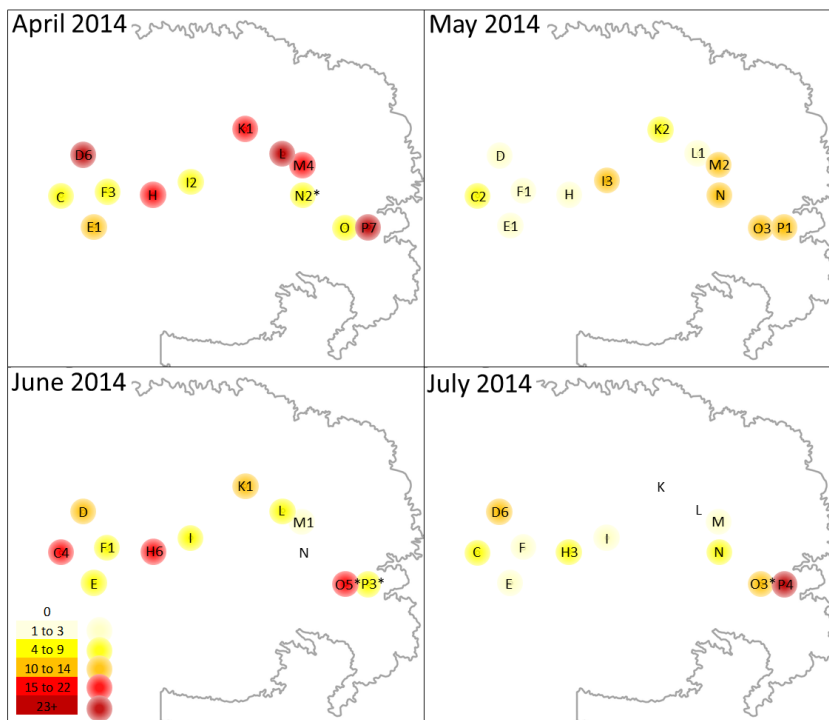


Fig. 7. Maned wolf roar-bark sequences recorded passively with 12 autonomous recorders (Song Meter SM2+) at Serra da Canastra National Park, MG/Brazil (gray contour). Circles have approximately 0.5 km radius with the center point being the recorder site. Heat colors represent the intensity of vocal activity (number of sequences). Letters indicate the site name and numbers following them on the circles indicate the amount of group vocalizations. * Indicate at least one sequence involved 3 animals (otherwise group vocalizations involve 2 animals).

and 17.28 (May-June: non-mating) recorded animals in 2016. Based on our estimates of recorded area and the reported maned wolf density in this park the number of animals would range from 4.24 to 15.62 individuals (low and maximum area estimate).

DISCUSSION

We passively recorded spontaneous long-distance calls (roar-barks) of maned wolves during eight months over two years in a protected park with the aim of elucidating the maned wolf's long-range acoustic behavior. As predicted, we found that there is an increase in vocal activity during the mating period (March and April). We also found a second smaller increase in June, coinciding with the peak period of parturition. Vocal activity was much higher at some recording sites than others and it was present in all months, suggesting that the species uses roar-barks as territory announcement and defense besides reproductive related purposes. We found that maned wolves vocalize more on moon illuminated nights,

especially during the waxing gibbous lunar phase. They concentrate their vocalizations from dusk to midnight, adjusting to the seasonal variation in sunset time. We had also predicted more roar-barks around dawn, but maned wolves vocalized very few near sunrise. Group vocalizations (detected vocal activity coming from 2 or more animals) did follow the seasonal variation of the general vocal activity, but not always the lunar or nightly vocal activity pattern, suggesting that environmental cues are less important for social interactions. Based on the solo and group vocalizations on consecutive nights, we estimate that between 6 and 11 different animals contributed to recordings.

The peak in vocal activity in March and April coincides with the reported mating season for the species (Carvalho & Vasconcellos 1995; Rodden et al. 2004). Female maned wolves stay fertile for a few days (Rodden et al. 2004). In this scenario, vocalizations could play an important role for normally solitary wolves to quickly locate their potential

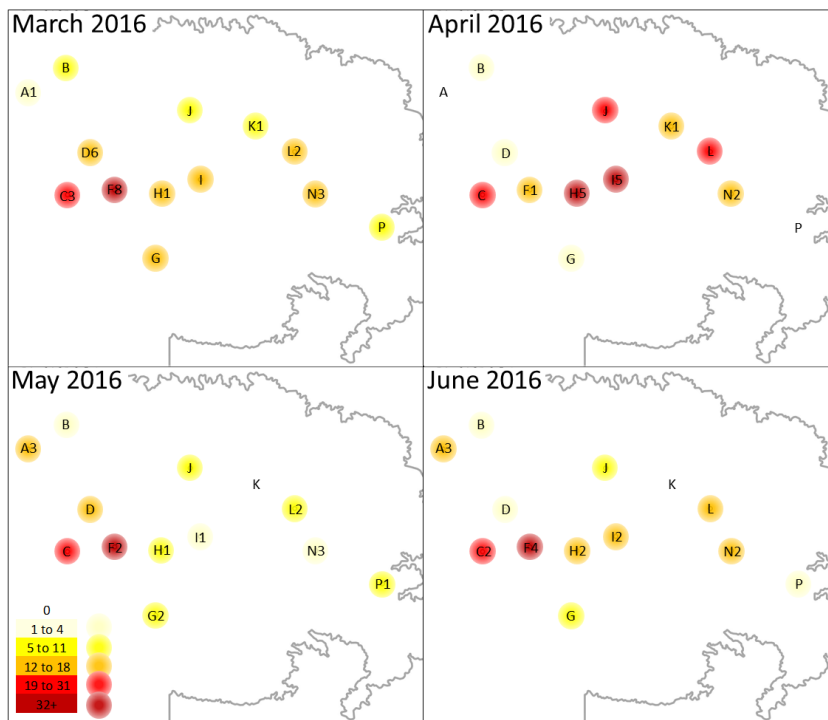


Fig. 8. Maned wolf roar-bark sequences recorded passively with 13 autonomous recorders (Song Meter SM2+) at Serra da Canastra National Park, MG/Brazil (gray contour). Circles have approximately 0.5 km radius with the center point being the recorder site. Heat colors represent the intensity of vocal activity (number of sequences). Letters indicate the site name and numbers following them indicate the amount of group vocalizations (sequences involving 2 animals).

mate or partner on an extensive home range. Our findings are in accordance with the literature and reinforce the role of roar-barks in partner attraction and possibly mate guarding.

We also found an increase in vocal activity in June, which coincides with the species' gestation period and the reported peak in births for the Serra da Canastra park (Dietz 1984; Melo et al. 2007; 2009). We have confirmation that at least one female in the area was lactating in July 2014 and 2016 (R. C. de Paula, personal communication). The use of roar-barks for intra-pair vocal communication is poorly discussed in the literature, but we speculate that, around parturition while pups are still dependent of parental care, acoustic communication may mediate family coordination, e.g. signal the location of females and their den to males, since females are known to shift pups' location often (Dietz 1984; Bestelmeyer 2000), or mediate negotiation/manipulation of parental care (Wachtmeister 2001). Another possible cause would be an increased urge for announcing and defending the territory, as other maned wolves, pumas, and

feral dogs could be a threat to the pups (Dietz 1984; Melo et al. 2009).

Despite the uncertain lunar role on the species' movement behavior (Sábato et al. 2006; Péron et al. 2016), here we found that maned wolves vocalize more on bright moon nights. Animals may be spending less energy pursuing prey while light probably helps in finding fruits (Prugh & Golden 2014). This would reduce time and energy investment in foraging and permit maned wolves to devote more to announcing territory ownership and interacting with conspecifics acoustically. Another speculation would be that light facilitates spotting trespassing conspecifics, which would induce vocalizations. This explanation is limited as the species' typical habitat has many tall grass/bushes and most of the time wolves are far enough that they would not see each other even in bright daylight (Jácomo et al. 2009). However, the moon phases when maned wolves increase their vocalization rates are those in which the first half of the night is illuminated. This portion of the night is also when we found they concentrate

their diel vocal activity (in all nights, not just bright ones), hinting on a more direct light influence.

To announce the territory ownership right at the start of the activity may be especially important as other wolves will also start moving around at this time and may decide to trespass or not (also suggested by Rocha et al. 2016). Conversely, the peak in vocal activity on the first hour of the night in 2016 was not accompanied by an increase in group vocalizations. Those interactions only appear later, sometimes one hour after a previous increase in vocal activity (Fig. 6). This suggests that the first roar-bark display is used to announce territory, before others can trespass. Later the partner can respond, or another wolf may dispute the area, creating group vocalizations. Also corroborating this idea, maned wolves only responded to playbacks between 17-19:40h (Ferreira et al. 2019).

Although peaks in the species' activity have been reported around both dusk and dawn (Paula 2016), here we registered very few roar-bark sequences preceding dawn. Like our findings on lunar vocal patterns, this highlights the importance of coupling the investigation of activity levels and vocalization levels, as they may not fluctuate together.

Our results also suggest solo and group vocalizations may have slightly different functions as they do not always follow the same temporal pattern. On several occasions, sequences appearing to come from different individuals were separated by 5-20 minutes, a time interval short enough to assume the second wolf heard the first wolf but chose not to alternate roar-barks with it. Conversely, on a playback experiment (Ferreira et al. 2019), wolves never alternated the response with the broadcasted roar-barks, even during an interactive playback (but alternated entire sequences). This suggests wolves intentionally choose to alternate roar-barks on some occasions but not on others.

We hypothesize group vocalizations happen more often when the response to a conspecific vocalization must be immediate, as territorial defense (versus passive territory ownership announcement), and/or when pair members must be located simultaneously, as for mate guard and joint territorial/offspring defense. Accordingly, group vocalizations increased in the mating period, and in 2014 near parturition, when those situations would happen more often. On the other hand, group vocalizations did not follow the lunar or diel solo vocalization pattern. Those facts indicate events of social interaction occur at any time and must be addressed independent of illumination and hour. As a final remark on this

topic, animals emitting group vocalizations were still several meters apart (>80m), that is, vocal interactions do not mean close physical interaction.

Our estimates of the number of animals that contributed to the recordings ranged from 4 to 17. On March 20, 2016, there were group vocalizations on both extremes of the park. Therefore, while we are certain that at least 4 different animals were recorded, we think 17 animals is an overestimate. Nevertheless, based on telemetry data obtained in our study area (Paula 2016) we estimate that 5 ranges could have been recorded, considering generally ranges do not change drastically (Dietz 1984; Emmons 2012). Each range would have a breeding pair, and occasionally up to 3 juveniles or adult offspring (maximum family size reported: Azevedo 2008; Emmons 2012). Additionally, transient animals could also vocalize and contribute to the maximum estimate, so it would be possible that 17 different animals were recorded.

In conclusion, maned wolves use roar-barks in many contexts, and more in the mating season, on better moonlit nights (or less on darker ones), and at the onset of their activity in the first part of the night. All of these findings support the role of this vocalization in territorial announcement and defense, partner attraction and guarding, and intra-family communication. This multi-functionality attests that maned wolves interact in complex ways and more frequently than previously thought. Additionally, we were able to identify when the mating (and possibly parturition) period was occurring in a wild population, which could be useful to plan protective measures for parks and against road-kills. We also were able to estimate the number of vocalizing individuals in a way useful to monitor populations and detect large scale fluctuations in the number of individuals at a low cost (passive acoustic monitoring). Those fluctuations would indicate serious environmental problems requiring urgent decision making and action. Also, the low estimated number of vocalizing animals highlight the fact that maned wolves occur in low densities and thus, large protected areas are needed for their conservation.

ACKNOWLEDGMENTS

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001 and was part of the Ph.D thesis of Luane S. Ferreira (Programa de Pós-graduação em Psicobiologia da Universidade Federal do Rio Grande do Norte), who received a CAPES scholarship. We thank Jean Pierre Santos and Marcello Montagno do Valle for equipment deployment and maintenance. We are grateful

for Jeff Podos, Julie Patris, Susan Parks, and Holger Klinck for comments and insights on the early version of the manuscript. We are also grateful for Roxana Zenuto and the anonymous reviewers for their time and suggestions.

LITERATURE CITED

- AZEVEDO, F. C. 2008. Área de vida e organização espacial de lobos-guará (*Chrysocyon brachyurus*) na região do Parque Nacional da Serra da Canastra, Minas Gerais, Brasil. Dissertação de mestrado. Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brasil. <https://doi.org/10.11606/d.10.2013.tde-17072014-113127>
- BALIEIRO, F., & P. F. MONTICELLI. 2019. Evidence of individual discrimination in the maned wolf long-distance extended-bark. Behavioural processes 158:219–227. <https://doi.org/10.1016/j.beproc.2018.12.004>
- BEARDER, S. K. ET AL. 2003. Species-typical patterns of infant contact, sleeping site use and social cohesion among nocturnal primates in Africa. Folia Primatologica 74:337–354. <https://doi.org/10.1159/000073318>
- BENDER, D. J., E. M. BAYNE, & R. M. BRIGHAM. 1996. Lunar condition influences coyote (*Canis latrans*) howling. American Midland Naturalist 136:413–417. <https://doi.org/10.2307/2426745>
- BESTELMEYER, S. V. 2000. Solitary, reproductive, and parental behavior of maned wolves (*Chrysocyon brachyurus*). PhD Thesis, Colorado State University, Fort Collins, U.S.A.
- BLUMSTEIN, D. T. ET AL. 2011. Acoustic monitoring in terrestrial environments using microphone arrays: applications, technological considerations and prospectus. Journal of Applied Ecology 48:758–767. <https://doi.org/10.1111/j.1365-2664.2011.01993.x>
- BOCCI, A., M. TELFORD, & P. LAIOLO. 2013. Determinants of the acoustic behaviour of red deer during breeding in a wild alpine population, and implications for species survey. Ethology Ecology and Evolution 25:52–69. <https://doi.org/10.1080/03949370.2012.705331>
- BRADY, C. A. 1981. The vocal repertoires of the bush dog (*Speothos venaticus*), crab-eating fox (*Cerdocyon thous*), and maned wolf (*Chrysocyon brachyurus*). Animal Behaviour 29:649–669. [https://doi.org/10.1016/s0003-3472\(81\)80001-2](https://doi.org/10.1016/s0003-3472(81)80001-2)
- BRADY, C. A., & M. K. DITTON. 1979. Management and breeding of Maned Wolf *C. brachyurus* at the National Zoological Park. Washington International Zoo Yearbook 19:171–176. <https://doi.org/10.1111/j.1748-1090.1979.tb00557.x>
- BROWN, T. J., & P. HANDFORD. 2003. Why birds sing at dawn: the role of consistent song transmission. Ibis 145:120–129. <https://doi.org/10.1046/j.1474-919x.2003.00130.x>
- CARVALHO, C. T. D., & L. E. VASCONCELLOS. 1995. Disease, food and reproduction of the maned wolf: *Chrysocyon brachyurus* (Illiger)(Carnivora, Canidae) in southeast Brazil. Revista Brasileira de Zoologia 12:627–640. <https://doi.org/10.5902/198050988459>
- CLUTTON-BROCK, T. H., & S. D. ALBON. 1979. The roaring of red deer and the evolution of honest advertisement. Behaviour 69:145–170. <https://doi.org/10.1163/156853979x00449>
- DIETZ, J. M. 1984. Ecology and social organization of the maned wolf (*Chrysocyon brachyurus*). Smithsonian Contribution to Zoology 392:1–51. <https://doi.org/10.5479/si.00810282.392>
- EMMONS, L. H. 2012. The maned wolves of Noel Kempff Mercado National Park. Smithsonian Contributions to Zoology 639:1–135. <https://doi.org/10.5479/si.00810282.639>
- FERREIRA, L. M. S. 2019. The call of the (Neotropical) wild-maned wolf long-range acoustic ecology. Tese de doutorado. Universidade Federal do Rio Grande do Norte, Natal, Rio Grande do Norte, Brasil. <https://doi.org/10.24873/jr.pemd.2019.05.446>
- FERREIRA, L. S., J. S. DAMO, V. SÁBATO, J. E. BAUMGARTEN, F. H. G. RODRIGUES, & R. SOUSA-LIMA. 2019. Using playbacks to monitor and investigate the behaviour of wild maned wolves. Bioacoustics 1–19. <https://doi.org/10.1080/09524622.2019.1691655>
- FIGUEROA, H. 2007. Extensible BioAcoustic Tool. XBAT R7. Cornell Bioacoustics Research Program, Ithaca, New York.
- FOX, M. W. 1975. The wild canids: their systematics, behavioral ecology and evolution. Van Nostrand Reinhold Company.
- GERKEMA, M. P., W. I. DAVIES, R. G. FOSTER, M. MENAKER, & R. A. HUT. 2013. The nocturnal bottleneck and the evolution of activity patterns in mammals. Proceedings of the Royal Society B: Biological Sciences 280:20130508. <https://doi.org/10.1098/rspb.2013.0508>
- JÁCOMO, A. T. ET AL. 2009. Home range and spatial organization of maned wolves in the Brazilian grasslands. Journal of Mammalogy 90:150–157. <https://doi.org/10.1644/07-mamm-a-380.1>
- JONES, K. E. ET AL. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90:2648–2648. <https://doi.org/10.1890/08-1494.1>
- KLEIMAN, D. G. 1972. Social behavior of the maned wolf (*Chrysocyon brachyurus*) and bush dog (*Speothos venaticus*): a study in contrast. Journal of Mammalogy 53:791–806. <https://doi.org/10.2307/1379214>
- KRONFELD-SCHOR, N. ET AL. 2013. Chronobiology by moonlight. Proceedings of the Royal Society B: Biological Sciences 280:20123088.
- LAROM, D., M. GARSTANG, K. PAYNE, R. RASPET, & M. LINDEQUE. 1997. The influence of surface atmospheric conditions on the range and area reached by animal vocalizations. Journal of experimental biology 200:421–431. <https://jeb.biologists.org/content/200/3/421.short>
- LUKAS, D., & T. H. CLUTTON-BROCK. 2013. The evolution of social monogamy in mammals. Science 341:526–530. <https://doi.org/10.1126/science.1238677>
- MAIA, O. B., & A. M. G. GOUVEIA. 2002. Birth and mortality of maned wolves *Chrysocyon brachyurus* (Illiger, 1811) in captivity. Brazilian Journal of Biology 62:25–32. <https://doi.org/10.1590/s1519-69842002000100004>
- MARQUES, T. A. ET AL. 2013. Estimating animal population density using passive acoustics. Biological Reviews 88:287–309.
- MELO, L. F. B., M. A. L. SÁBATO, E. M. VAZ MAGNI, R. J. YOUNG, & C. M. COELHO. 2007. Secret lives of maned wolves (*Chrysocyon brachyurus* Illiger 1815): as revealed by GPS tracking collars. Journal of Zoology 271:27–36. <https://doi.org/10.1111/j.1469-7998.2006.00176.x>
- MELO, L. F. B., M. A. L. SÁBATO, E. M. VAZ MAGNI, R. J. YOUNG, & C. M. COELHO. 2009. First observations of nest attendance behavior by wild maned wolves, *Chrysocyon brachyurus*. Zoo Biology: Published in affiliation with the American Zoo and Aquarium Association 28:69–74. <https://doi.org/10.1002/zoo.20213>
- MORTON, E. S. 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. The American Naturalist 111:855–869. <https://doi.org/10.1086/283219>
- PAULA, R. C., P. MEDICI, & R. G. MORATO (EDS.). 2008. Maned wolf action plan: population and habitat viability assessment. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, Centro Nacional de Informação, Tecnologias Ambientais e Editoração. <https://doi.org/10.11606/d.18.2017.tde-10022017-084955>
- PAULA, R. C., F. H. G. RODRIGUES, D. QUEIROLO, R. P. S. JORGE, F. G. LEMOS, & L. DE ALMEIDA RODRIGUES. 2013. Avaliação do risco de extinção do lobo-guará *Chrysocyon brachyurus* (Illiger, 1815) no Brasil. Biodiversidade Brasileira 1:146–159. <https://doi.org/10.22614/resc-v8-n1-1140>
- PAULA, R. C. D. 2016. Adequabilidade ambiental dos biomas brasileiros à ocorrência do lobo-guará (*Chrysocyon brachyurus*) e efeitos da composição da paisagem em sua ecologia espacial, atividade e movimentação. Tese de doutorado. Universidade

- de São Paulo, São Paulo, Brasil. <https://doi.org/10.11606/t.11.2016.tde-05072016-114911>
- PÉRON, G., C.H. FLEMING, R. C. DE PAULA, & J. M. CALABRESE. 2016. Uncovering periodic patterns of space use in animal tracking data with periodograms, including a new algorithm for the Lomb-Scargle periodogram and improved randomization tests. *Movement ecology* 4:19. <https://doi.org/10.1186/s40462-016-0084-7>
- PRUGH, L. R., & C. D. GOLDEN. 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *Journal of Animal Ecology* 83:504–514. <https://doi.org/10.1111/1365-2656.12148>
- QUEIROLO, D., & J. C. MOTTA-JUNIOR. 2007. Prey availability and diet of maned wolf in Serra da Canastra National Park, southeastern Brazil. *Acta Theriologica* 52:391–402. <https://doi.org/10.1007/bf03194237>
- R CORE TEAM. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- ROCHA, L. H., L. S. FERREIRA, B. C. PAULA, F. H. RODRIGUES, & R. S. SOUSA-LIMA. 2015. An evaluation of manual and automated methods for detecting sounds of maned wolves (*Chrysocyon brachyurus* Illiger 1815). *Bioacoustics* 24:185–198. <https://doi.org/10.1080/09524622.2015.1019361>
- ROCHA, L. H., L. S. FERREIRA, E. M. VENTICINQUE, F. H. RODRIGUES, & R. S. SOUSA-LIMA. 2016. Temporal and environmental influences on long-distance calling by free-ranging maned wolves (*Chrysocyon brachyurus*). *Journal of Mammalogy* 98:302–311. <https://doi.org/10.1093/jmammal/gyw171>
- RODDEN, M., F. RODRIGUES, & S. BESTELMEYER. 2004. Maned wolf (*Chrysocyon brachyurus*). Canids: Foxes, Wolves, Jackals and Dogs, Status Survey and Conservation Action Plan (C. Sillero-Zubiri, M. Hoffmann, & D. W. MacDonald, eds.). 1st ed. IUCN/SSC Canid Specialist Group, Cambridge, United Kingdom 38–43. <https://doi.org/10.2307/j.ctv39x6vm.3>
- RODRIGUES, F. H. G. 2002. Biologia e conservação do lobo-guará na Estação Ecológica de Águas Emendadas, DF. Tese de doutorado. Universidade Estadual de Campinas, Campinas, Brasil. <https://doi.org/10.26512/2015.06.d.19520>
- RODRIGUES F. H. G., A. L. J. DESBIEZ, R. L. S. C. GRANDO, A. C. R. LACERDA, A. HASS, & W. R. SILVA. 2013. Conservation of a population of maned wolves, *Chrysocyon brachyurus*, on a small reserve in the Cerrado. Ecology and conservation of the maned wolf: multidisciplinary perspectives (A. G. Consorte-McCrea, & E. F. Santos, eds.). 1st ed. Boca Raton (FL): CRC Press 131–151. <https://doi.org/10.1201/b15607-14>
- SÁBATO, M. A. L., L. F. B. MELO, E. M. V. MAGNI, R. J. YOUNG, & C. M. COELHO. 2006. A note on the effect of the full moon on the activity of wild maned wolves, *Chrysocyon brachyurus*. *Behavioural processes* 73:228–230. <https://doi.org/10.1016/j.beproc.2006.05.012>
- SÁBATO, V. 2011. Aspectos do comportamento acústico do lobo-guará *Chrysocyon brachyurus* (Illiger 1815). Dissertação de mestrado. Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil. <https://doi.org/10.14393/19834071.2016.36163>
- SILLERO-ZUBIRI, C., M. HOFFMANN., & D. W. MACDONALD (EDS.). 2004. Canids: foxes, wolves, jackals, and dogs: status survey and conservation action plan. 1st ed. IUCN/SSC Canid Specialist Group, Cambridge, United Kingdom. <https://doi.org/10.2307/j.ctv39x6vm.3>
- SILVEIRA L. 1999. Ecologia e conservação da comunidade de carnívoros do Parque Nacional das Emas, GO. Dissertação de mestrado. Universidade Federal de Goiás, Goiânia, Goiás, Brazil. [https://doi.org/10.17138/tgft\(2\)207-213](https://doi.org/10.17138/tgft(2)207-213)
- VAN PARIJS, S. M. ET AL. 2009. Management and research applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales. *Marine Ecology Progress Series* 395:21–36. <https://doi.org/10.3354/meps08123>
- WACHTMEISTER, C. A. 2001. Display in monogamous pairs: a review of empirical data and evolutionary explanations. *Animal Behaviour* 61:861–868. <https://doi.org/10.1006/anbe.2001.1684>

ONLINE SUPPLEMENTARY MATERIAL

Supplement 1

Table S1. Total and monthly summary of maned wolf's vocal activity in 2014 and 2016.

Table S2. Concentration of maned wolf vocal activity on each of the eight moon cycles recorded. Mean moon phase, mean angle \pm circular standard deviation, and Rayleigh test statistics are reported.

Fig. S1. Maned Wolf roar-barks registered between 17-19h showing the vocal activity following the seasonal variation in sunset.

Fig. S2. Examples of nightly maned wolf vocal activity recorded and their spatial distribution across the autonomous recorders' sites.