Communication in an Endangered Canid: Towards a Better Understanding of the Vocalisation Repertoire of African wild dogs (*Lycaon pictus*)



Kate Malone
Minor Research Project
Environmental Biology
Behavioural Ecology track
Solis ID: 6885225

Supervisor, first examiner: **Assoc. Prof. Dr. Damien Paris**
Second examiner: **Assistant Prof. Dr. Anne Marijke Schel**
Additional Supervisors: **Pia Riddell, Assoc. Prof. Dr. Monique Paris**

Acknowledgements

This work would not have been possible without the involvement and investment of several people. To Damien, Monique, and Pia: thank you for taking a chance on me. I was a stranger on the other end of an email, determined to study African wild dogs and you opened the door for me to explore the wonderful, frustrating, important, and complicated world of wildlife conservation in South Africa. It couldn't have happened without your tireless efforts, and I sincerely appreciate everything.

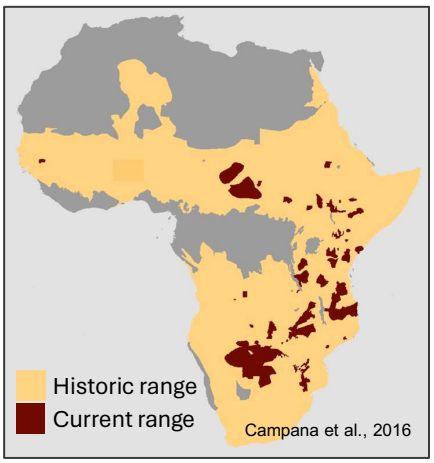
Thank you to the institutes and organisations that facilitated our access to their animals, without which this work also could not have happened; Bothongo Rhino and Lion Reserve, Johannesburg Zoo, and especially to Reilly Mooney and Clinton Venter of the Waterberg Wild Dog Initiative; the heroes that the last remaining free-roaming wild dogs in South Africa need and deserve.

To Anne Marijke, thank you for your calm and measured guidance and particularly for the discussions on social complexity and vocalisation, and help with presenting confidently before I felt ready to share my work.

And of course, to the dogs themselves, especially to the memory of the six TOOG Waterberg dogs killed in the months following data collection. Thank you for being wonderful, if at times frustrating, study animals and members of the most fascinating and wonderful species anywhere on Earth- though I may be a little biased there.

A particular thanks to Pia for many, many things over the past year but especially for a breath-taking, bucket-list-ticking trip to Kruger National Park which I am so grateful for. And finally, thank you to the people whose hospitality and kindness made South Africa a welcoming place: Alex, Manda, Andre, JJ, and Chipo in Pretoria, and Leonard and Nicky in the Waterberg.

Layman's Summary



African wild dogs are an endangered canine species that lives primarily in Eastern and Southern Africa. In the past, over 500,000 wild dogs lived across thirty-five countries in sub-Saharan Africa, however the current population is just below 7,000 dogs in fourteen countries. Their survival is threatened by several factors including predation by lions, diseases such as rabies and canine distemper, and human-derived threats including road collisions and human persecution, especially by farmers who may see them as a threat to their livelihood.

African wild dogs live in packs, usually with approximately seven to fifteen members, with one alpha male and one alpha female. There are strong social bonds within packs which are important for success and survival, because wild dogs care for each other more than most wild animals. They share meat when they make a kill, and they also chase away threats such as hyenas and lions together. The whole pack contributes to raising puppies, and they feed old or injured pack members. Since their social bonds are important, wild dogs must be able to communicate with each other well.

Vocalisations are used for a wide range of purposes across the animal kingdom, from young animals begging for food, to older animals defending territory and mating. In African wild dogs, vocalisations can be studied to try to discover how they communicate with each other and how they co-ordinate group behaviours. It is also important to know if there are differences in the way that different groups 'speak' to each other, in case it is necessary to combine packs. Such as, do African wild dogs in a zoo or in a wildlife park 'speak' differently than those in the wild? Are there situations, such as when they are eating, that they use specific vocalisations? To study this, we recorded the vocalisations and behaviours of three wild dog packs. One pack was housed in a traditional zoo enclosure, one in a larger open-range enclosure, and the last was a free-roaming wild pack being monitored for conservation purposes. Their calls were recorded using a powerful microphone and their behaviour was filmed using a video camera, which allowed us to investigate the relationship between specific vocalisations and behaviours.

We found some differences in the way that each of the packs vocalized and behaved. Both captive packs used showed dominance when keepers were inside their enclosures. While eating, the open-range pack vocalized much more than the other packs. This may have been because they were fed with several pieces of meat and therefore the dominant pack members tried to control all the pieces, while the wild pack ate from one piece, allowing the alphas to have complete control over the food. Alternatively, there may be social explanations behind the differences. The zoo pack vocalized less than other packs and were also the smallest pack, suggesting that vocalisations are mostly social. These findings will allow us to determine more easily whether a pack has strong social bonds by listening to their vocalisations. This is especially important when a pack will be released from captivity into the wild, where survival depends on social bonds. By improving our understanding of their vocalisations and behaviour, we aim to continue conserving this charismatic African mammal.

Abstract

African wild dogs (*Lycaon pictus*) are an endangered, highly social canid facing population decline due to a mixture of ecological factors and human-imposed threats. In South Africa, the remaining animals are managed as a metapopulation consisting of several packs in Kruger National Park, several in fenced reserves, and only two free-roaming packs, while most other packs live in captivity in zoos and wildlife parks. Wild dogs show complex social behaviour characterised by co-operative breeding, collective hunting, and communal care of young, old and injured pack members. This complex sociality is accompanied by the most complex vocal repertoire of any known canid, which consists of over twenty distinct vocalisation types, but remains under-studied. Here we use recordings of vocalisations and behaviours to compare vocalisation use across different social contexts and across three packs; one wild, free-roaming, one zoo-housed, and one housed in a larger, fenced open-range enclosure. We found stronger associations between vocalisations and behaviours relating to agonistic interactions, particularly dominance and aggression. The open-range zoo pack vocalised at a higher rate than the traditional zoo or wild packs during feeding, which is a potentially competitive context that wild dogs typically mediate using submission and appeasement. The traditional zoo-housed pack had the lowest rate of vocalisation and was also the smallest pack, highlighting the social nature of much of the wild dog vocal repertoire. Social cohesion within packs is important to the success of wild dog management, and an improved understanding of vocalisations can contribute to more effective management, for example monitoring the differences between natural hierarchy establishment and problematic aggression. These findings contribute to a greater understanding of African wild dog vocal and social complexity, which feeds into the larger goal of informing evidence-based conservation management initiatives for the species.

Introduction

African wild dogs (hereafter wild dogs; *Lycaon pictus*) are an endangered, highly social carnivore that have disappeared from much of their historic range. They are threatened primarily by human activity including snaring, shooting, vehicle collisions, and diseases transmitted by domestic dogs (Woodroffe et al., 2007; Prager et al., 2012). Additionally, elements of the species' ecology make them vulnerable to habitat loss, such as their large home ranges and naturally low population densities driven by the risks of predation and kleptoparasitism by other large carnivores (Creel & Creel, 1998). These factors also make them particularly prone to conflict with humans, and increasingly result in fragmented habitats that are unable to support or protect viable populations (Creel & Creel, 1996; Mills & Gorman, 1997). Wild dogs are now found in less than 10% of their historic range (Woodroffe & Sillero-Zubini, 2011; Rabaiotti et al., 2021) so it is imperative that effective management strategies are put in place for their ongoing survival.

While the simplest method of conserving wild populations is protecting large, undisturbed swathes of land to allow for proper dispersal patterns, sufficient prey density, and protection from human persecution, this is not a practically or politically viable solution. There thus remains a need for more intensive management initiatives (Woodroffe & Ginsberg, 1999).

Range expansion projects, for example, aim to increase the suitable habitat available for populations that could ultimately disperse naturally or be reintroduced (Whittington-Jones et al., 2014). Management strategies with an emphasis on reintroduction have historically shown limited success; the origin of the animals impacts survivorship post-release, with wild-caught faring better then captive-born individuals across carnivore species (Jule et al., 2008). Captive breeding programmes are another tool in the conservation kit; these populations offer a stock of genetic material that may be lacking in the wild, and may represent a more genetically diverse effective population than can be found in the wild (Witzenberger & Hochkirch, 2011). This can act as a backup to supplement small populations vulnerable to genetic drift or catastrophic environmental events (Leus, 2011), whether by direct reintroduction, as a genetic insurance population, or by boosting genetic diversity through artificial insemination (Paris et al., 2024). Translocation and artificial pack formation are two strategies currently used across fourteen highly fragmented populations that make up the managed metapopulation in South Africa (Davies-Mostert et al., 2009; Nicholson et al., 2020). Artificial pack formation aims to boost pack numbers and post-reintroduction success by allowing the new packmates to bond prior to release, increasing the likelihood of remaining together and persisting long-term (Gusset et al., 2006, 2008).

The success of these management strategies depends on understanding the underlying behaviours that drive social cohesion in this species. Wild dogs hunt collectively, and cooperate to raise young, care for old or injured pack members, and guard territory (Creel & Creel, 2002). This high degree of reliance on cooperation and collective behaviours means that social cohesion, and by extension, effective teamwork, impact survival and reproductive success (Marneweck et al., 2019). Translocation of captive-raised wild dog packs typically results in poor survival post-reintroduction; however this effect can be mitigated by socially integrating captive-raised with wild-caught individuals. These packs fare considerably better post-release than all-captive groups (Woodroffe et al., 1997; Gusset et al., 2008), which have fewer vital survival skills than wild groups. Social integration of wild and captive groups pre-release allows for a cohesive pack to form (Somers & Gusset, 2009) with the skills to survive in the wild. Social factors such as sex ratio, group size, odour familiarity, rates of long-distance contact calling, and methods of separation and reintroduction are known to impact the success of pack formation attempts (Gusset et al., 2006; Potgieter et al., 2015; Marneweck et al., 2019). This suggests an important role for both behaviours and vocalisations in social cohesion, warranting further research into the vocal repertoire of wild dogs as potentially important indicators of social interaction.

Vocalisations are a key part of the behavioural repertoire of social animals, enabling communication and facilitating social relationships and organisation (Bartholomew & Collias, 1962; Whitehead et al., 2012). Vocalisations have been linked to a range of functions across taxa including co-ordinating group movement (sifakas; Trillmich et al., 2004), indicating sexual competitive ability (baboons; Fischer et al., 2004), threatening competitors (dolphins; King et al., 2019), attracting mates (barn swallows; Hasegawa & Arai, 2016), and to enabling social partner and offspring recognition (bats; Boughman & Wilkinson, 1998; mink; Malmkvist, 2019). Several social mammals show threat-specific, apparently functionally referential, alarm calls that communicate the source or degree of potential danger to group

mates (vervet monkeys; Seyfarth at al., 1980; marmots; Blumstein & Armitage 1997; capuchin monkeys; Wheeler 2010; meerkats; Rauber & Manser 2017).

Across the Canidae family, vocalisations are thought to reflect context-specific signals and mediate social behaviour (Yin & McCowan 2004; Siniscalchi et al. 2018). In the wild, vocalisations also function to maintain territory and hierarchy, signal and drive away threats, facilitate individual recognition, locate separated pack members, and communicate social bonds, among other functions (Lehner 1978; Harrington & Mech 1979, 1983; Robbins 2000; Mitchell et al. 2006; Clarke & Déaux 2013; Kershenbaum et al. 2016). Social and vocal behaviours are closely linked, for example relationship quality affects howling behaviour in timber wolves, with separation from higher-ranked individuals or affiliative partners prompting more howling (Mazzini et al., 2013). Similarly, the familiarity of the howler and the properties of the howl both affect the behavioural response of Iberian wolves (Palacios et al., 2015). Several canid species are known to encode group- or individual-specific information in their vocalisations including coyotes (Hallberg, 2007), dingoes (Déaux & Clarke, 2013), timber wolves (Tooze et al., 1990) and wild dogs (Hartwig, 2005). Given the importance of vocalisations to social canids, a better understanding of vocal behaviour could shed further light on their social behaviour (Kershenbaum et al., 2016) and by extension on social cohesion.

Wild dogs show among the highest number of distinct vocalisations of any canid (Déaux & Clarke, 2013), with at least 11 vocal classes and 18 subclasses identified (Table 1; Robbins 2000; Walker et al. 2017). This includes seven vocalisations thought to be unique to wild dogs: twitters, begging cries, gurgles, buzz moans, rumbles, howl barks, and hoo calls. These calls can be context-specific and reflect wild dogs' social lifestyles; for example, spar twitters may be used as affiliative vocalisations, or antagonistically during high-arousal play (Robbins, 2000). Hoo calls carry across considerable distances and are thought to help locate separated pack members (Estes & Goddard, 1967) or seek groups of the opposite sex during dispersal (Frame et al., 1979; Robbins, 2000). Vocalisations can cause a cascade of behavioural change within a pack such as hoo calls bringing the entire pack to their feet when a member is missing (Estes & Goddard, 1967). Pups and other adults use yelps and muzzle-to-muzzle contact to induce regurgitation of meat from adults after a hunt (Robbins & McCreery, 2003), and sneeze-like exhalations from high ranking individuals increase the likelihood of collective movement (Walker et al., 2017). Despite this, research into wild dog vocalisations remains limited. While Robbins (2000) and Robbins and McCreery (2003) worked towards characterising the entire vocal repertoire of wild dog adults and pups, these observations were made primarily when the animals were at rest, limiting the contexts for which these conclusions are applicable. There remains therefore a lack of variation in the contexts in which wild dog vocalisations have been studied.

Feeding behaviour in wild dogs proceeds differently to other species of large carnivore, and again highlights the sociality central to wild dog society. Priority of access to carcasses runs generally from youngest to oldest; starting with pups, followed by the alpha pair, then yearlings, next youngest and so on (Jordan et al., 2022). This queue is thought to be socially and behaviourally reinforced by the alpha pair (McNutt, 1996), as opposed to many large carnivore species in which feeding competition may involve high levels of aggression, with dominant

individuals controlling or ‘owning’ the carcass (Packer et al., 2001). In wild dogs, however, aggression is minimised during feeding by the frequent use of appeasement behaviours that appear to derive from infantile begging (Estes & Goddard, 1967), especially during instances of direct competition in which the use of submissive behaviours seems to hold aggression at bay (Kühme, 1965). An improved understanding of the use of vocalisations associated with feeding behaviour could therefore shed further light on the feeding process and the social cohesion underpinning its counterintuitively non-competitive nature.

As many of the wild dog packs in South Africa reside in captivity, potential differences between wild and captive populations’ use of vocalisations should be considered. Captivity, whether temporary or permanent, is known to increase stress hormone levels in wild dogs (Crossey et al., 2020). As wild dogs are naturally wide-ranging, they are likely to experience captivity more negatively than other species, especially as their natural foraging patterns are also disrupted in captivity (Clubb & Mason, 2003). Together, these suggest that captive wild dog individuals and packs may experience higher levels of stress than their wild counterparts, so a comparison of understudied elements of behaviour such as vocalisation use between these housing types may continue to illustrate these differences.

The existential threats facing wild dogs, particularly those originating from humans, are unlikely to recede in the near future. With this in mind, further loss of wild dog numbers should be avoided, and the success of conservation management events should be prioritised to boost population numbers and avoid further loss of genetic diversity (Paris et al., 2024). These may rely on successful social bonding of unrelated wild dogs, so contributions towards understanding social cohesion and its constituent behavioural and vocal parts is valuable towards wild dog conservation.

We therefore aim to:

(i) investigate the vocalisation repertoire of wild dogs and improve our understanding of the associations between vocalisations and behaviours.
(ii) investigate the associations between vocalisations and behaviour in socially relevant contexts including feeding, rest, and the presence of human keepers.
(iii) investigate the associations between vocalisations and behaviour between three differently housed packs.

We expect to find differences between the use of vocalisations in wild and captive dogs originating from the insurmountable social constraints present in captivity. Not only could this be valuable to monitor the integrity of existing established packs in permanent captivity, but it may also prove an informative indicator of bonding success during translocation and artificial pack formation initiatives in temporary bomas in the wild. Moreover, our research may help to uncover pack-specific differences in communication, which can inform management decisions at a pack-specific level, rather than species-specific, one-size-fits-all level.

Methods

Overview

Data was collected between March and July 2023 using 3 packs (n = 32) of wild dogs located in Gauteng and Limpopo provinces in north-eastern South Africa (Fig. 1). All packs were mixed sex, with 9 female and 23 male adults in total and each pack was housed and fed differently (Table 1).

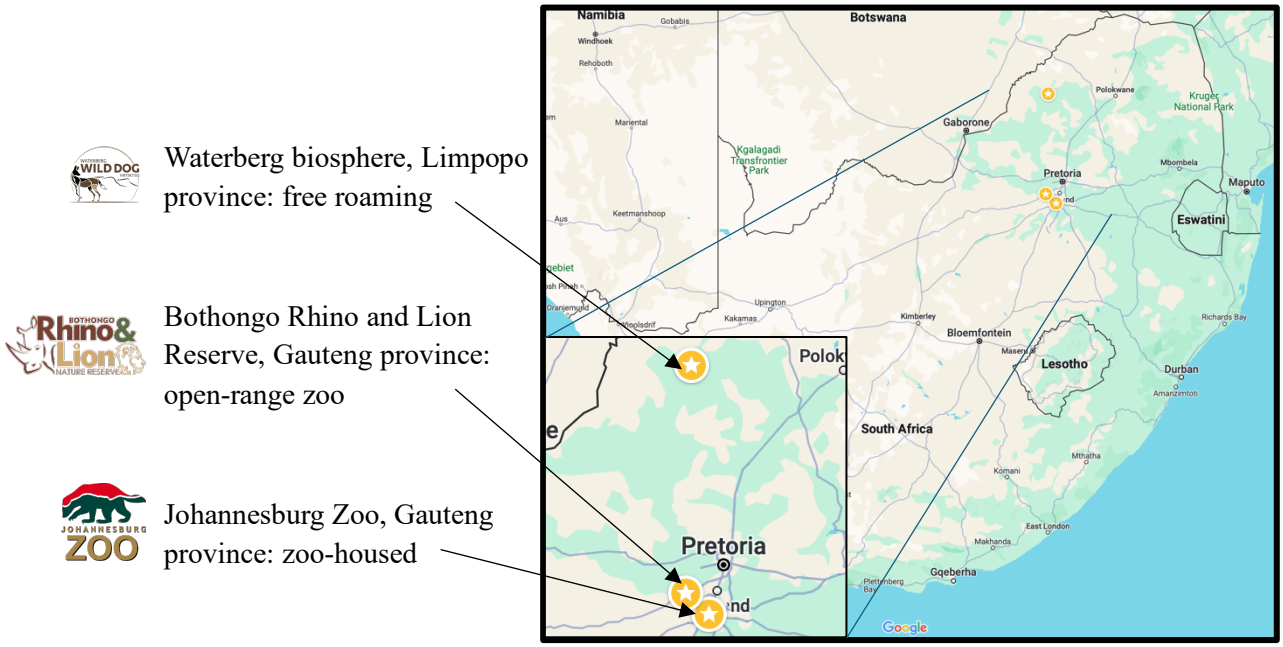


Figure 1: Location of the 3 study packs in Limpopo and Gauteng Provinces of north-eastern South Africa.

Table 1: African wild dog pack identity, location, demographics, husbandry, and length of video and audio recorded per pack.

Pack	Location	Pack size (♂:♀)	Age (years)	Housing	Feeding	Rec. time (h:m)
Bothongo (BOT)	Bothongo Rhino and Lion Reserve	15 (10:5)	4-12	Open-range zoo enclosure ~15 acres	5x per week	9:46
Joburg (JOB)	Johannesburg Zoo	2 (1:1)	12+	Traditional zoo enclosures, ~2350 & 1350 m^2	Daily	14:39
Waterberg TOOG (WAT)	Waterberg Biosphere	10-15* (12:3)	1-12**	Free roaming, wild	Daily, supplemental	3:32

* 5 dogs dispersed in the middle of data collection but returned before the end of data collection
** Puppies were also present in this pack but were never directly observed

The Joburg pack consisted of 2 individuals housed in separate but adjacent traditional zoo enclosures. The Bothongo pack of 15 dogs were housed in a large drive-through style open-range enclosure adjacent to two lion enclosures. The Waterberg pack is one of two remaining

free-roaming wild packs in South Africa managed by the Waterberg Wild Dog Initiative. This pack receives supplemental feeding once per day during denning season to lessen the impact of predation on nearby farms; this permits daily observation of those dogs during feeding.

Recording

Video was recorded primarily using a Sony FDR-AX100E 4K hand-held digital video camera and where necessary supplemented with a Canon EOS Rebel T3i digital SLR camera. Audio was recorded using a Rhodes NTG-2 directional condenser microphone connected to a Zoom H8 Handy Recorder.

Video and audio were recorded in 15-minute increments. For the two captive packs, Bothongo and Joburg, recording amounted to approximately 3 hours per day: 1.5-2 hours in the morning and 1-1.5 hours in the afternoon. For the wild pack, Waterberg, audio and video of animals was recorded opportunistically whenever dogs were present. This resulted in longer observation times for both captive packs than the wild pack (Table 1) as the dogs were always present. By contrast, the wild pack was only visible just before, during and immediately after their daily supplementary feeding and were not pursued outside of this time.

The Joburg pack was recorded from the visitor-accessible viewing point directly in front of their enclosure, while the Bothongo pack was recorded from a vehicle within their enclosure along visitor-accessible or permitted management drive routes. The Waterberg pack was recorded from a Waterberg Wild Dog Initiative (WWDI) open-top safari vehicle, to which the dogs were habituated, parked approximately 20 meters from the carcass the dogs were fed.

Vocalisation and Behaviour Scoring

Audio files were examined using Kaleidoscope Lite software v5.5.2 (Wildlife Acoustics Inc., Maynard MA, USA) and scored according to ethograms compiled from previous classification of wild dog vocalisations (Table 2, Supplementary Tables 1 and 2; Robbins 2000, Riddell in prep.).

Video and audio were indexed by narrating the pack, day, and time at the start of both types of recordings, however technical difficulties often resulted in audio and video becoming unsynchronised. Therefore, audio and video recordings were re-calibrated when necessary, using other audio cues that appeared in both. When a vocalisation occurred in am audio recording, it was scored according to the vocalisation ethogram, and the corresponding behaviour from the video recording was scored according to a modified ethogram from Van den Berghe et al., (2019; Supplementary Table 3). If no corresponding behaviour could be determined from the video recordings, the vocalisation was excluded from the dataset.

The overarching context in which a particular vocalisation - behaviour combination occurred was also noted, and included feeding, rest, keeper interaction and travel. As such, two identical vocalisation-behaviour combinations, for example social twitters and active submission, could

Table 2: Classification and behavioural context of the African wild dog vocalisation repertoire (adapted from Robbins 2000).

Vocal class	Subclass	Behavioural context
Twitter *	Social twitter	Used during greeting behaviours, possibly for bond reinforcement Used during rest when individuals approach each other
	Spar twitter	Used during vigorous play by subadults Used during appeasement and pack formation
	Mob twitter	Used by adults mobbing other pack members and hunting Used while chasing hyenas or vultures Used by pups to warn adults while resting
	Attack twitter	Used while chasing hyenas, during interpack encounters, and by resting pups approached by adults
Begging cries *	General begging cry	Used during food solicitation, greeting behaviours, social solicitation May indicate distress
	Gurgle *	Episodes of high arousal
Yelps / squeals	Yelp + Whistle squeal	Used with submissive behaviours by subordinate dogs in response to / anticipation of pain Used during appeasement and solicitation Used when being chased by hyenas
	Begging squeal	Used during greeting and social solicitation, sometime accompanying spar twitters
Whimpers		Used when dogs approach each other, during greeting ceremonies, and when repositioning themselves at rest Used by adults calling to pups Used by dogs mobbing each other
Moans	Full moan	Used during apparent frustration while attempting to access kills or pups in dens
	Buzz moan *	Used during high-intensity greeting ceremonies, with begging cries and gurgles
Rumbles *		Used in the initial phases of greeting ceremonies
Growls	Social	Used during intra-pack antagonistic interactions
	Alarm	Used (repeatedly) as a warning to pack members when potential threats are present
Barks	Alarm	Common alarm barks used similarly to alarm growls but appear to indicate higher intensity Tremolo alarm barks used in higher arousal situations, when lions or humans approach
	Threat	Used towards pups soliciting food, indicating muted aggression
	Attack	Used while chasing hyenas
	Howl *	Used with tremolo alarm barks during inter-pack encounters
	Clear bark	Used in alarm Used by adults in affiliative interactions with pups
	Yelp bark	Used when mobbing hyenas Used by adults in affiliative interactions with pups
Hoo calls *		Used as a long distance contact call May indicate distress depending on context
Pack calls		Used during inter-pack encounters by both pack Used when pack members are reunited
Mixed vocalisations		Sounds of different classes may be mixed, either by succession or superimposition, increasing the diversity of sounds in the repertoire
Sneeze**		Co-ordinating collective movement away from rest, likely to begin hunting

* thought to be unique to African wild dogs. ** vocalization identified in Walker et al. (2017).

be further characterised by the context in which they occurred, for example one may have occurred during feeding, the other during rest. While the wild Waterberg pack did not interact with a traditional keeper, any instances in which their behaviours and vocalisations were directed towards the vehicle and its occupants were recorded as keeper interactions. The duration in which each pack was recorded in each context was also noted from the video recordings for further analysis.

In some instances, it was not possible to score a specific behaviour associated with a given vocalisation. This typically occurred when dogs were huddled closely together, predominantly around a carcass during feeding, and the closest dog obscured the rest from view. Thus, behaviours categorised as 'feeding' may also include behaviours belonging to other categories, for example agonistic interactions, in which the specific behaviours were not visible.

Statistical Analysis

Individual behaviours were grouped by their broader category to facilitate statistical analysis. Not every behavioural category was observed in every pack, and behavioural categories associated with very few vocalisations, or not observed at all, were removed from the analysis (sexual behaviour, vigilance behaviour, stereotypy, hunting). Similarly, contexts which did not occur across all three packs were excluded from the analysis (visitor interaction, veterinary or management intervention, greeting ceremony, hunting, predator interaction).

Each vocalisation was therefore associated with a specific behaviour, its corresponding behaviour category, a context, and a pack. Rates of vocalisations were calculated by counting the number of vocalisations per day, filtering by the desired factor(s), and dividing by the amount of time that audio and video was recorded for. For example, the rate of vocalisation per pack during feeding was calculated by counting the number of vocalisations per pack associated with the feeding context each day, and dividing by the amount of time each pack was recorded in the feeding context each day. Daily rates of vocalisation were calculated by dividing each pack's total number of scored vocalisations by total amount of time recorded per day.

Data were placed into heatmaps and contingency tables to assess differences in the vocalisations associated with each behaviour category, overall and per context. Rates of vocalisation overall and per context were compared per pack by ANOVAs and post-hoc Tukey tests. Statistical analyses were performed in R Studio v1.3.1093 (Posit, Boston, MA, USA), and results considered significant when $p \leq 0.05$.

Results

(i) Association between vocalisations and behaviours

The total rate of each type of vocalisation and its corresponding behaviour category is shown for all packs in Fig. 2. For three behaviour categories: affiliative, aggression, and play, relatively few vocalisations were recorded, so little variation in vocalisation type across the behaviour categories was recorded. However, in the other categories, specifically within dominance and feeding behaviours, more variation in the use of certain vocalisations was found. For dominance behaviours, these included alarm barks, alarm growls, attack barks, attack twitters, buzz gurgle moans, full moans, howl barks, and tremolo alarm barks. Comparatively, for feeding behaviours these included huffs, mob twitters, rumbles, sneezes, staccato begging cries, yelps and whines.

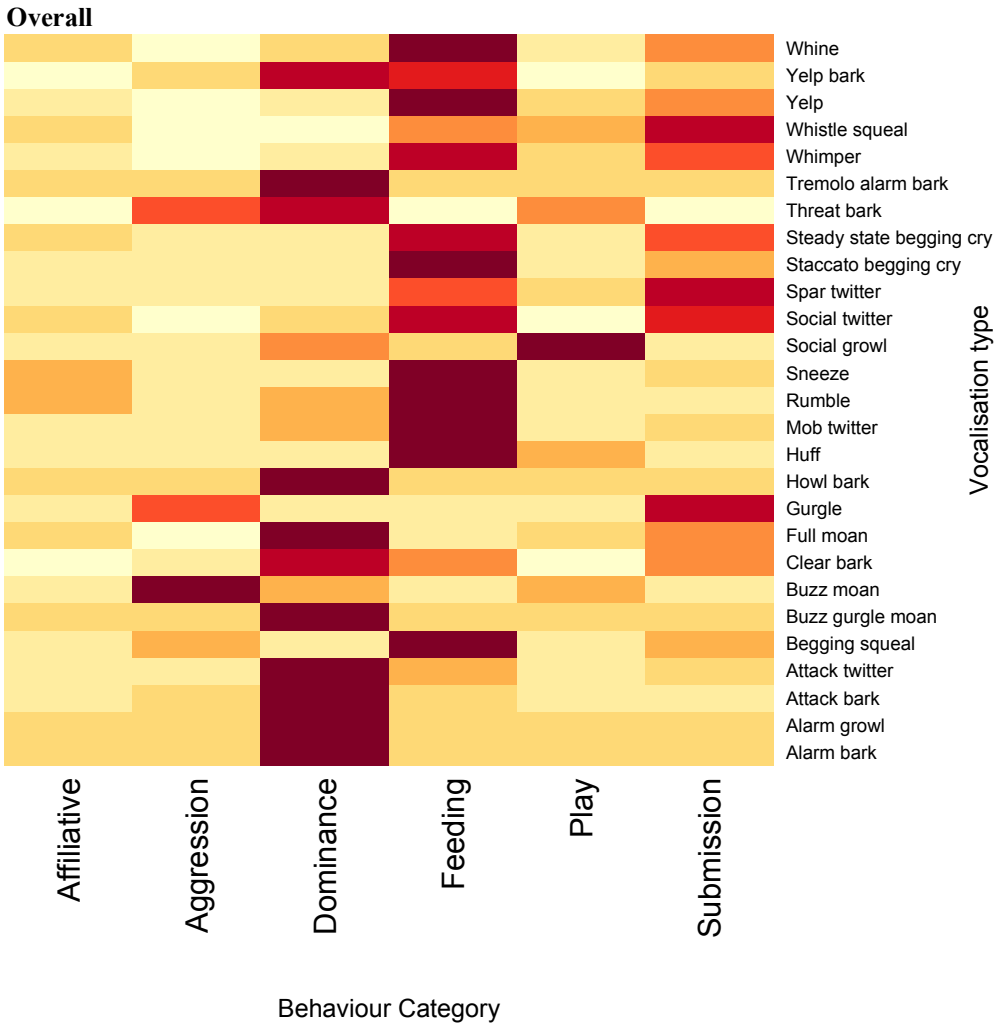


Figure 2, Heatmap of Vocalisations and Behaviour Categories across three packs of African wild dogs (n = 32): Heatmap showing the vocalisation types and the rates at which they were observed occurring with each category of behaviour within the observation period. Columns are independently clustered such that each category of behaviour has its own scale for the rate of vocalisation. Lighter cells correspond to lower rates, and darker cells to higher rates.

The total number of times that each vocalisation was recorded in combination with each behaviour category is shown for all packs in Table 3. Vocalisations were excluded from this table if they were not observed across any of the six behaviour categories presented below.

Table 3: Contingency table showing the number of times each type of vocalisation was recorded in association with each category of behaviour across three packs of African wild dogs, n = 3 packs, 32 individuals. Vocalisations that were not observed across any category of behaviour were excluded for clarity.

Vocalisation	Behaviour Category - Overall					
	Affiliative	**Aggression**	**Dominance**	**Feeding**	**Play**	**Submission**
Alarm bark	0	0	13	0	0	0
Alarm growl	0	0	36	0	0	1
Attack bark	0	28	289	5	0	0
Attack twitter	0	0	15	3	0	1
Begging squeal	3	29	2	90	4	25
Buzz gurgle moan	0	0	2	0	0	0
Buzz moan	0	7	2	0	2	0
Clear bark	0	1	6	3	0	3
Full moan	2	0	6	1	2	3
Gurgle	0	2	0	0	0	3
Howl bark	0	0	1	0	0	0
Huff	0	0	0	12	2	0
Mob twitter	1	2	31	81	9	11
Rumble	1	0	1	3	0	0
Sneeze	7	0	2	23	0	5
Social growl	0	0	2	1	4	0
Social twitter	18	0	16	51	3	43
Spar twitter	0	0	0	14	4	19
Staccato begging cry	0	0	0	20	0	4
Steady state begging cry	6	0	0	39	0	27
Threat bark	0	3	4	0	2	0
Tremolo alarm bark	0	0	8	0	0	0
Whimper	4	0	10	50	12	37
Whine	10	0	7	29	5	17
Whistle squeal	2	0	0	5	4	9
Yelp	2	0	3	30	6	14
Yelp bark	0	3	8	7	0	2

Some vocalisations were used more frequently and along with more categories of behaviour than others. Eight vocalisations were seen associated with only one or two categories of behaviour: alarm barks, alarm growls, buzz gurgle moans, howl barks, and tremolo alarm barks are almost exclusively associated with dominance behaviour, which contributes useful information towards the determination of the emotional state of packs using vocalisations. Gurgles, huffs, and staccato begging cries were also observed with two categories of behaviour:

gurgles with aggression and submission, huffs with feeding and play, and staccato begging cries with feeding and submission. However, some of these were observed very few times so it remains difficult to say with confidence that they are strongly associated with one type of behaviour: for example, buzz gurgle moans were observed only twice, and howl barks were observed only once. In contrast, alarm barks and alarm growls were recorded frequently, and almost exclusively in combination with dominance behaviours. Most vocalisations were associated with three to five categories of behaviour, indicating a broader use. Two types of vocalisations were observed with every category of behaviour: these were mob twitters and begging cries, which are both high-frequency sounds that were observed very frequently. More broadly used vocalisations show lower potential for use in diagnosing cohesion successes and failures, particularly without further detailed analysis of acoustic properties that could identify subtle variation for these more ubiquitous calls.

(ii) Association between vocalisations and behaviours per context

The associations between vocalisations and categories of behaviour were broken down into their corresponding contexts: feeding, rest, and keeper presence.

Context: Feeding

The total rate of vocalisations and their corresponding behaviour categories are shown for all packs during the context of feeding in Fig. 3. As in Fig. 2, very few vocalisations were recorded for some behaviour categories, while other behaviour categories were associated with a higher diversity and rates of vocalisation.

The total number of times that each vocalisation was recorded in combination with each behaviour category within the context of feeding is shown for all packs in Table 4. Vocalisations were excluded from this table if they were not observed across any of the six behaviour categories.

There are some differences in the way that vocalisations were used within the feeding context compared to their overall use. Firstly, only two vocalisations- threat bark and full moan- were associated with aggression or dominance behaviours in the feeding context. Most were associated with feeding behaviour, which does not fully identify the more subtle interactions that may have occurred but were not visible. Although dominance and aggression vocalisations were not common in the feeding context, the presence of threat barks and full moans does indicate that some of these interactions were occurring and were mediated by these vocalisations. There were also a relatively large number of vocalisations associated with submission behaviours in this context, and a broad spread of vocalisation types that were used with submissive behaviours, particularly gurgles, spar twitters, and whistle squeals.

Additionally, some vocalisations that were frequently observed overall were not observed at all during feeding, specifically alarm barks, alarm growls, or attack barks. Overall, those three vocalisations were used primarily with dominance behaviours, which we observed very little

of during the feeding context. Begging squeals were also used differently during feeding compared to their overall use, as they were not associated with aggression during feeding, so this context does not account for the aggression-related begging squeals found overall. Yelp barks, attack twitters, and spar twitters showed a similar pattern to begging squeals, as they were not associated with dominance or aggression during feeding, in contrast to the overall findings. However, both yelp barks and attack twitters were observed infrequently so this may not constitute a strong pattern. Mob twitters were the only vocalisation observed across every category of behaviour during feeding, but with most, as was the general pattern within the feeding context, observed with feeding behaviour.

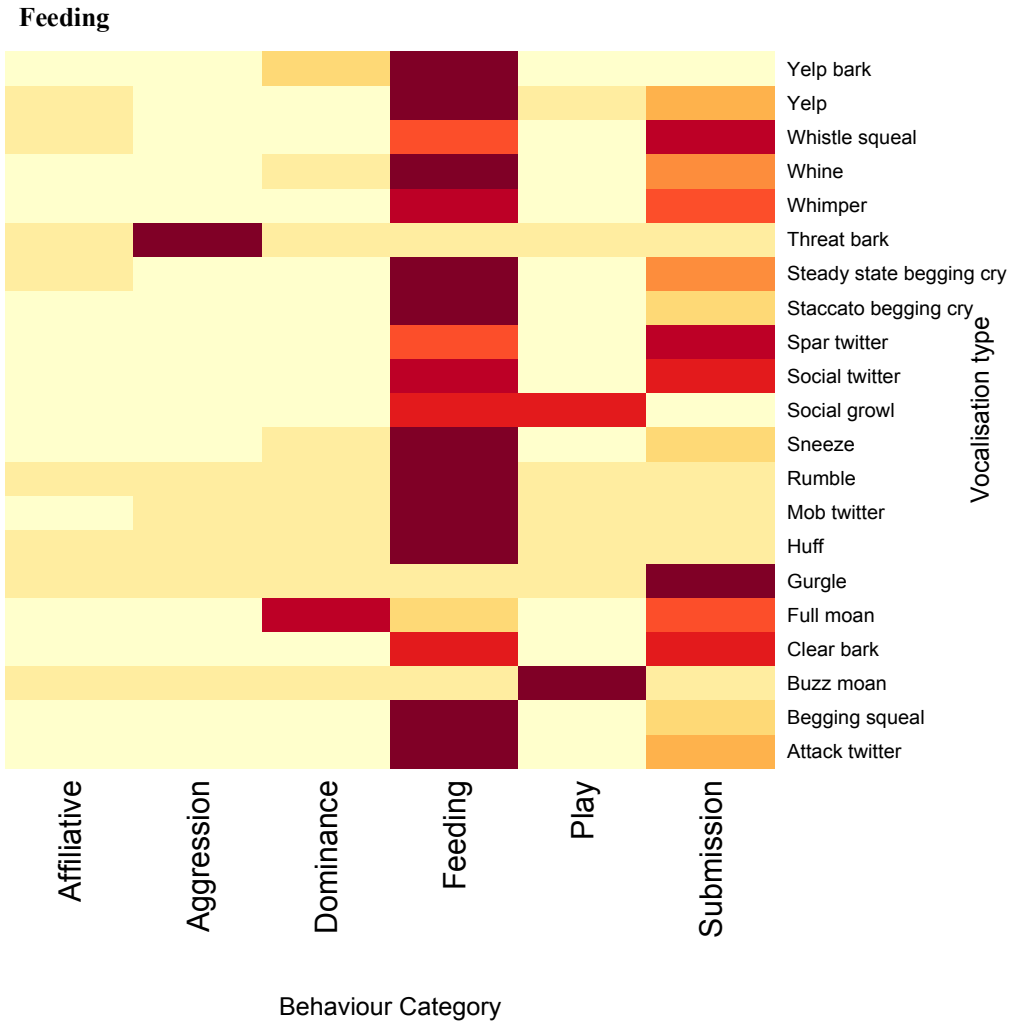


Figure 3, Heatmap of Vocalisations and Behaviour Categories within the Context of Feeding across three packs of African wild dogs (n = 32): Columns are independently clustered such that each category of behaviour has its own scale for the rate of vocalisation. Lighter cells correspond to lower rates, and darker cells to higher rates. Vocalisations were excluded from this heatmap if they were never observed in combination with any of these six behaviour categories.

Table 4: Contingency table showing the number of times each type of vocalisation was recorded in association with each category of behaviour within the context of feeding across three packs of African wild dogs, *n* = 3 packs, 32 individuals. Vocalisations that were not observed across any category of behaviour were omitted for clarity.

Vocalisation	Behaviour Category - Feeding context					
	Affiliative	**Aggression**	**Dominance**	**Feeding**	**Play**	**Submission**
Attack twitter	0	0	0	3	0	1
Begging squeal	0	0	2	90	1	23
Buzz moan	0	0	0	0	1	0
Clear bark	0	0	0	2	0	2
Full moan	0	0	3	1	0	2
Gurgle	0	0	0	0	0	2
Huff	0	0	0	12	0	0
Mob twitter	1	2	3	72	3	8
Rumble	0	0	0	1	0	0
Sneeze	0	0	2	23	0	4
Social growl	0	0	0	1	1	0
Social twitter	6	0	3	51	0	43
Spar twitter	0	0	0	14	0	18
Staccato begging cry	0	0	0	20	0	4
Steady state begging cry	3	0	0	39	0	20
Threat bark	0	1	0	0	0	0
Whimper	2	0	2	49	0	31
Whine	2	0	3	29	0	16
Whistle squeal	1	0	0	5	0	6
Yelp	2	0	1	30	2	10
Yelp bark	0	0	1	6	0	0

Context: Rest

The total number of times that vocalisations were recorded in combination with behaviour categories within the context of rest is shown for all packs in Table 5. For this context, no heatmap is shown because one single vocalisation, a yelp, was recorded across all three packs, in combination with any of the six behaviour categories presented, as rest is not a highly vocal context for wild dogs.

Context: Keeper Presence

The total rate of vocalisations and their corresponding behaviour category within the context of keeper presence is shown for all packs in Fig. 4. For some behaviour categories, very few vocalisations were recorded, while other behaviour categories, specifically dominance and feeding, were associated with a higher diversity of types and rates of vocalisation.

Table 5: Contingency table showing that within the context of rest, only one vocalisation was recorded in combination with any of the six behaviour categories presented, across three packs of African wild dogs, *n* = 3 packs, 32 individuals. Vocalisations that were not observed across any category of behaviour were excluded for clarity.

Vocalisation	Behaviour Category - Rest context					
	Affiliative	Aggression	Dominance	Feeding	Play	Submission
Yelp	0	0	0	0	0	1

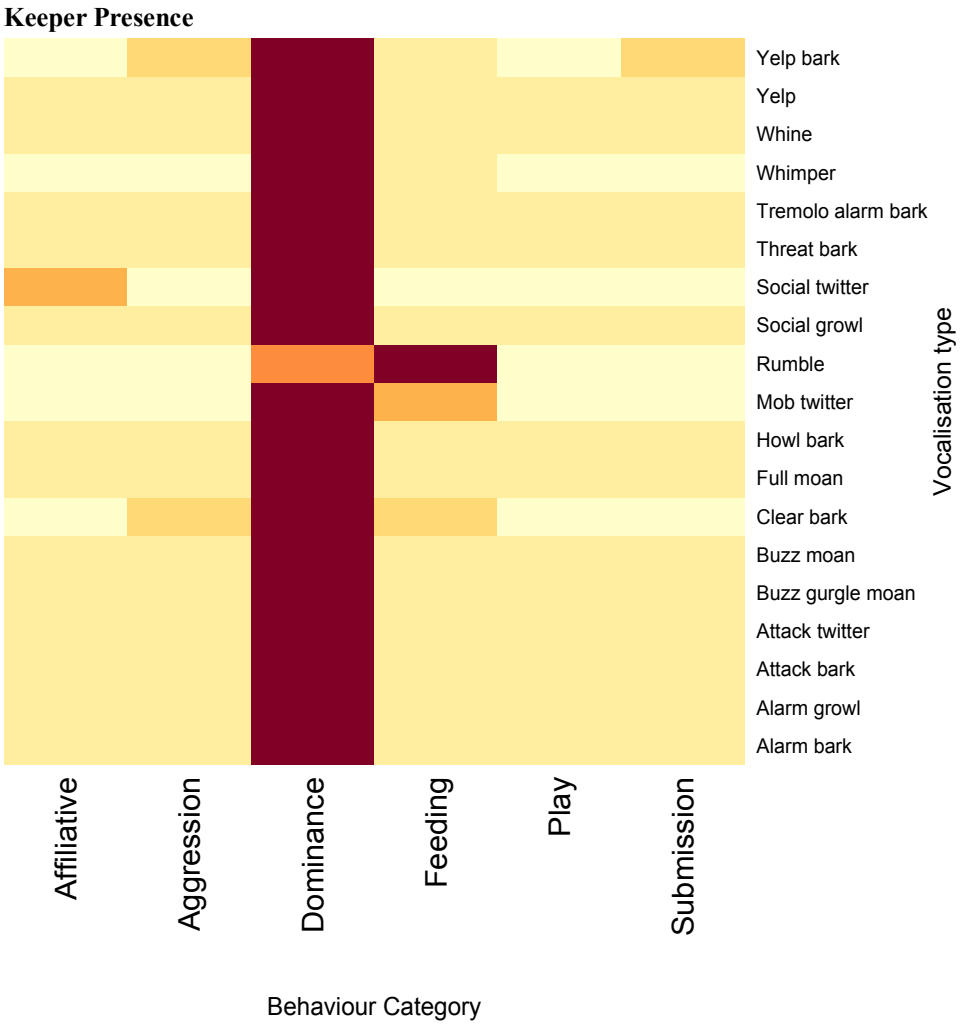


Figure 4, Heatmap of Vocalisations and Behaviour Categories within the Context of Keeper Presence across three packs of African wild dogs (n = 32): Columns are independently clustered such that each category of behaviour has its own scale for the rate of vocalisation. Lighter cells correspond to lower rates, and darker cells to higher rates. Vocalisations were excluded from this heatmap if they were never observed in combination with any of these six behaviour categories.

The total number of times that each vocalisation was recorded in combination with each behaviour category within the context of keeper presence is shown for all packs in Table 6. Vocalisations were excluded from this table if they were not observed across any of the six behaviour categories.

There were differences in vocalisation use within this context compared to their overall use, most significantly that this context was dominated by dominance-associated vocalisations, as every type of vocalisation used within this context was used with dominance behaviour. These were: alarm barks, alarm growls, attack barks, attack twitters, buzz gurgle moans, buzz moans, clear barks, full moans, howl barks, mob twitters, rumbles, social growls, social twitters, threat barks, tremolo alarm barks, whimpers, whines, yelps, and yelp barks. This showed a stronger focus on a single category of behaviour compared to both the overall vocalisation use or the feeding context and indicates that agonistic behaviours are the primary way that wild dogs respond to the presence of human keepers.

Notably, attack barks, alarm growls, and mob twitters were recorded more than 25 times with dominance behaviour, and fewer than ten times in any other category within this context. In addition to using a broad diversity of vocalisations with dominance, some of the calls were used at particularly high rates, with attack barks recorded 289 times. The near-complete overshadowing by a single category of behaviour, in addition to the high frequency with which some of those vocalisations were used, suggests that human presence elicits primarily dominant, agonistic responses from wild dogs.

Keepers came into proximity with the wild dogs for a few purposes, but the primary one was to feed the pack. There were therefore some vocalisations associated with feeding which fell into the keeper presence context, which were rumbles, and to a lesser extent, mob twitters. The combination of feeding behaviour with keeper presence may indicate a more nuanced use of these vocalisations as food guarding from threats.

(iii) Association between vocalisations and behaviours per pack and per context

The associations between vocalisations and categories of behaviour were broken down by pack to examine whether these relationships were consistent across each pack of wild dogs. The total number of times that each vocalisation was recorded in combination with each behaviour category for Bothongo is shown in Table 7, for Joburg in Table 8, and for Waterberg in Table 9. Vocalisations were excluded from these tables if they were not observed across any of the behaviour categories.

Table 6: Contingency table showing the number of times each type of vocalisation was recorded in association with each category of behaviour within the context of keeper presence across three packs of African wild dogs, *n* = 3 packs, 32 individuals. Vocalisations that were not observed across any category of behaviour were removed for clarity.

Vocalisation	Behaviour Category – Keeper presence context					
	Affiliative	**Aggression**	**Dominance**	**Feeding**	**Play**	**Submission**
Alarm bark	0	0	13	0	0	0
Alarm growl	0	0	36	0	0	1
Attack bark	0	10	289	5	0	0
Attack twitter	0	0	15	0	0	0
Buzz gurgle moan	0	0	2	0	0	0
Buzz moan	0	0	2	0	0	0
Clear bark	0	1	6	1	0	0
Full moan	0	0	3	0	0	0
Howl bark	0	0	1	0	0	0
Mob twitter	0	0	27	9	0	0
Rumble	0	0	1	2	0	0
Social growl	0	0	2	0	0	0
Social twitter	5	0	13	0	0	0
Threat bark	0	0	4	0	0	0
Tremolo alarm bark	0	0	8	0	0	0
Whimper	0	0	8	1	0	0
Whine	0	0	4	0	0	0
Yelp	0	0	2	0	0	0
Yelp bark	0	2	7	1	0	2

The Bothongo pack showed the most vocalisations associated with dominance, followed by feeding. A notably high number of attack barks were used, accounting for approximately 90% of the total attack bark use across all three packs and occurring entirely within the aggression and dominance categories. Despite the high number of dominance vocalisations, this pack primarily used attack barks in this category; although seventeen different vocalisation types were used with dominance, attack barks accounted for over 75% of these. In contrast, the next most vocal category of behaviours was feeding, where the most-used vocalisation accounted for under 25% of total feeding-associated vocalisations, and five vocalisation types were used over 35 times. This pack appears, therefore, to use attack barks as their primary way to communicate dominance. Submission-associated vocalisations were also prominent in this pack, which suggests that the most vocal behaviours observed in the Bothongo pack were used in agonistic interactions.

Table 7, Bothongo: Contingency table showing the number of times each type of vocalisation was recorded in association with each category only within the Bothongo pack (n = 15). Vocalisations that were not observed across any category of behaviour were omitted for clarity.

Vocalisation	Behaviour Category - Bothongo					
	Affiliative	**Aggression**	**Dominance**	**Feeding**	**Play**	**Submission**
Alarm bark	0	0	3	0	0	0
Alarm growl	0	0	4	0	0	0
Attack bark	0	18	274	0	0	0
Attack twitter	0	0	13	3	0	0
Begging squeal	0	29	0	85	0	12
Buzz gurgle moan	0	0	2	0	0	0
Buzz moan	0	7	2	0	0	0
Clear bark	0	0	1	0	0	1
Full moan	1	0	3	1	0	1
Gurgle	0	2	0	0	0	2
Howl bark	0	0	1	0	0	0
Huff	0	0	0	9	0	0
Mob twitter	0	0	26	58	0	8
Rumble	1	0	0	1	0	0
Sneeze	7	0	0	9	0	3
Social growl	0	0	2	0	1	0
Social twitter	5	0	14	39	0	15
Spar twitter	0	0	0	14	0	15
Staccato begging cry	0	0	0	19	0	4
Steady state begging cry	1	0	0	38	0	25
Threat bark	0	2	2	0	0	0
Tremolo alarm bark	0	0	2	0	0	0
Whimper	3	0	4	38	4	22
Whine	6	0	4	10	0	7
Whistle squeal	2	0	0	3	2	8
Yelp	1	0	2	19	0	8
Yelp bark	0	1	0	2	0	0
Totals:	**27**	**59**	**359**	**348**	**7**	**131**

Similarly to both Bothongo and Waterberg, Joburg employed a range of vocalisation types with feeding behaviours, however in contrast to both of those packs, these vocalisations were all keeper-directed due to the separate housing condition. As a result, Joburg used attack barks and mob twitters as their primary feeding-associated vocalisations, in contrast to the more frequent use of begging and solicitation vocalisations observed primarily in Bothongo, and to a lesser extent also in Waterberg. The Joburg pack was less engaged in inter-individual communication than the others, and likely shows only agonistic communication in its current setup.

Table 8, Joburg Zoo: Contingency table showing the number of times each type of vocalisation was recorded in association with each category only within the Joburg Zoo pack (n = 2). Vocalisations that were not observed across any category of behaviour were excluded for clarity.

Vocalisation	Behaviour Category - Joburg			
	Aggression	**Dominance**	**Feeding**	**Submission**
Alarm bark	0	10	0	0
Alarm growl	0	32	0	1
Attack bark	10	15	5	0
Attack twitter	0	2	0	0
Clear bark	1	5	1	0
Huff	0	0	0	0
Mob twitter	0	1	9	0
Rumble	0	1	2	0
Sneeze	0	0	0	0
Threat bark	0	2	0	0
Tremolo alarm bark	0	6	0	0
Whimper	0	4	1	0
Yelp bark	2	7	2	2
Totals:	**13**	**85**	**20**	**3**

The Waterberg pack showed the most vocalisations associated with feeding, followed by submission. This pack showed few aggression or dominance behaviours compared to the other packs, indicating either that relatively little aggression and dominance behaviours occurred in this pack, or that they were not communicated vocally. More submission-related vocalisations were recorded in this pack, which indicates either that the submission was more often actively offered by this pack, or that in agonistic interactions, the submission response was more vocal than a preceding dominant or aggressive behaviour. Feeding and submission behaviours were also associated with higher diversities of vocalisation types; thirteen types with feeding and fourteen with submission. Social twitters, begging squeals, whimpers, whines, and yelps were used across all the categories except aggression, and mob twitters were used similarly with the addition of two aggression-related instances. The spread in use for these vocalisations, with most use focused on feeding, submission, and play, suggests that this pack uses these with some flexibility but primarily around ‘positive’ social, less agonistic behaviours. The Waterberg pack was overall more vocal with submissive and feeding-related behaviours compared to the more dominance-focused vocalisation usage in both Bothongo and Waterberg.

Table 9, Waterberg: Contingency table showing the number of times each type of vocalisation was recorded in association with each category only within the Waterberg pack (n = 15). Vocalisations that were not observed across any category of behaviour were omitted for clarity.

Vocalisation	Behaviour Category - Waterberg					
	Affiliative	**Aggression**	**Dominance**	**Feeding**	**Play**	**Submission**
Attack twitter	0	0	0	0	0	1
Begging squeal	3	0	2	5	4	13
Buzz moan	0	0	0	0	2	0
Clear bark	0	0	0	2	0	2
Full moan	1	0	3	0	2	2
Gurgle	0	0	0	0	0	1
Huff	0	0	0	3	2	0
Mob twitter	1	2	4	14	9	3
Sneeze	0	0	2	14	0	2
Social growl	0	0	0	1	3	0
Social twitter	13	0	2	12	3	28
Spar twitter	0	0	0	0	4	4
Staccato begging cry	0	0	0	1	0	0
Steady state begging cry	5	0	0	1	0	2
Threat bark	0	1	0	0	2	0
Whimper	1	0	2	11	8	15
Whine	4	0	3	19	5	10
Whistle squeal	0	0	0	2	2	1
Yelp	1	0	1	11	6	6
Yelp bark	0	0	1	3	0	0
Totals:	**29**	**3**	**20**	**99**	**52**	**90**

The overall rate of vocalisation per hour per pack was calculated to facilitate between-pack comparisons (Fig. 5a). A significant difference was found overall (p = 0.0496, F = 4.117), however no significant pairwise differences were detected (Bot-Job, p = 0.058; Job-Wat p = 0.131; Bot-Wat p = 0.715). The two captive packs had a near-significant difference, indicating that they had more difference in vocal rate compared with both wild - captive comparisons. The Bothongo pack also had higher variation in the rate of vocalisations per hour compared to the Joburg Zoo or Waterberg packs, which likely reflects the wide variation in the vocal rate depending on the pack's activity; feeding events in Bothongo encompassed the presence of keepers and the consumption of food, and therefore produced a high volume of vocalisations, while the pack made relatively few vocalisations during the non-feeding portions of the observation time.

The rate of vocalisations per hour per pack within the contexts of feeding, rest, and keeper presence are shown in Fig. 5b-d. A significant difference between packs was detected during feeding ($p < 0.001$, F = 57.01). Pairwise comparisons showed that the rate of vocalisations in the Bothongo pack was significantly higher than both Joburg ($p < 0.001$) and Waterberg ($p < 0.001$), but Joburg and Waterberg were not significantly different from each other (p = 0.730).

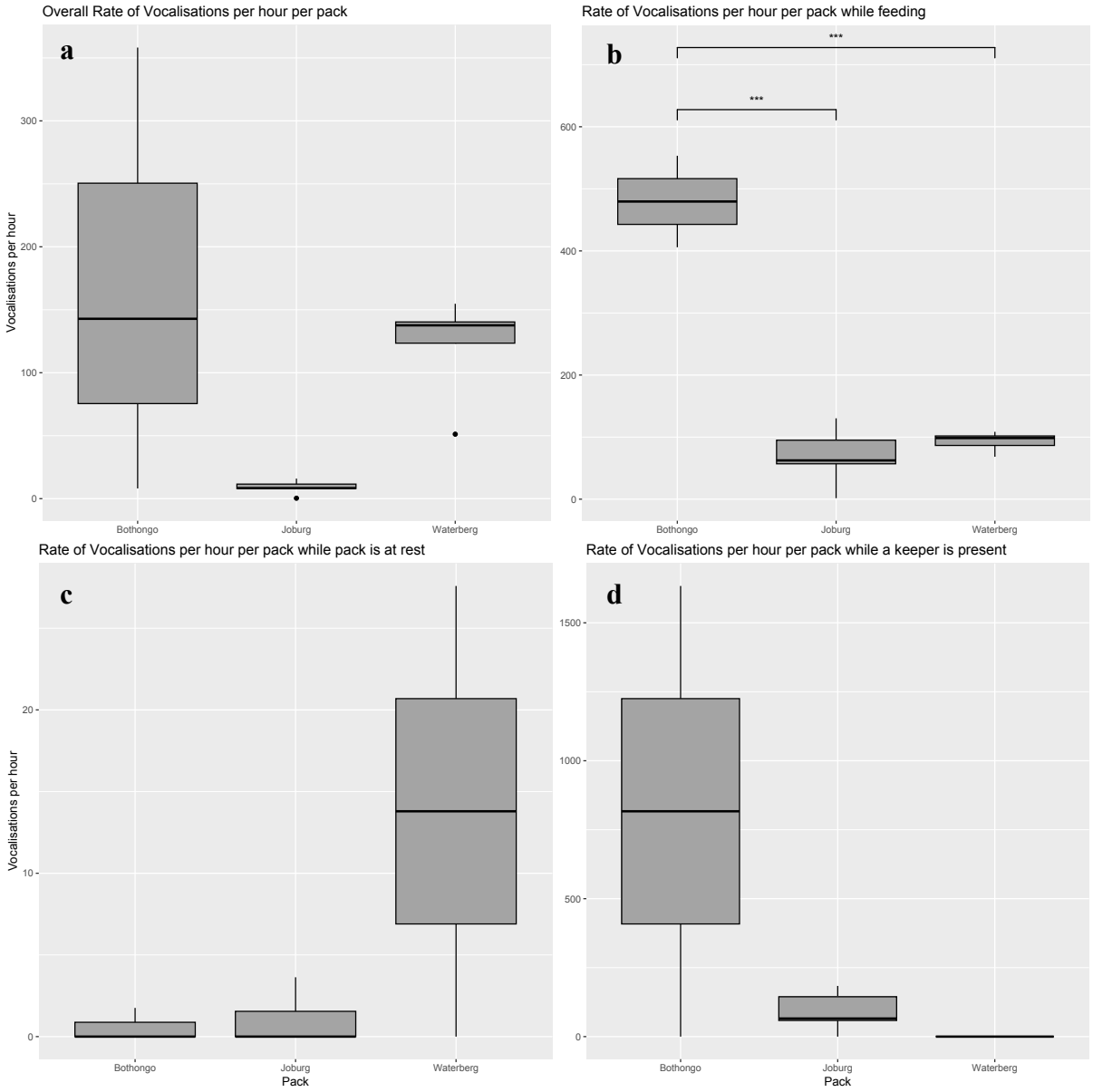


Figure 5a-d: Boxplots showing the rate of vocalisation per pack, which was compared by ANOVA overall and by post-hoc Tukey tests for pairwise comparisons (a) overall (p = 0.0496*, F = 4.117;Bot-Job p = 0.0581; Job-Wat p = 0.131; Bot-Wat p = 0.715), (b) in the context of feeding (p = 7.75e-06***, F = 57.01; Bot-Job p = 0.0000084***; Bot-Wat p = 0.000138***; Job-Wat p = 0.73), (c) in the context of rest, (p = 0.162, F = 2.386; Bot-Job p = 0.996; Job-Wat p = 0.174; Bot-Wat p = 0.199) and (d) in the context of keeper presence (p = 0.303, F = 1.533; Bot-Job p = 0.304; Job-Wat p = 0.986; Bot-Wat p =0.463).

During rest, no significant differences between packs were found (overall p = 0.162, F = 2.386; Bot-Job p = 0.996; Job-Wat p = 0.174; Bot-Wat p = 0.199). Similarly, no significant differences were found between any packs in the context of keeper presence (overall p = 0.303, F = 1.533; Bot-Job p = 0.304; Job-Wat p = 0.986; Bot-Wat p =0.463). The Waterberg pack showed the most variation in their rate of vocalisation at rest, despite only one presented vocalisation in the rest context. Rest was not observed often in any pack, including Waterberg, in which the

pack spent under 30 minutes at rest throughout the observation period. Further, in this pack, a small number of vocalisations were recorded at rest with behaviours that were not ultimately included in further analysis because they occurred in only one pack or with very few vocalisations, primarily vigilance-related behaviours. As a result, these are not reflected in Table 5, but contribute to the rate of vocalisation at rest.

Discussion

This study aimed to elucidate the associations between vocalisations and behaviour in wild dogs. We found stronger associations between vocalisations and agonistic behaviours such as dominance and aggression, compared to social behaviours such as affiliation and play, which were associated with a broader range of vocalisations. Different patterns of vocalisation use were found in the context of feeding compared to keeper presence. While feeding, there were fewer vocalisations associated with dominance and aggression behaviours compared to overall use, which is consistent with wild dogs' reportedly peaceful feeding behaviour. While keepers were present, more dominance associated vocalisations were used. We also found differences in vocalisation use between packs. Both captive packs vocalised primarily in combination with dominance behaviours, while the wild pack vocalised more in combination with submission and play behaviours. In each of the packs, the behaviours with the largest range of vocalisation types associated were also the most vocal categories; these were dominance in both Bothongo and Joburg, and feeding and submission in Waterberg. Two of the packs, Bothongo and Waterberg, consisted of fifteen individuals each, while the other consisted of two separate but adjacently housed dogs. The two larger groups showed vocalisations associated with a wider range of inter-individual interactions, whether putatively 'negative' or 'positive' social interactions, as both showed some affiliation and play, compared to the Joburg dogs which could not make physical contact and consequently lacked inter-individual interaction and the associated vocalisations. Additionally, there was a significantly higher rate of vocalisation during feeding in one of the captive packs, which can likely be attributed to a combination of the feeding methods used, as well as the demographic and social differences between each pack.

Vocalisations were first examined overall, without splitting into contexts and packs. Eight vocalisation types were associated with only one or two categories of behaviour. Of these, five vocalisation types were observed almost exclusively occurring in combination with dominance behaviours. These were alarm barks, alarm growls, buzz gurgle moans, howl barks, and tremolo alarm barks. Some of these vocalisations were observed infrequently, for example buzz gurgle moans were observed twice, and howl barks only once, making it difficult to confidently conclude their meaning. The others, however, were observed more often and are likely more strongly associated with dominance. Alarm barks, alarm growls, and tremolo alarm barks, which were previously classified by Robbins (2000) as associated with potential threats to the pack such as approaching lions, were found to be most often associated with dominance in the current study. While these finding are not perfectly consistent, they both indicate that these vocalisations are used to communicate agonism and as warnings, whether towards fellow pack

members or directed at higher intensity threats. This makes them potentially good candidates with which to detect negative emotional states as a potential measure of poor social cohesion within packs. Vocalisation monitoring has already proven useful in monitoring social cohesion during artificial pack formations (Potgieter et al., 2015), so the framework for ongoing assessment of vocalisations is present. Increasing rates of these possible warning vocalisations could therefore signal deteriorating cohesion, while decreasing rates could imply improvement.

The other vocalisations associated with one or two categories of behaviour were gurgles, staccato begging cries, and huffs. Gurgles were previously classified as occurring with excitatory, high intensity interactions (Robbins, 2000), and our findings link gurgles to both aggression and submission. While these categories of behaviour are seemingly opposite, submission is a response to aggressive behaviours, so both can be expected in one agonistic interaction. This finding lends some support to Robbins' idea that gurgles may be indicative of the level of arousal and intensity of agonistic interaction, as aggressive interactions are associated with higher arousal which is expected to impact vocalisation use (Ordóñez-Gómez et al., 2015), and more severe aggression is more likely to provoke vocal responses from the victim (Szipl et al., 2017). Gurgles therefore appear to mark the intensity of an interaction more so than being a reliable indicator of who is the aggressor and who is the recipient of the aggression.

Staccato begging cries were previously classified as food solicitation and social solicitation (Robbins, 2000) and we found that staccato begging cries were used with feeding and submission behaviours. These are consistent findings, as both food solicitation and social solicitation involve submission and appeasement behaviours in wild dogs (Rütten & Fleissner, 2004). Wild dogs use submissive behaviours, particularly appeasement, to mediate group feeding (Estes & Goddard, 1967), and our findings suggest that staccato begging cries are one of the communication tools used in these interactions. Finally, huffs have not been previously described in the vocal repertoire of wild dogs (but see Walker et al., 2017). We found that huffs were associated with play and feeding behaviours. Play behaviours consist of a mixture of mock-aggressive, dominant, and submissive behaviours (Van den Berghe et al., 2019), as well as the submission and solicitation expected around feeding. Huffs may therefore serve as a solicitation vocalisation, whether towards play partners or feeding partners. Further research which examines the specific behaviours associated with both huffs and staccato begging cries could clarify this; solicitation vocalisations would be expected early in play sequences from an initiator, or could prompt food sharing during feeding.

While some vocalisation types were more clearly associated with categories of behaviour, most others showed associations with a larger range of behaviours, however there are still patterns present. Attack barks and clear barks were observed across three categories: aggression, dominance, and feeding behaviours. 'Feeding behaviours' as a category includes some interactions which likely belong to other categories but were not sufficiently visible while coding behaviour. Therefore, it is likely that these vocalisations, particularly attack barks, are associated with aggression and dominance, including aggression and dominance interactions that occur during feeding. Although dominance and aggression are separable categories of

behaviours, they differ primarily by degree, where aggressive behaviours are more extreme than dominant behaviour, and include more physical contact . We can therefore group attack barks and clear barks as similar in intention to alarm barks, alarm growls, and tremolo alarm barks; these vocalisations all appear to be indicative of agonistic interactions and likely come from a more dominant individual or an aggressor.

Several other vocalisation types were observed across more categories of behaviour, but some inferences can still be made. For example, begging squeals were seen across all categories of behaviour, but primarily during feeding, then aggression and submission. As noted, the feeding category likely encompasses some unseen interactions, in this case, possibly more aggression and submission interactions. Similarly to gurgles, begging squeals may be indicative of high-arousal agonistic interactions that involve aggressors and victims. In isolation, a begging squeal may therefore not tell us whether the vocaliser is the aggressor or the victim, but can inform us that high-arousal agonistic interactions are occurring. While mob twitters were also observed across every category of behaviour, their second-highest use behind feeding was dominance, indicating a difference in the way these two vocalisation types are used.

Our findings have identified several types of vocalisations which are primarily associated with agonistic interactions. More detailed analysis of the specific behaviours and interactions underlying these vocalisations would benefit management by improving the ability to distinguish between dominance-related barks and growls and aggression-related barks and growls. These are important distinctions for management purposes; asymmetric interactions with one individual asserting dominance over another are a natural and expected element of hierarchy establishment and maintenance in a hierarchical species (Drews, 1993), whereas aggression can be fatal and severely hinder wild dog conservation efforts (Potgieter et al., 2012). A proper understanding of the distinct vocalisations associated with each is therefore important, such that natural hierarchy establishment may be facilitated, but potentially threatening conflicts can be recognised and de-escalated as early as possible.

Vocal communication repertoires are known to be context-specific in related species including wolves (Faragó et al., 2014), domestic dogs (Yin & McCowan, 2004) and dingoes (Déaux & Clarke, 2013). The present study therefore also aimed to examine contexts relevant to our study packs to determine patterns within the vocal repertoire. Two of our study packs were captive, while one was wild but habituated to human presence, so the contexts which were effectually comparable between all three were feeding and keeper presence.

Six of the vocalisation types that were recorded overall were not observed at all during feeding. These are six of the previously described vocalisations associated with aggression and dominance. Instead, begging squeals and social twitters were used the most often during feeding, and were associated most often with feeding and submission behaviours. Wild dog feeding behaviour is more peaceful than is usually described for large carnivores, with potential conflicts primarily mediated by submissive and infantile behaviours between adults (Kühme, 1965; Estes & Goddard, 1967), Based on our findings, this is likely communicated through begging squeals and social twitters. Within the feeding context, begging squeals are used in a

more restricted way- with no aggression behaviours- compared to their overall use, in which they were more often observed associated with aggression. This suggests a degree of context dependence for begging squeals and lends support to the idea that they, similarly to gurgles, may be better indicators of the intensity of an interaction as opposed to reliable markers of whether, for management purposes, an interaction is ‘positive’; or ‘negative’.

The keeper presence context was dominated by vocalisations associated with dominance behaviour. This accounts for the majority of vocalisations strongly associated with dominance overall, including attack barks and alarms growls. Attack barks were used notably often in this context, and were also found with aggressive behaviours, suggesting that their use can escalate with the severity of the agonistic behaviour. The use of several vocalisation types within this category may be due to the target being human; if a vocalisation is intended to drive away a perceived threat, the wild dogs may expect the target of their behaviour to retreat. In the case of a human keeper, the behavioural response is different, as they will not move away. The pack may then use progressively escalating vocalisations and behaviours to address the threat, driving a higher diversity of vocalisation types in this context. Threat intensity is known to drive changes in the acoustic parameters of aggressive vocalisations (Sun et al., 2018), and the complexity of wild dog call types on top of modulation of acoustic parameters may represent an extension of this. Future research should entail a more detailed look at how vocalisations and behaviours progress throughout a wild dog-keeper interaction, and track whether vocalisation type and their acoustic parameters change over time and in response to a keeper’s retreat or lack thereof.

The social complexity hypothesis posits that more complex social systems will drive the evolution of more complex vocal communication repertoires (McComb & Semple, 2005), which may provide the context for understanding variation in wild dog vocalisation use. In comparing vocalisation use and behaviour, we find the strongest associations between vocalisation type and behaviour category in dominance and aggression related vocalisations, compared to a higher diversity of vocalisation types associated with affiliation and play. In the feeding context, a wider range of vocalisations were employed across more categories of behaviour in contrast to the keeper presence context, where vocalisations were primarily dominance-associated. Physical play is a socially complex behaviour, and necessitates complex communication (Palagi et al., 2016), which may drive the evolution of a particularly complex sub-repertoire of vocalisation. Additionally, the social complexity of wild dogs is often exemplified by unique elements of their feeding behaviour, such as younger pack members feeding before older ones (Jordan et al., 2022). Feeding may therefore be a context in which the complexity of behaviours and interactions drives a complexity of communication. There are also several types of vocalisations associated with dominance behaviours, however this is possibly due to the presence and behavioural responses of a human keeper. To investigate this possibility further, the focus should be on capturing a larger diversity of behavioural contexts, such as collective movement and hunting, and examining whether the diversity of vocalisations may be driven by complexity of behaviours. Also, distinctions between external threat-directed vocalisations and intra-pack dominance and aggression behaviours could further clarify what drives the complexity of vocalisation repertoires.

For vocalisation types that are associated with multiple categories of behaviour, analysis of the acoustic parameters of individual vocalisations should be carried out. Parameters including fundamental frequency and inter-syllable interval show correlations with arousal levels in other mammals (Briefer et al., 2015; Scheumann et al., 2012), and the physical structure of short-range vocalisations is proposed to be broadly associated with the context for which the vocalisation is used (Morton, 1977; Robbins & McCreery, 2003). Acoustic analysis of wild dog vocalisations is ongoing with this dataset (Pia Riddell, pers. comm.), which may further clarify the patterns we observed between vocalisations and behaviours, for example to determine if there is detectable variation between the same vocalisation when associated with agonistic or social behaviours, or even aggression compared to dominance.

There was also variation in both the repertoire and rates of vocalisation between each study pack. The Joburg pack used relatively few vocalisation types compared to the other packs, and all of their vocalisations were associated with dominance behaviours. As separately but adjacently housed wild dogs, this suggests that the vocalisations lacking from their repertoire are more likely to be social vocalisations used for inter-individual communication. The two larger packs, correspondingly, showed more positive social behaviours such as affiliation and play, and these were associated with similar vocalisations between these two packs, such as social twitters, whimpers and whines. In the context of management, observing these types of vocalisations might therefore indicate social interaction and positive social contact within packs.

The Bothongo and Waterberg packs showed more similarity between their vocal repertoires, though some differences remained. Both used begging squeals across a few categories of behaviour, but Bothongo showed associations between begging squeals and both aggression and submission, while Waterberg showed only the association with submission. From our data, it remains unclear whether the Waterberg pack simply shows less aggressive behaviour, or is less vocal while showing aggressive behaviour, or whether there is a true difference in the ways that these packs use these vocalisations. These different uses suggest a flexible role for begging squeals; further research should incorporate more packs to determine whether these calls are used differently across packs, or reflect a difference in our specific study packs, as Bothongo was generally a highly vocal pack.

The rate of vocalisation during feeding was significantly higher in Bothongo compared to both Joburg and Waterberg. Feeding behaviour in group-living carnivores is often hierarchical and consists of dominance, aggression, and submission interactions. For example, in spotted hyaenas, feeding proceeds according to a linear dominance hierarchy (Tilson & Hamilton, 1984), and in African lions, aggressive competition is frequent at carcasses and an individual's size dictates carcass ownership (Packer et al., 2001). In contrast, wild dogs have remarkably peaceful group feeding behaviour dominated by submissive and appeasing behaviours, in which feeding priority proceeds largely from youngest to oldest, with alpha individuals feeding after the youngest group (Estes & Goddard, 1967; Jordan et al., 2022; Kühme, 1965). The Joburg pack did not show group feeding behaviour, leaving the more interesting comparison between Bothongo and Waterberg.

The Bothongo pack was fed from approximately four carcass sections simultaneously dropped into the feeding area of their enclosure. In contrast, the Waterberg pack was fed from a single carcass, or carcass section. The latter more closely resembles wild-typical feeding habits, as wild dog packs generally feed from a single item of prey (Estes & Goddard, 1967). A single food source can be monopolised more easily by whichever part of the feeding queue has the present priority, while several pieces of food prevent monopolisation. Feeding priority is behaviourally enforced in wild dogs (McNutt, 1996) and as such, monopolising a more spread-out food source requires more interaction and assertions of dominance which can be communicated vocally. The Bothongo pack showed a higher rate of vocalisation during feeding and more dominance-associated vocalisations overall, supporting the idea that feeding is associated with more agonistic interactions in this pack as individuals displace each other from feeding. This is further supported by the frequency of submission-associated vocalisations recorded in the Waterberg pack, as begging for carcass access involves submission (Kühme, 1965; Creel & Creel, 2002), and begging would only be necessary if access to food is not otherwise immediately available.

Hierarchy stability may also play a role in the different rates of vocalisation between the Bothongo and Waterberg packs. In the wild, wild dogs typically disperse before four years of age (McNutt, 1996), however this is restricted by captivity. While ideal captive programmes allow for the exchange of animals to mimic the behavioural and genetic drivers of dispersal, this can be limited by a range of factors and, consequently, many groups consist of group structures different to those found in the wild. In this case, Bothongo consists primarily of the adult offspring of one pair, which are all above five years of age. In contrast, the Waterberg pack is wild and consists of the alpha and beta pairs, several two-year-olds, yearlings, and the pups from the present season. With an un-altered, natural group structure, and no observed hierarchy challenges (Clinton Venter, Waterberg Wild Dog Initiative Field Officer, pers. comm.), it is likely that feeding in the Waterberg pack resembled the documented peaceful feeding queue and few conflicts were necessary to establish feeding priority. In Bothongo, however, likely due to the age of the non-dispersing pack members, the pack had undergone a number of suspected hierarchy disruptions in the months prior to data collection, even prompting management to remove some individuals from the group (Gavin Swart, Bothongo Carnivore Keeper, pers. comm.), suggesting that the dominance of the aging alpha pair is not unchallenged. Without a clearly defined alpha pair, or with an alpha pair whose dominance is contested, more individuals may attempt to feed outside the socially enforced order and therefore require more consistent intervention by individuals asserting- or attempting to assert-dominance. We saw more dominance associated vocalisations in the Bothongo pack compared to the Waterberg pack, which lends support to this explanation.

An alternative, though related, explanation is that the heightened stress that comes with an unstable hierarchy during a potentially competitive event- in this case feeding- leads to a higher arousal level in all dogs. Chronic arousal and stress are associated with maintaining dominance in social hierarchies (Milewski et al., 2022), which may extend to individuals attempting to assert dominance where a hierarchy is not well established. The rate of food calls have previously been linked to arousal levels (Clay et al., 2012), raising the possibility that a higher

rate of vocalisation, and in this case, more dominance-associated vocalisations, indicates high arousal levels in dogs in a more stressful social surrounding. The lower rate of vocalisation in Waterberg is also consistent with this explanation, as we can expect that the dominance hierarchy is not being challenged, leading to an overall lower rate of vocalisation.

Distinguishing between these explanations would require a more intensive video recording setup, with multiple camera angles that would allow us better visual access to the dogs while feeding to determine whether previously unseen agonistic interactions are happening. For management purposes, the differences in vocalisation use and behaviour during feeding is important. Establishing a social hierarchy is a vital element of successful pack formation (Marneweck et al., 2019), and while providing more food sources may aim to reduce competition, it may not have the intended effect in the context of the social complexity of wild dogs. It may therefore be wise to dedicate further study to feeding methods as an important element of species husbandry, and as a potential tool to monitor social cohesion during pack formation.

It is worth noting a particular limitation to this study, which is that data collection was, somewhat naturally, and in some cases necessarily, biased towards certain contexts and scenarios. The most unavoidable instance of this was that the Waterberg wild dogs, being a wild, free roaming pack, were not possible to follow and record in the same way as the captive packs. Our Waterberg data is therefore biased towards feeding, as this was our sole opportunity to observe these dogs. Another unavoidable factor was the difference in size between our study packs, with two fifteen-strong packs and one consisting of two individuals housed separately. The data was not divided to produce individual rates or numbers; this would not, comparatively, have affected Bothongo or Waterberg, and for Joburg, it would not accurately reflect vocalisation use and would therefore not be comparable to the larger packs in which social interaction was possible. This should have biased the larger packs towards larger rates and numbers of vocalisations. In this case though, the findings suggest that the decision not to account for pack size was at least interesting; rate differences between Bothongo and Waterberg were found during feeding, and no difference was found between any pack's overall, resting, or keeper presence related rate. Finally, rest was an under-represented context considering wild dogs spend much of the midday at rest (Creel et al., 1997). The rest context was less vocal than the feeding events and in both captive packs, where more freedom over data collection patterns was possible, predicatble periods of rest were more often used for breaks in collection, and were therefore recorded less, introducing a possible bias in the data towards more active and vocal contexts. Calculating rates and examining contexts separately does work towards overcoming this, however there is undoubtedly some amount of bias present towards more vocal events.

A more general limitation to this study was that a small dataset forced some data to be grouped, limiting the detail with which vocalisations and behaviours could be linked. For example, when linking specific vocalisations with behaviours, dominance behaviour directed towards other pack members was not distinguished from dominance behaviours directed towards the keeper. These types of distinctions could help to understand vocalisations and behaviour in more detail,

such as whether the vocalisations used during a display of dominance show a particular pattern of use, and whether communication used within the pack is distinct from vocalisations directed externally. Additionally, behaviours that are not associated with vocalisations should also be scored, such that the strength of the association can be measured by objective, robust statistical methods. This would facilitate a more detailed analysis of vocalisation and behaviour, for example whether the less-often observed vocalisations may be used within stricter contexts.

Previous literature seems to lack a precedent for such an approach: Salmi et al. (2013) makes some progress towards a distinction between general-use or context-specific vocalisation types, but still primarily relies on rates of vocalisation for analysis. In Déaux & Clarke (2013), the variability of both acoustic parameters of vocalisations and the contexts with which they were associated ruled out a systematic quantification of the associations between behaviour and vocalisation. Wadewitz et al. (2015) describes objective, quantitative methods of describing vocal repertoires, but with a focus on the acoustic structure of vocalisations, however this also proved challenging due to the gradation between call types in complex vocal repertoires. Ultimately, as in Brady (1981), Knörnschild et al. (2010), and Robbins (2000), characterisations of vocal repertoires typically rely on qualitatively matching the contexts and behaviours with vocalisations. There are, however, statistical methods which can model the relationship between multiple categorical variables, which may facilitate this type of behaviour-vocalisation association model but require a larger dataset than was presently collected. A systematic statistical analysis of the relationships between vocalisations and their associated behaviours could provide a more accurate interpretation of vocalisations; for wild dogs, this could translate into more directed management tools, for example to acutely assess social cohesion in temporary captivity.

This study adds another piece to the puzzle of wild dog vocalisations and behaviour, but also raises further questions. For example, Robbins (2000) discusses the frequent use of mixed vocalisations by wild dogs, which add another layer of complexity to the function and acoustic qualities of the wild dog vocal repertoire. Mixed vocalisations were not specifically addressed in this study, primarily because it was too challenging to determine whether overlapping or rapidly produced vocalisations originated from one or multiple dogs. Some of the previously suggested improvements could shed light on mixed vocalisations; for example, more camera angles could help to distinguish which dog is vocalising.

The classification of wild dog vocalisations, and those of other mammals, could be benefitted by the application of automatic recognition. This has been deployed successfully to automate the recognition of bird species (Xie et al., 2023) and to some extent bat species (Russo & Voigt, 2016), however an initial attempt to automate the classification of wild dog vocalisations was unsuccessful (Pia Riddell, pers. comm.). If only one development could be made to the methodology of this study, it would be integrating automated vocalisation recognition to improve the efficiency of vocalisation classification.

Some vocalisations are used more frequently and along with more categories of behaviour than others. Eight vocalisations are seen associated with only one or two categories of behaviour:

alarm barks, alarm growls, buzz gurgle moans, howl barks, and tremolo alarm barks are almost exclusively associated with dominance behaviour, which contributes useful information towards the determination of the emotional state of packs using vocalisations. Gurgles, huffs, and staccato begging cries were also observed with two categories of behaviour: gurgles with aggression and submission, huffs with feeding and play, and staccato begging cries with feeding and submission. However, some of these were observed very few times so it remains difficult to say with confidence that they are strongly associated with one type of behaviour: for example, buzz gurgle moans were observed only twice, and howl barks

Conclusion

The vocal repertoire of wild dogs is complex, but there are patterns of association between vocalisation use and behaviour. The vocal repertoire associated with agonistic interactions, particularly dominance and aggression behaviours, consists of at least five vocalisation types: alarm barks, alarm growls, attack barks, tremolo alarm barks, and attack twitters, which are used extensively when human keepers are present. Affiliative and play behaviours show a wider range of associated vocalisations, which may reflect the social and communicative complexity inherent to these behaviours. Similarly, feeding is a context associated with complex vocalisation use, but this differs between packs, possibly due to demographic or husbandry differences. Both captive packs used more dominance related vocalisations compared to the wild pack, in which more submission related vocalisations were found. In general, studies aiming to classify vocal repertoires of any species could benefit from the use of artificial intelligence technologies to improve the efficiency of classification and to facilitate analysis of specific acoustic parameters, which may also be key to analysing variation. These findings have the potential to inform management decisions for wild dogs by providing indicators for which vocalisations may relate to unwanted or dangerous behaviours, however identifying specific reasons behind these behaviours is likely to require further research.

Bibliography

Bartholomew, G. A., & Collias, N. E. (1962). The role of vocalization in the social behaviour of the northern elephant seal. *Animal Behaviour*, *10*(1–2), 7–8. https://doi.org/10.1016/0003-3472(62)90124-0

Blumstein, D. T., & Armitage, K. B. (1997). Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls. *Animal Behaviour*, *53*(1), 143–171. https://doi.org/10.1006/anbe.1996.0285

Boughman, J. W., & Wilkinson, G. S. (1998). Greater spear-nosed bats discriminate group mates by vocalizations. *Animal Behaviour*, *55*(6), 1717–1732. https://doi.org/10.1006/anbe.1997.0721

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*(3), 649–669. https://doi.org/10.1016/S0003-3472(81)80001-2

Briefer, E. F., Maigrot, A. L., Mandel, R., Freymond, S. B., Bachmann, I., & Hillmann, E. (2015). Segregation of information about emotional arousal and valence in horse whinnies. *Scientific Reports*, *4*, 1–12. https://doi.org/10.1038/srep09989

Campana, M. G., Parker, L. D., Hawkins, M. T. R., Young, H. S., Helgen, K. M., Szykman Gunther, M., Woodroffe, R., Maldonado, J. E., & Fleischer, R. C. (2016). Genome sequence, population history, and pelage genetics of the endangered African wild dog (Lycaon pictus). *BMC Genomics*, *17*(1), 1–11. https://doi.org/10.1186/s12864-016-3368-9

Clay, Z., Smith, C. L., & Blumstein, D. T. (2012). Food-associated vocalizations in mammals and birds: What do these calls really mean? *Animal Behaviour*, *83*(2), 323–330. https://doi.org/10.1016/j.anbehav.2011.12.008

Clubb, R., & Mason, G. (2003). Captivity effects on wide-ranging carnivores. *Nature*, *425*(6957), 473–474. https://doi.org/10.1038/425473a

Creel, S., & Creel, N. M. (1996). Limitation of African Wild Dogs by Competition with Larger Carnivores. *Conservation Biology*, *10*(2), 526–538. http://www.jstor.org/stable/2386867

Creel, S., & Creel, N. M. (1998). Six ecological factors that may limit African wild dogs, Lycaon pictus. *Animal Conservation*, *1*(1), 1–9. https://doi.org/10.1111/j.1469-1795.1998.tb00220.x

Creel, S., & Creel, N. M. (2002). *The African Wild Dog: Behavior, Ecology, and Conservation*.

Creel, S., Creel, N. M., Mills, M. G. L., & Monfort, S. L. (1997). Rank and reproduction in cooperatively breeding african wild dogs: Behavioral and endocrine correlates. *Behavioral Ecology*, *8*(3), 298–306. https://doi.org/10.1093/beheco/8.3.298

Crossey, B., Chimimba, C., Plessis, C. Du, Hall, G., & Ganswindt, A. (2020). Using faecal glucocorticoid metabolite analyses to elucidate stressors of African wild dogs Lycaon pictus from South Africa. *Wildlife Biology*, *2020*(1), 1–10. https://doi.org/10.2981/wlb.00646

Davies-Mostert, H. T., Mills, M. G. L., & Macdonald, D. W. (2009). A Critical Assessment of South Africa's Managed Metapopulation Recovery Strategy for African Wild Dogs. In M. J. Somers & M. W. Hayward (Eds.), *Reintroduction of Top-Order Predators* (pp. 10–42). Wiley-Blackwell, ZSL.

Déaux, É. C., & Clarke, J. A. (2013). Dingo (Canis lupus dingo) acoustic repertoire: form and contexts. *Behaviour*, *150*(1), 75–101. https://doi.org/10.1163/1568539X-00003038

Drews, C. (1993). The concept and definition of dominance in animal behaviour. *Behaviour*, *125*(3–4), 283–313. https://doi.org/10.1163/156853993X00290

Estes, R. D., & Goddard, J. (1967). Prey Selection and Hunting Behavior of the African Wild Dog. *The Journal of Wildlife Management*, *31*(1), 52–70.

Faragó, T., Townsend, S., & Range, F. (2014). The Information Content of Wolf (and Dog) Social Communication. In *Biocommunication of Animals* (Vol. 9789400774, pp. 41–62). Springer Netherlands. https://doi.org/10.1007/978-94-007-7414-8_4

Fischer, J., Kitchen, D. M., Seyfarth, R. M., & Cheney, D. L. (2004). Baboon loud calls advertise male quality:

acoustic features and their relation to rank, age, and exhaustion. *Behavioral Ecology and Sociobiology*, *56*(2), 140–148. https://doi.org/10.1007/s00265-003-0739-4

Frame, L. H., Malcolm, J. R., Frame, G. W., & van Lawick, H. (1979). Social Organization of African Wild Dog on the Serengeti Plains. *Zeitschrift Für Tierpsychologie*, *50*, 225–2. https://repository.si.edu/bitstream/handle/10088/11584/Frame1979.pdf

Gusset, M., Ryan, S. J., Hofmeyr, M., van Dyk, G., Davies-Mostert, H. T., Graf, J. A., Owen, C., Szykman, M., Macdonald, D. W., Monfort, S. L., Wildt, D. E., Maddock, A. H., Mills, M. G. L., Slotow, R., & Somers, M. J. (2008). Efforts going to the dogs? Evaluating attempts to re-introduce endangered wild dogs in South Africa. *Journal of Applied Ecology*, *45*(1), 100–108. https://doi.org/10.1111/j.1365-2664.2007.01357.x

Gusset, M., Slotow, R., & Somers, M. J. (2006). Divided we fail: the importance of social integration for the re-introduction of endangered African wild dogs (Lycaon pictus). *Journal of Zoology*, *270*(3), 502–511. https://doi.org/10.1111/j.1469-7998.2006.00168.x

Hallberg, K. I. (2007). *Information in a long-distance vocal signal: chorus howling in the coyote (Canis latrans)* [The Ohio State University]. file:///C:/Users/USUARIO/Desktop/NEUROSICOLOGIA2/NEUROPSICOLOGÍA CLÍNICA (Ardila y Roselli)2.pdf

Harrington, F. H., & Mech, L. D. (1979). Wolf Howling and Its Role in Territory Maintenance. *Behaviour*, *68*(3–4), 207–249. https://doi.org/10.1163/156853979X00322

Harrington, F. H., & Mech, L. D. (1983). Wolf pack spacing: Howling as a territory-independent spacing mechanism in a territorial population. *Behavioral Ecology and Sociobiology*, *12*(2), 161–168. https://doi.org/10.1007/BF00343208

Hartwig, S. (2005). Individual acoustic identification as a non-invasive conservation tool: An approach to the conservation of the african wild dog lycaon pictus (temminck, 1820). *Bioacoustics*, *15*(1), 35–50. https://doi.org/10.1080/09524622.2005.9753537

Hasegawa, M., & Arai, E. (2016). Female Attraction to Higher Pitched Male Enticement Calls in Barn Swallows. *Ethology*, *122*(5), 430–441. https://doi.org/10.1111/eth.12492

Jordan, N. R., Golabek, K. A., Behr, D. M., Walker, R. H., Plimpton, L., Lostrom, S., Claase, M., van der Weyde, L. K., & McNutt, J. W. (2022). Priority of access to food and its influence on social dynamics of an endangered carnivore. *Behavioral Ecology and Sociobiology*, *76*(1). https://doi.org/10.1007/s00265-021-03115-z

Jule, K. R., Leaver, L. A., & Lea, S. E. G. (2008). The effects of captive experience on reintroduction survival in carnivores: A review and analysis. *Biological Conservation*, *141*(2), 355–363. https://doi.org/10.1016/j.biocon.2007.11.007

Kershenbaum, A., Root-Gutteridge, H., Habib, B., Koler-Matznick, J., Mitchell, B., Palacios, V., & Waller, S. (2016). Disentangling canid howls across multiple species and subspecies: Structure in a complex communication channel. *Behavioural Processes*, *124*(JANUARY), 149–157. https://doi.org/10.1016/j.beproc.2016.01.006

King, S. L., Allen, S. J., Krützen, M., & Connor, R. C. (2019). Vocal behaviour of allied male dolphins during cooperative mate guarding. *Animal Cognition*, *22*(6), 991–1000. https://doi.org/10.1007/s10071-019-01290-1

Knörnschild, M., Glckner, V., & Helversen, O. Von. (2010). The vocal repertoire of two sympatric species of nectar-feeding bats (Glossophaga soricina and G. commissarisi). *Acta Chiropterologica*, *12*(1), 205–215. https://doi.org/10.3161/150811010X504707

Kühme, W. (1965). Communal Food Distribution and Division of Labour in African Hunting Dogs. *Nature Publishing Group*, *208*(5007), 239–241.

Lehner, P. N. (1978). Coyote vocalizations: A lexicon and comparisons with other canids. *Animal Behaviour*, *26*(PART 3), 712–722. https://doi.org/10.1016/0003-3472(78)90138-0

Leus, K. (2011). Captive breeding and conservation. *Zoology in the Middle East*, *54*(2011), 151–158.

https://doi.org/10.1080/09397140.2011.10648906

Malmkvist, J. (2019). Early recognition of offspring vocalisation by mink mothers. *Applied Animal Behaviour Science*, *212*, 109–113. https://doi.org/10.1016/j.applanim.2018.12.011

Marneweck, C., Becker, P. A., Beverley, G., Davies-Mostert, H. T., du Plessis, C., Forssman, K., Graf, J. A., Gusset, M., Hofmeyr, M., Kelly, C., Kilian, P. J., Marchal, A. F. J., Marneweck, D. G., Marnewick, K., Owen, C., Postiglione, G., Slotow, R., Somers, M. J., Szykman Gunther, M., … Parker, D. M. (2019). Factors affecting the success of artificial pack formation in an endangered, social carnivore: the African wild dog. *Animal Conservation*, *22*(5), 493–502. https://doi.org/10.1111/acv.12490

Marneweck, D. G., Druce, D. J., & Somers, M. J. (2019). Food, family and female age affect reproduction and pup survival of African wild dogs. *Behavioral Ecology and Sociobiology*, *73*(5), 65. https://doi.org/10.1007/s00265-019-2676-x

Mazzini, F., Townsend, S. W., Virányi, Z., & Range, F. (2013). Wolf howling is mediated by relationship quality rather than underlying emotional stress. *Current Biology*, *23*(17), 1677–1680. https://doi.org/10.1016/j.cub.2013.06.066

McComb, K., & Semple, S. (2005). Coevolution of vocal communication and sociality in primates. *Biology Letters*, *1*(4), 381–385. https://doi.org/10.1098/rsbl.2005.0366

McNutt, J. W. (1996). Sex-biased dispersal in African wild dogs, Lycaon pictus. *Animal Behaviour*, *52*(6), 1067–1077. https://doi.org/10.1006/anbe.1996.0254

Milewski, T. M., Lee, W., Champagne, F. A., & Curley, J. P. (2022). Behavioural and physiological plasticity in social hierarchies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *377*(1845). https://doi.org/10.1098/rstb.2020.0443

Mills, M. G. L., & Gorman, M. L. (1997). Factors Affecting the Density and Distribution of Wild Dogs in the Kruger National Park. *Conservation Biology*, *11*(6), 1397–1406. http://www.jstor.org/stable/2387366

Mitchell, B. R., Makagon, M. M., Jaeger, M. M., & Barrett, R. H. (2006). Information Content of coyote barks and howls. *Bioacoustics*, *15*(3), 289–314. https://doi.org/10.1080/09524622.2006.9753555

Morton, E. S. (1977). On the Occurrence and Significance of Motivation-Structural Rules in Some Bird and Mammal Sounds. *The American Naturalist*, *111*(981), 855–869. https://doi.org/10.1086/283219

Nicholson, S. K., Marneweck, D. G., Lindsey, P. A., Marnewick, K., & Davies-Mostert, H. T. (2020). A 20-Year Review of the Status and Distribution of African Wild Dogs (Lycaon pictus) in South Africa. *African Journal of Wildlife Research*, *50*(1), 8–19. https://doi.org/10.3957/056.050.0008

Ordóñez-Gómez, J. D., Dunn, J. C., Arroyo-Rodríguez, V., Méndez-Cárdenas, M. G., Márquez-Arias, A., & Santillán-Doherty, A. M. (2015). Role of Emitter and Severity of Aggression Influence the Agonistic Vocalizations of Geoffroy's Spider Monkeys (Ateles geoffroyi). *International Journal of Primatology*, *36*(2), 429–440. https://doi.org/10.1007/s10764-015-9833-5

Packer, C., Pusey, A. E., & Eberly, L. E. (2001). Egalitarianism in female African lions. *Science*, *293*(5530), 690–693. https://doi.org/10.1126/science.1062320

Palacios, V., Font, E., Márquez, R., & Carazo, P. (2015). Recognition of familiarity on the basis of howls: A playback experiment in a captive group of wolves. *Behaviour*, *152*(5), 593–614. https://doi.org/10.1163/1568539X-00003244

Palagi, E., Burghardt, G. M., Smuts, B., Cordoni, G., Dall'Olio, S., Fouts, H. N., Řeháková-Petrů, M., Siviy, S. M., & Pellis, S. M. (2016). Rough-and-tumble play as a window on animal communication. *Biological Reviews*, *91*(2), 311–327. https://doi.org/10.1111/brv.12172

Paris, D. B. B. P., Riddell, P., Joone, C., de la Rey, M., Ganswindt, A., & Paris, M. C. J. (2024). Cold dogs: Sperm freezing, artificial insemination & non-invasive monitoring tools to facilitate a hybrid conservation management approach for endangered African wild dogs. *Theriogenology Wild*, *4*(January), 100073. https://doi.org/10.1016/j.therwi.2024.100073

Potgieter, K.R., Whittington-Jones, B., Gusset, M., Mills, M. G. L., & Davies-Mostert, H. T. (2012). *The South African Wild Dog Metapopulation Compendium*. *January*.

Potgieter, Katherine R., O'Riain, M. J., & Davies-Mostert, H. T. (2015). Behavioural Cues Can be Used to Predict the Outcome of Artificial Pack Formation in African Wild Dogs (Lycaon pictus). *African Journal of Wildlife Research*, *45*(2), 215. https://doi.org/10.3957/056.045.0215

Prager, K. C., Mazet, J. A. K. K., Dubovi, E. J., Frank, L. G., Munson, L., Wagner, A. P., & Woodroffe, R. (2012). Rabies Virus and Canine Distemper Virus in Wild and Domestic Carnivores in Northern Kenya: Are Domestic Dogs the Reservoir? *EcoHealth*, *9*(4), 483–498. https://doi.org/10.1007/s10393-013-0815-9

Rabaiotti, D., Groom, R., McNutt, J. W., Watermeyer, J., O'Neill, H. M. K., & Woodroffe, R. (2021). High temperatures and human pressures interact to influence mortality in an African carnivore. *Ecology and Evolution*, *11*(13), 8495–8506. https://doi.org/10.1002/ece3.7601

Rauber, R., & Manser, M. B. (2017). Discrete call types referring to predation risk enhance the efficiency of the meerkat sentinel system. *Scientific Reports*, *7*(November 2016), 1–9. https://doi.org/10.1038/srep44436

Robbins, R. L. (2000). Vocal communication in free-ranging African wild dogs (Lycaon pictus). *Behaviour*, *137*(10), 1271–1298. https://doi.org/10.1163/156853900501926

Robbins, R. L., & McCreery, E. K. (2003). African Wild Dog Pup Vocalizations with Special Reference to Morton's Model. *Behaviour*, *140*(3), 333–351. http://www.jstor.org/stable/4536030

Russo, D., & Voigt, C. C. (2016). The use of automated identification of bat echolocation calls in acoustic monitoring: A cautionary note for a sound analysis. *Ecological Indicators*, *66*, 598–602. https://doi.org/10.1016/j.ecolind.2016.02.036

Rütten, S., & Fleissner, G. (2004). On the function of the greeting ceremony in social canids – exemplified by African wild dogs Lycaon pictus. *Canid News*, *7.3*.

Salmi, R., Hammerschmidt, K., & Doran-Sheehy, D. M. (2013). Western Gorilla Vocal Repertoire and Contextual Use of Vocalizations. *Ethology*, *119*(10), 831–847. https://doi.org/10.1111/eth.12122

Scheumann, M., Roser, A. E., Konerding, W., Bleich, E., Hedrich, H. J., & Zimmermann, E. (2012). Vocal correlates of sender-identity and arousal in the isolation calls of domestic kitten (Felis silvestris catus). *Frontiers in Zoology*, *9*, 1–14. https://doi.org/10.1186/1742-9994-9-36

Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour*, *28*(4), 1070–1094. https://doi.org/10.1016/S0003-3472(80)80097-2

Siniscalchi, M., d'Ingeo, S., Minunno, M., & Quaranta, A. (2018). Communication in dogs. *Animals*, *8*(8). https://doi.org/10.3390/ani8080131

Somers, M. J., & Gusset, M. (2009). The Role of Social Behaviour in Carnivore Reintroductions. *Reintroduction of Top-Order Predators*, *May*, 270–281. https://doi.org/10.1002/9781444312034.ch12

Sun, C., Jiang, T., Kanwal, J. S., Guo, X., Luo, B., Lin, A., & Feng, J. (2018). Great Himalayan leaf-nosed bats modify vocalizations to communicate threat escalation during agonistic interactions. *Behavioural Processes*, *157*(September), 180–187. https://doi.org/10.1016/j.beproc.2018.09.013

Szipl, G., Ringler, E., Spreafico, M., & Bugnyar, T. (2017). Calls during agonistic interactions vary with arousal and raise audience attention in ravens. *Frontiers in Zoology*, *14*(1), 1–13. https://doi.org/10.1186/s12983-017-0244-7

Tilson, R. L., & Hamilton, W. J. (1984). Social dominance and feeding patterns of spotted hyaenas. *Animal Behaviour*, *32*(3), 715–724. https://doi.org/10.1016/S0003-3472(84)80147-5

Tooze, Z. J., Harrington, F. H., & Fentress, J. C. (1990). Individually distinct vocalizations in timber wolves, Canis lupus. *Animal Behaviour*, *40*(4), 723–730. https://doi.org/10.1016/S0003-3472(05)80701-8

Trillmich, J., Fichtel, C., & Kappeler, P. M. (2004). Coordination of group movements in wild Verreaux's sifakas (Propithecus verreauxi). *Behaviour*, *141*(9), 1103–1120. https://doi.org/10.1163/1568539042664579

van den Berghe, F., Paris, M. C. J., Sarnyai, Z., Millar, R. P., Ganswindt, A., Cozzi, A., Pageat, P., & Paris, D. B. B. P. (2019). Dog Appeasing Pheromone prevents the testosterone surge , and may reduce contact-dominance and active-submission behaviours after interventions in captive African wild dogs (Lycaon

pictus). Discussion-Conclusion. *PLoS ONE*, *14*(3), e0212551.

Wadewitz, P., Hammerschmidt, K., Battaglia, D., Witt, A., Wolf, F., & Fischer, J. (2015). Characterizing vocal repertoires - Hard vs. Soft classification approaches. *PLoS ONE*, *10*(4), 1–16. https://doi.org/10.1371/journal.pone.0125785

Walker, R. H., King, A. J., McNutt, J. W., & Jordan, N. R. (2017). *Sneeze to leave African wild dogs Lycaon pictususe use variable quorum thresholds facilitated by sneezes in collective decisions*.

Wheeler, B. C. (2010). Production and perception of situationally variable alarm calls in wild tufted capuchin monkeys (Cebus apella nigritus). *Behavioral Ecology and Sociobiology*, *64*(6), 989–1000. https://doi.org/10.1007/s00265-010-0914-3

Whitehead, H., Antunes, R., Gero, S., Wong, S. N. P., Engelhaupt, D., & Rendell, L. (2012). Multilevel Societies of Female Sperm Whales (Physeter macrocephalus) in the Atlantic and Pacific: Why Are They So Different? *International Journal of Primatology*, *33*(5), 1142–1164. https://doi.org/10.1007/s10764-012-9598-z

Whittington-Jones, B. M., Parker, D. M., Bernard, R. T. F., & Davies-Mostert, H. T. (2014). Habitat selection by transient African wild dogs (Lycaon pictus) in northern KwaZulu-Natal, South Africa: Implications for range expansion. *African Journal of Wildlife Research*, *44*(2), 135–147. https://doi.org/10.3957/056.044.0201

Witzenberger, K. A., & Hochkirch, A. (2011). Ex situ conservation genetics: A review of molecular studies on the genetic consequences of captive breeding programmes for endangered animal species. *Biodiversity and Conservation*, *20*(9), 1843–1861. https://doi.org/10.1007/s10531-011-0074-4

Woodroffe, R., Davies-Mostert, H. T., Ginsberg, J., Graf, J. A., Leigh, K., McCreery, K., Robbins, R. L., Mills, G., Pole, A., Rasmussen, G., Somers, M. J., & Szykman, M. (2007). Rates and causes of mortality in Endangered African wild dogs Lycaon pictus : lessons for management and monitoring. *Oryx*, *41*(2), 215–223. https://doi.org/10.1017/S0030605307001809

Woodroffe, R., Ginsberg, J. ., & Macdonald, D. . (1997). The African Wild Dog Status Survey and Conservation Action PLan. In *IUCN/SSC Canid Specialist Group*.

Woodroffe, R., & Ginsberg, J. R. (1999). Conserving the African wild dog Lycaon pictus. I. Diagnosing and treating causes of decline. *Oryx*, *33*(2), 132–142. https://doi.org/10.1046/j.1365-3008.1999.00052.x

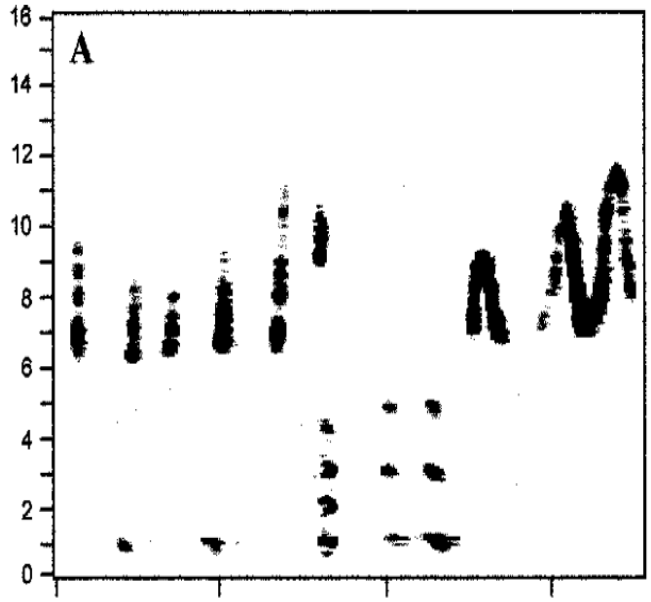
Woodroffe, R., & Sillero-Zubini, C. (2011). African wild dog (Lycaon pictus): Supplementary Material. *The IUCN Red List of Threatened Species*, 1–7. http://www.speciesconservation.org/case-studies-projects/african-wild-dog/1421

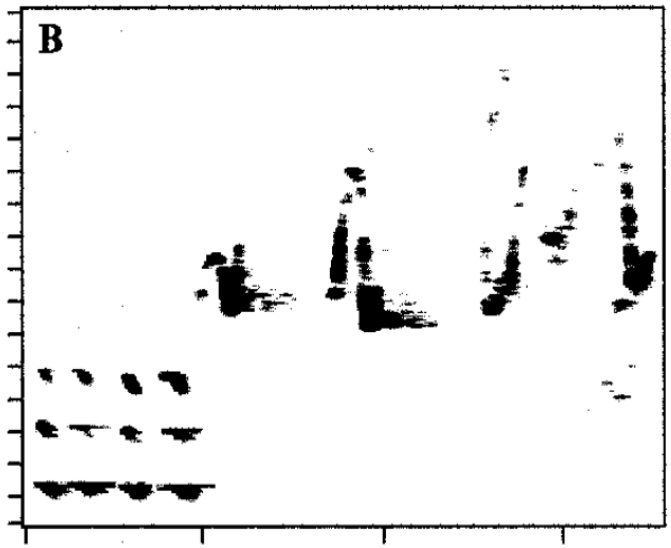
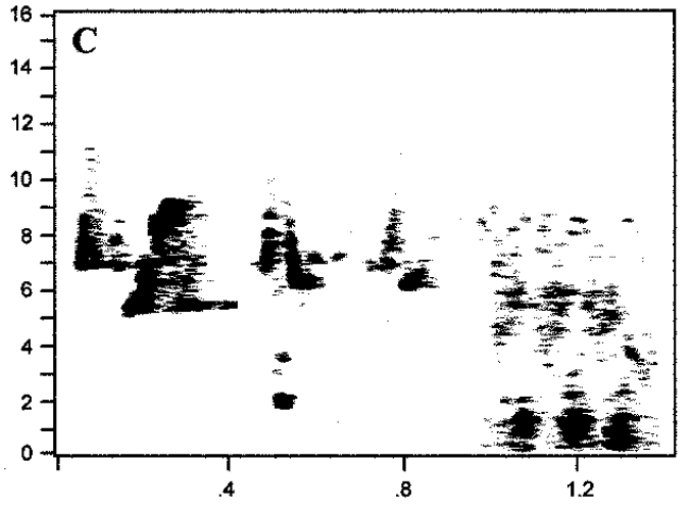
Xie, J., Zhong, Y., Zhang, J., Liu, S., Ding, C., & Triantafyllopoulos, A. (2023). A review of automatic recognition technology for bird vocalizations in the deep learning era. *Ecological Informatics*, *73*(November 2022), 101927. https://doi.org/10.1016/j.ecoinf.2022.101927

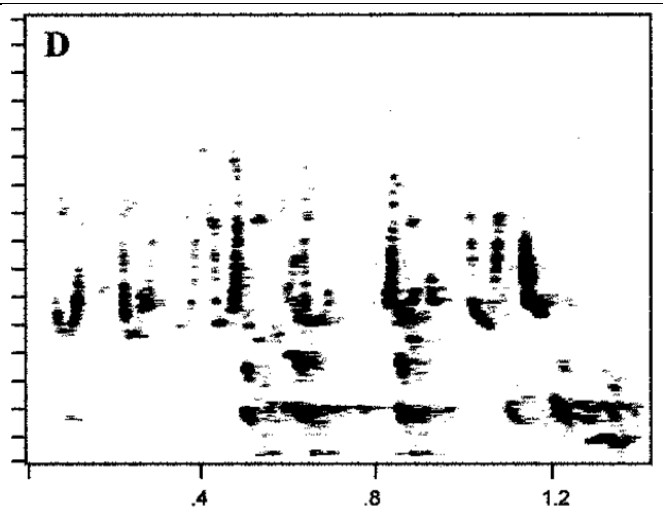
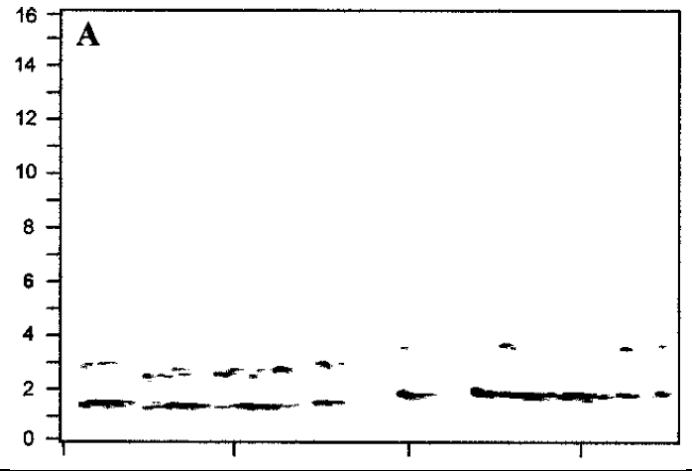
Yin, S., & McCowan, B. (2004). Barking in domestic dogs: context specificity and individual identification. *Animal Behaviour*, *68*(2), 343–355. https://doi.org/10.1016/j.anbehav.2003.07.016

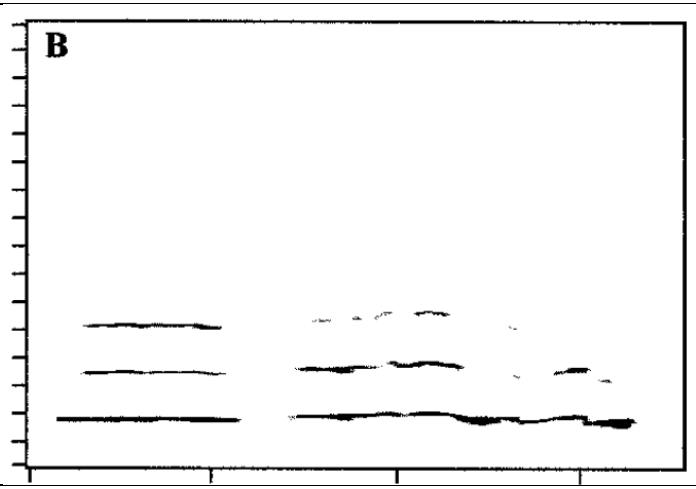
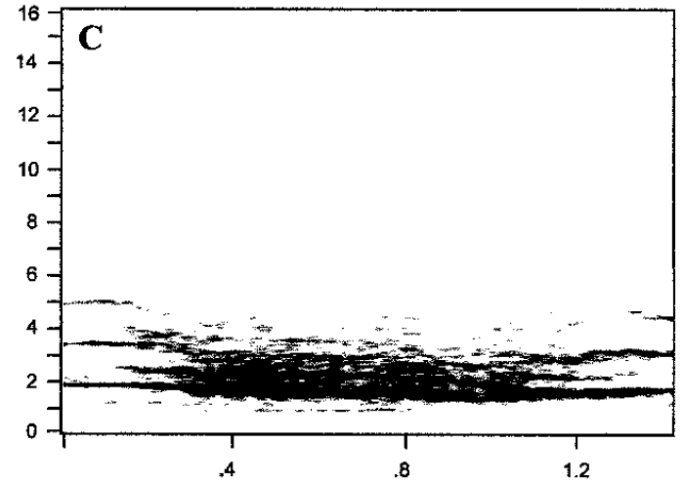
Supplementary Material

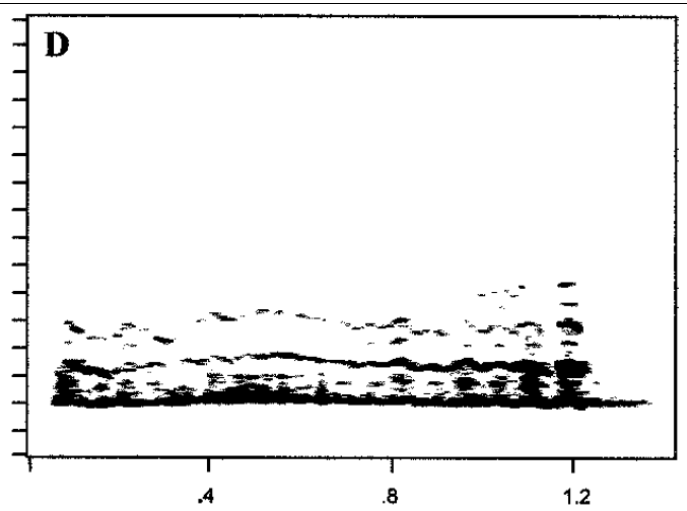
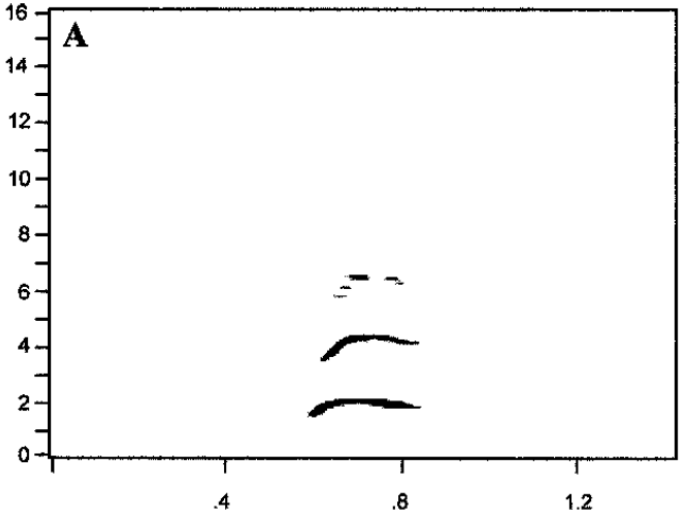
Supplementary Table 1: Vocal ethogram of vocalisations, contexts and acoustic parameters from African wild dogs (*Lycaon pictus*; modified from Robbins 2000)

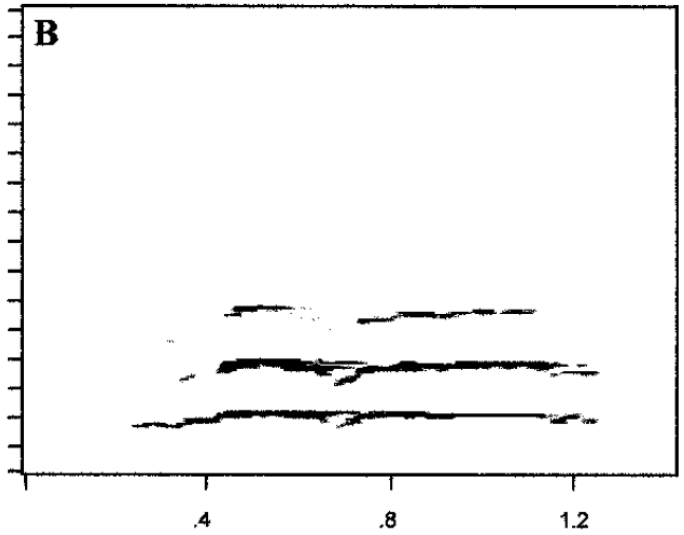
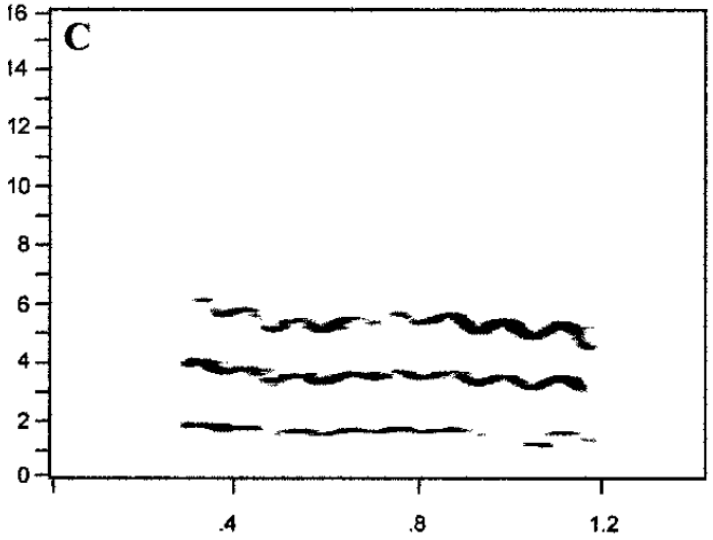
Call ID	**Spectrogram**	**Context**	**Acoustic burst lengths**	**Bouts**
Twitters				
Social Twitter - Low and high freq range (high predominant) - Noisy and harmonic		Vocal accompaniments in greeting ceremonies and along with gestures, serve to reinforce social bonds. Sometimes given during resting when individuals reposition themselves or approach another animal. Typically given during high arousal	0.2-6.0 sec	Up to 83.0 sec

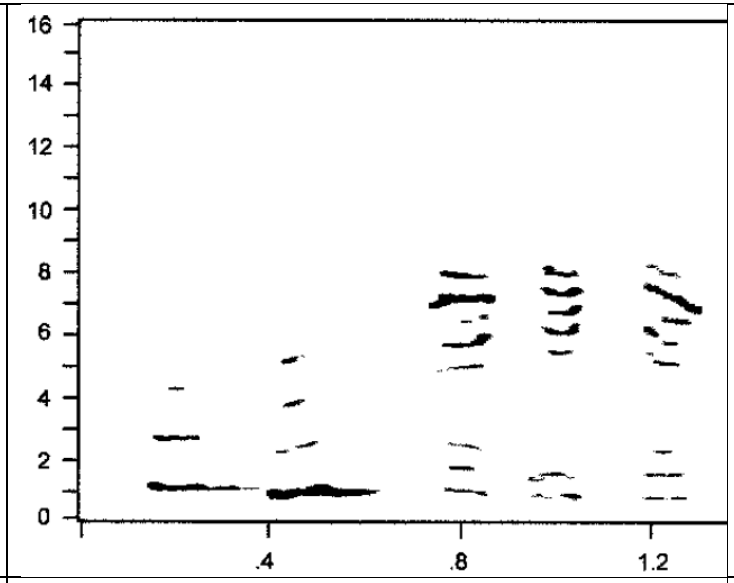
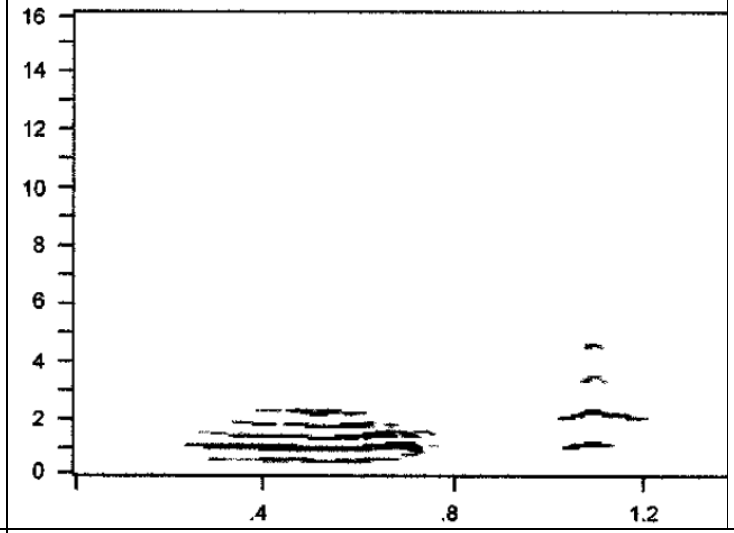
Spar Twitter - Low frequency component more common - High freq components often chevron shaped and energy uneven - Harmonic intervals greater and inter-syllable interval shorter		Vigorous play Appeasement Engaged in social investigation during pack formation	0.3-1.0 sec	Up to 6.3 sec
Mob Twitter - Low frequency generally suppressed - Noisy with breathy quality - Disyllabic with first syllable vertical – 0.05-0.2 sec and 0.2-0.5s between pairs		Mobbing other pack members Pursuing prey Chasing kleptoparasites from prey Resting pups when approached by adults as warning	0.9-1.8 sec	9.7 sec

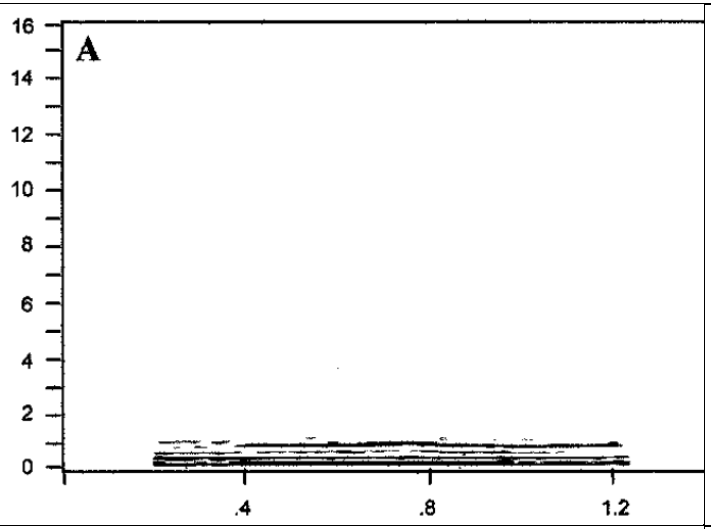
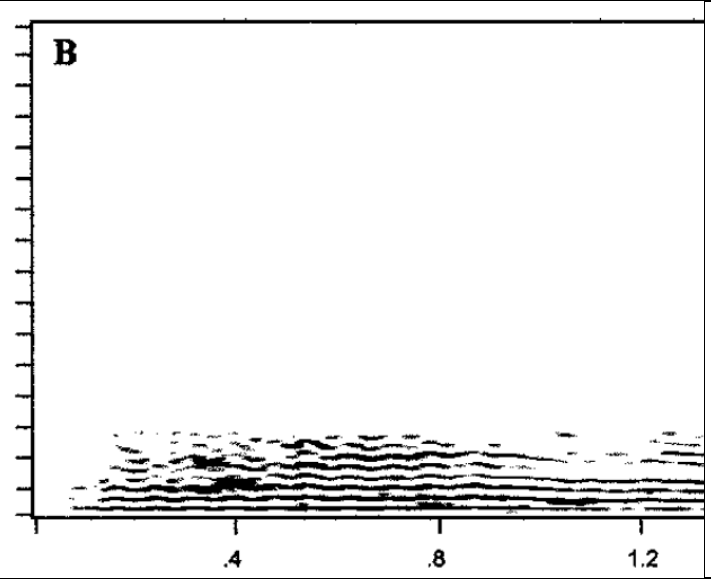
Attack twitter - Lower components more pronounced - Mostly noisy, low frequency - Nasal sound - High pitched U-shaped twitters		Packs chasing hyenas Interpack encounters Resting pups approached by adults	0.3-0.8 sec	Up to 6.8 sec
Begging cries				
Staccato		Food solicitation Greeting ceremonies (social solicitation) Distress (spectrally noisier	0.3-11.1 sec	0.5-137.0sec

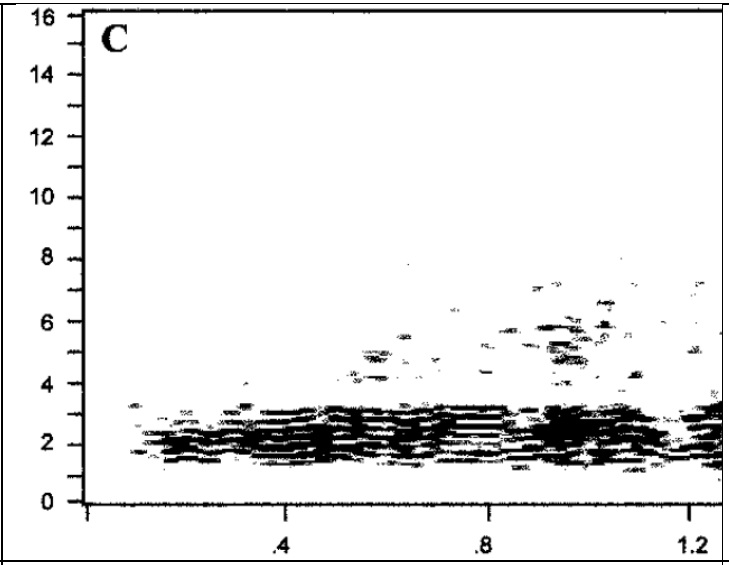
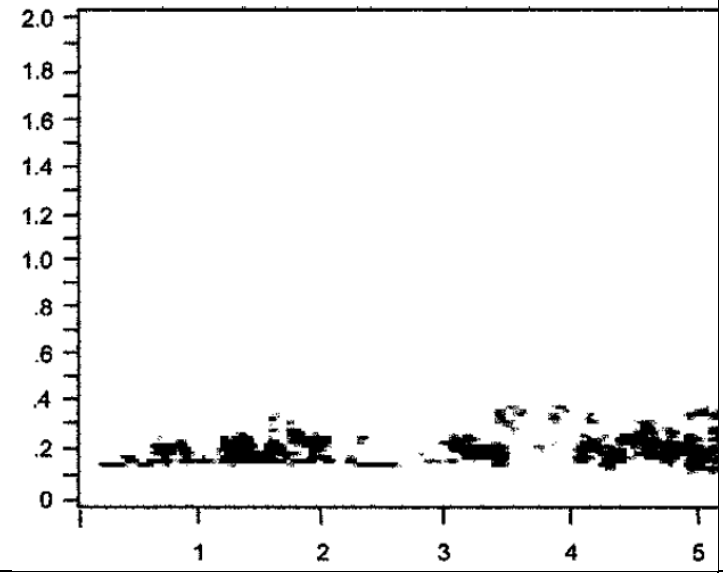
Steady-state and modulated		Food solicitation Greeting ceremonies (social solicitation) Distress (spectrally noisier		
Scream		Food solicitation Greeting ceremonies (social solicitation) Distress (spectrally noisier		

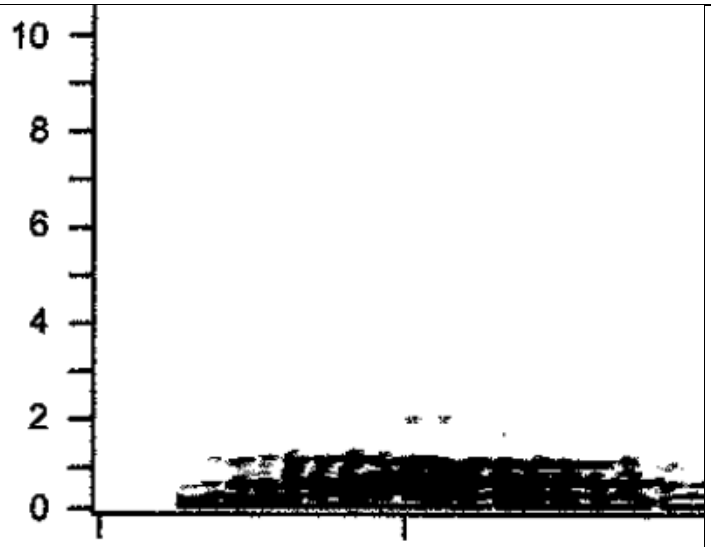
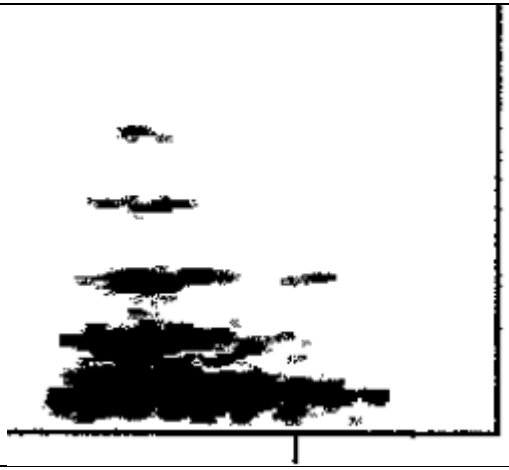
Gurgle		During peak arousal, begging cries can encapsulate noisy components that range from 0.1-0.3s in length and 1.0-3.0kHz in frequency. Aside from buzz moans longest syllable lengths		
Yelps/Squeals				
Yelps - Short, sharp sounds - Diagnostically convex		Submission by subordinates, anticipation or response to pain Given in appeasement and solicitation during greeting ceremonies		

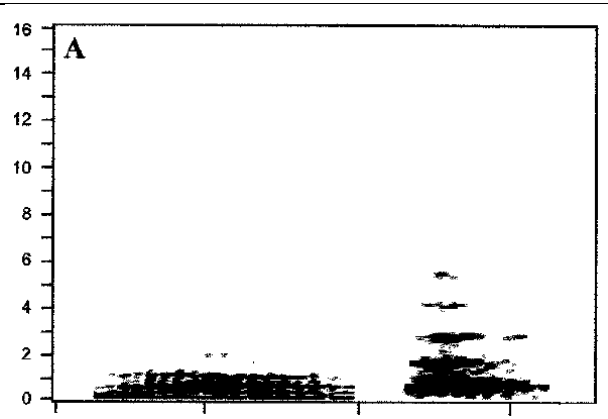
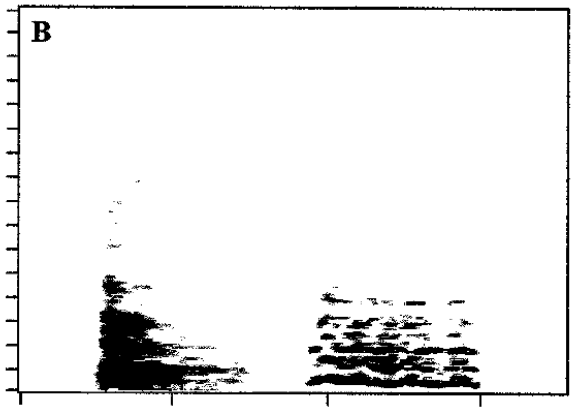
Whistle Squeals - Steady state or modulated - Syllable length 3x yelps - Single or multiple syllables - Intersyllable interval 0.04-0.06s		Similar contexts to yelps		
Begging Squeals - Diagnostically sinusoidal - Higher fundamentals and narrower freq ranges than yelps or whistle squeals		Greeting ceremonies Begging cry displays as an expression of solicitation and appeasement Can also accompany spar twitters		

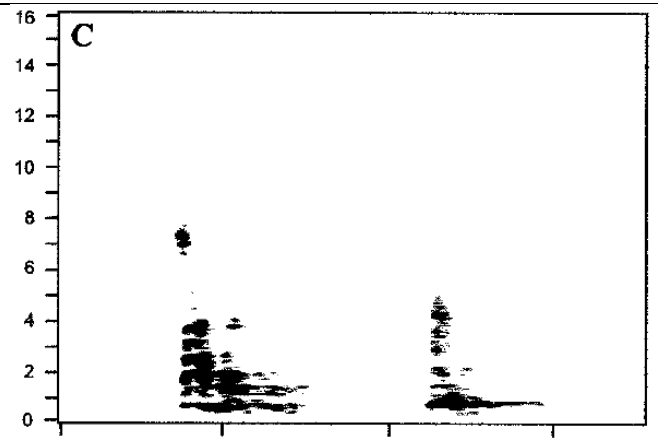
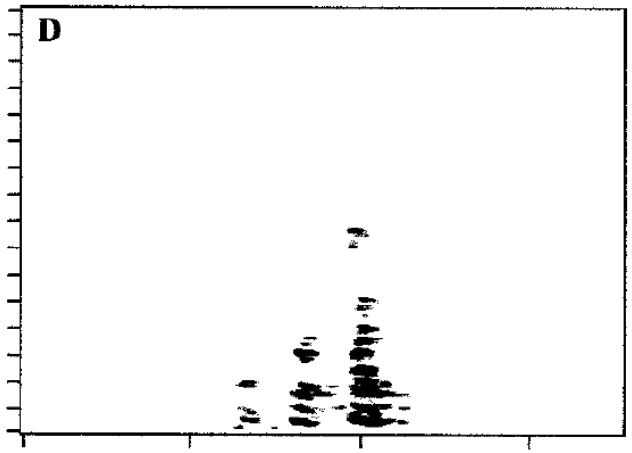
Whimpers - Low frequency, low-medium amplitude		Usually repetitive Given when dogs approach one another or reposition themselves during resting When pups call from den Greeting ceremonies Can be a sign of ambivalence during mobbing		
Whines - Low to high freq and low-med amplitude - Steady state or modulated - Harmonics pronounced and syllables not repeated		Mew like during greeting ceremonies Solicitation frustration		
Moans				

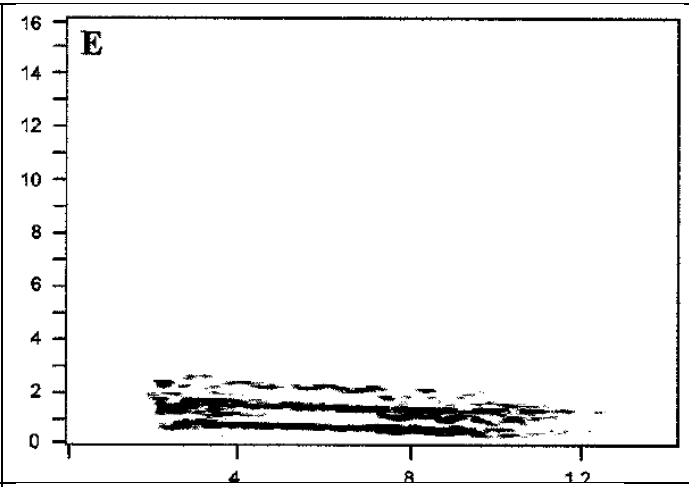
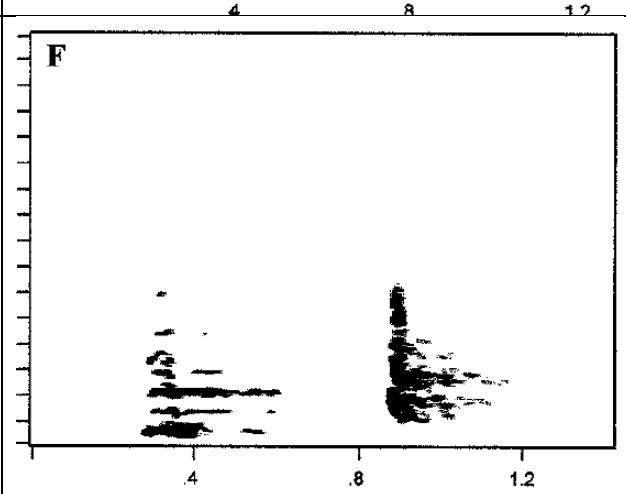
Full moan - Shortest syllables and narrowest freq		Indicate frustration		
Buzz moan - Longest syllable length of any vocalisations		Context specific to the initial excitatory phase of high intensity greeting ceremonies and begging cry displays		

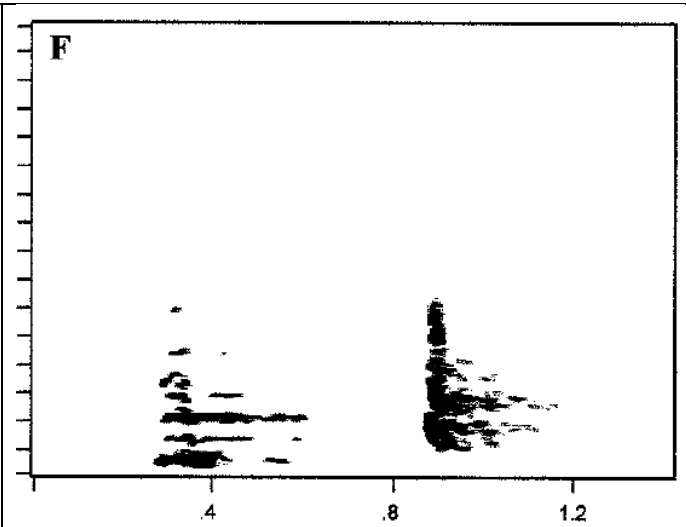
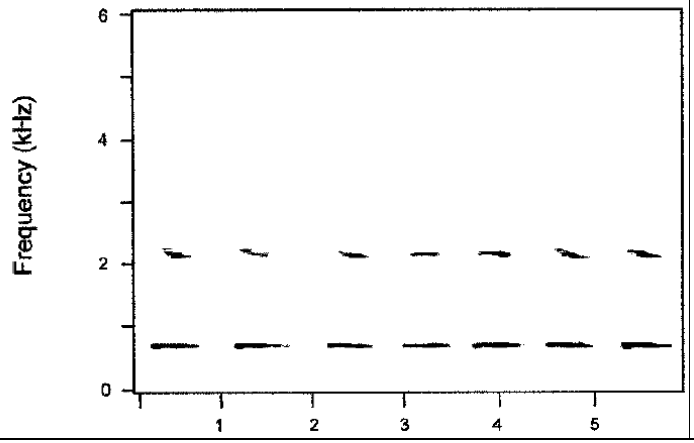
Buzz gurgle moan		Have greater fundamental freq. range than buzz moans alone		
Rumbles - Lowest sound - Staccato-like guttural components		Given during initial excitatory phase of greeting ceremonies		10 sec
Growls				

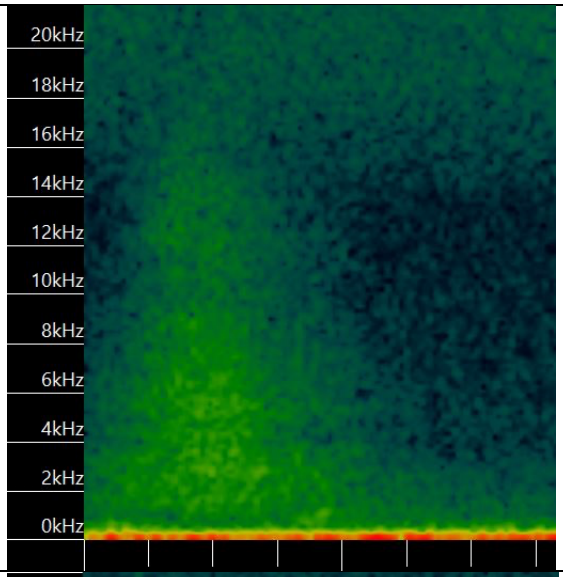
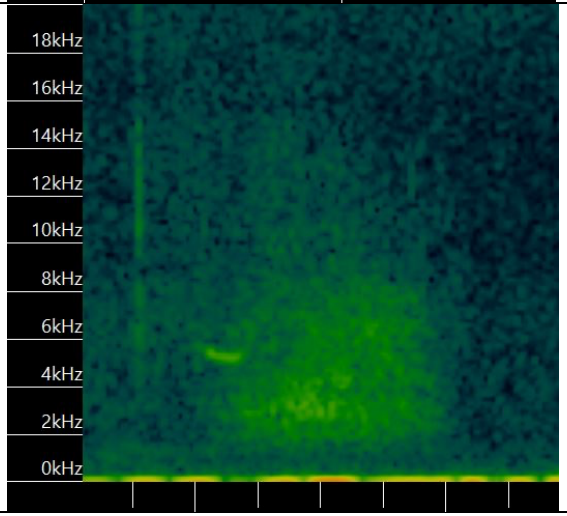
Social growls - Medium amplitude - Relatively uniform - Tight banded harmonics		Antagonistic interactions with other pack members		
Alarm growls - Shorter - Greater frequency spread - More amplified		Warn packs when confronted with a possible threat	0.5-6.3sec	13.5-106 sec
Barks				

Alarm barks (left) Common alarm bark growl like in appearance and auditory quality		Same motivational intensity as alarm growls, serve similar function		
Alarm bark Tremolo alarm bark Indicates higher level of arousal than common alarm bark		More harmonic & longer than common alarm bark More uniform distribution of energy over time Given in presence of lions or humans approaching Occasionally issued repeatedly with intersyllable intervals		

Threat barks Shorter than alarm Disyllabic Each syllable same relative length, separated by intervals 0.1-0.3sec		Express motivational ambivalence Given towards pups soliciting food Appear to signal muted aggression		
Attack Bark Shortest bark and most harmonic Harmonics strong and tightly banded Low to medium amplitude Nasal quality		Pack members chasing hyenas		

Howl Bark Longest bark Least frequency spread Uttered with tremolo		Frequency:0.3-0.5kHz Individual dogs running excitedly during intra-pack encounters		
Clear Bark (left) Mostly harmonic		Not often emitted Sharp barks Indicate alarm or affiliative interaction with pups		

Yelp Bark (right) Mostly noisy		Aggressively given when pack mobbing hyenas Can be affiliative		
Hoo Call Pulsed Monotonic Concatenations of single syllables		Long distance contact call Issued when dogs separated,		

Sneeze Rapid exhalation from the nose, apparently involuntarily and often repeated		Possibly used to co-ordinate collective movement (Walker et al, 2017), more distinction between the two is required		single
Huff Similar to sneezes, but less rapid and seemingly voluntary and not often repeated				single

Supplementary Table 2: Vocal ethogram of vocalisations and acoustic parameters from African wild dogs (*Lycaon pictus*; modified from Robbins (2000)).

Vocalisation	**Spectral type**	**Frequency range (kHz)**	**Syllable length (ms)**	**Intersyllable interval (ms)**	**Distinguishing features**
Twitters					
Social twitters	Low & high frequency: noisy /harmonic	0.4-2.5	30	100	At high frequency vertical and chevron components
Spar twitters	Low & high frequency: noisy /harmonic	0.4-25	30-300	50-300	At high frequency chevron components
Mob twitters	Medium frequency: noisy /harmonic High frequency: mostly noisy	0.5-14.0	20-50	50-800	Low frequency supressed Noisy with breathy quality Disyllabic with first syllable vertical
Attack twitters	Low frequency: mostly noisy High frequency: noisy /harmonic	0.2-12.0	20-60	40-400	Low frequency components more pronounced Nasal sounding High-pitched U-shaped twitters present
Begging cry	harmonic	0.5-5.5	30-220	20-600	Staccato, steady state, modulated or screams are spectrally different
Gurgles	Noisy /harmonic	0.3-1.8	300-5500	500-7000	Can encapsulate the noisy component of begging cries ranging from 0.1-0.3 seconds in length and 1.0-3.0kHz in frequency. Second longest syllable length of any vocalisation.
Yelp/squeal					
Yelp	Harmonic	0.7-7.0	100-300	NA	Short, sharp sound. Convex spectral shape

Whistle	harmonic	0.7-7.0	400-1000	NA	Steady-state or modulated. Single or multiple syllables.
Begging	harmonic	1.0-7.0	500-1000	NA	Sinusoidal shape to spectrogram.
Whimper	harmonic	0.-8.0	100-400	200-1500	Low frequency components with low-medium amplitude
Whine	Harmonic/richly harmonic	0.4-5.0	200-2700	NA	Low to high frequency range with low to medium amplitude. Can be steady-state or modulated. Harmonics pronounced and syllables not repeated.
Moans					
Full	Richly harmonic	0.1-1.2	200-1200	NA	Short syllables and narrow frequency bands.
Buzz	Richly harmonic	0.2-3.0	500-10,000	NA	Longest syllable length of any vocalisation.
Buzz Gurgle	Richly harmonic/noisy	0.2-30	500-10,000	NA	Greater fundamental frequency than buzz moans.
Rumbles	Mostly noisy	0.2-0.5	100-1300	20-200	Lowest sound. Staccato-like guttural components present.
Growls					
Social	Mostly noisy	0.2-1.5	400-800	NA	Relatively uniform frequency. Tight harmonic banding.
Alarm	Mostly noisy	0.3-2.0	200-400	500-6300	Greater frequency spread than social growls & greater amplification.
Barks					
Alarm (common)	Mostly noisy	0.2-4.5	100-600	500-6300	Growl-like in appearance and auditory quality.
Alarm (Tremolo)	Noisy/harmonic	0.5-4.5	600-700	500-6300	Tremolo bark. More harmonic and longer than common barks with more uniform distribution.
Threat	Noisy/harmonic	0.5-4.0	200-300	100-300	Disyllabic and each syllable approximately the same length.
Howl	Mostly harmonic	0.5-3.0	700-1200	4100-9300	Longest bark call Least amount of frequency spread of any vocalisation Uttered with tremolo.

Attack	Mostly harmonic	0.3-4.0	40-100	30-50	Shortest & most harmonic bark. Harmonics strong & tightly banded. Low to medium amplitude Nasal quality.
Clear	Mostly harmonic	0.3-4.0	100-400	NA	
Yelp	Mostly noisy harmonic	0.6-6.5	100-200	NA	
Hoo calls	harmonic	0.6-0.8	100-800	100-1400	Pulsatile, monotonic concatenations of single syllables.

Supplementary Table 3: Behaviour ethogram for African wild dogs (*Lycaon pictus*; modified from Van den Berghe et al., 2019b)

Behaviour	Description
Aggressive behaviour	
Assault	A brusque approach at full speed, often followed by an aggressive physical contact.
Severe biting	The actor has closed jaws and teeth having a strong hold of any part of the actor's body e.g. legs, tail, throat or head. The bite is with full strength (uninhibited).
Chase away	The actor walks or runs in pursuit to elicit a flee response from the recipient.
Push Down	The actor presses down the recipient by an inhibited bite in the neck.
Aggressive Embrace	The actor embraces the neck of the recipient from the front, the recipient can stand on four or two hind legs.
Snout bite	The actor seizes the snout of the recipient between its jaws from the side or from above and holds it gently for a short time.
Scruff bite	Scruff-orientated inhibited bite.
Snap	The actor lunges with a bite movement towards the recipient, without making contact and often with an audible sound of the jaws, when they come together.
Ritualized approach	A restrained gallop in high posture towards the recipient, not resulting in physical contact.
Dominant behaviour	
Scruff-orientated approach	The actor approaches the scruff of the recipient without biting.
Stalk approach	The actor slowly approaches the recipient with a prowling posture; that is with the head and neck in a straight line below the shoulder, the ears folded back, the tail relaxed or in a straight horizontal line and without losing eye-contact with the recipient.
Food approach	The actor approaches the recipient while looking at him in the context of food acquisition.
Intervention by approach, stand or threat	The actor stops an interaction between two interactants by approach, stand in between or threaten towards one of the recipients.

Fixating	The actor looks straight at the recipient from a distance, motionless, in a high posture and with the ears forward.
Mark over urine or food	The actor secretes, with one (or both) feet lifted from the ground, a small amount of urine over a previous urine mark or food item on the ground.
Freezing	The actor stands stiff with the head straight to the ground and the eyes fixated, either on the ground or on the recipient; the behaviour is shown mostly as a reaction to 'food approach'.
Inguino-genital inspection	The actor initiates an inguinal contact and investigates the genitals of the recipient while the latter remains passive.
Point	The actor directs, with an abrupt movement of his head or a short jump, towards the recipient.
Mount	The actor places both its forepaws on the back of the recipient. It may do so from behind or from the side.
Stand over position	The actor stands across a lying recipient.
Approach in high posture	The actor moves towards the recipient in a high posture, while looking at him.
High posture snout contact	The actor brings his nose close to or pushes it towards the nostrils of the recipient while being in a high posture.
High posture face lick	The actor licks the nose, lips and mandibular region of the recipient while being in a high posture.
Submissive behaviour	
Escape/flight	The actor runs away from the recipient, often seen during conflicts
Retreat	The actor moves away from the recipient in a low position after having been approached by him. This also includes a retreat in the context of food acquisition.

Jump back	The actor jumps back from the recipient, after being approached by him.
Avoid	The actor stands aside for the recipient, after being approached by him, slower or calmer than jumping back.
Active submission	A behavioural complex - the actor actively seeks contact with a recipient by approaching him in a crouched manner with curved back and bent legs, while the tail is curled down, often wagging, and while the ears are folded back. From this position, the actor tries to contact the recipient by licking its nose.
Passive submission	The actor pushes himself down in front of the recipient.
Head turning	The actor turns his head and avoid eye contact with the recipient, exposing the neck region towards the recipient.
Low posture standing	Stand in a low position, with the ears pulled back.
Approach in low posture	The actor moves towards the recipient in a low posture while looking at him.
Low posture snout contact	The actor brings his nose close to, or pushes it towards, the nostrils of the recipient while being in a low posture.
Present body	The actor rolls on his side in front of the recipient or rolls towards them, awaiting inspection.
Food solicit	The actor approaches or walks in parallel with the recipient while begging for food and trying to reach for his mouth corners. There is some resemblance with 'greeting', which is an affiliative behaviour, but the context is limited to around feeding, and the behaviour is not likely to be reciprocated.
Low posture face lick	The actor licks the nose, lips and mandibular region of the recipient while being in a low posture.
Affiliative behaviour	
Approach in neutral posture	The actor moves towards the recipient in a neutral posture while looking at him.
Neutral posture snout push	The actor brings his nose close to, or pushes it towards the nostrils of, the recipient while being in a neutral posture.

Neutral posture face lick	The actor licks the nose, lips and mandibular region of the recipient while being in a neutral posture.
Pass under head	The actor passes from a lateral side close under the head of the recipient, usually in a somewhat crouching manner; often a short nose-chin contact with the recipient is evident.
Head under	The actor pushes with his head towards the ventral-lateral side of the recipient, occasionally lifting the recipient's back quarters from the ground with his head.
Fur sniff/licking	The actor sniffs or licks the fur on the recipient's body; anywhere not otherwise covered by a specific behaviour.
Paw/head on	The actor places a paw or its head on the back of the recipient.
Grin	Only clear facial expression shown by AWDs. The mouth corners remain retracted, and the mouth may be slightly open so that the teeth become visible.
Greeting	The actor stands or walks in parallel with the recipient, tries to contact his muzzle, and performs a complex of behaviours including food-solicit or inspection behaviour, the facial expression 'grin'.
Parallel walk or run	Two animals walking side-by-side in the same direction.
Regurgitation	Expulsion of undigested food from the mouth, pharynx, or oesophagus.
Rub on	The actor establishes intensive latero-lateral contact with the recipient. This may occur while both animals are in motion.
Play behaviour	
Play solicit	The actor initiates a play interaction with the recipient by solicitation behaviours such as nose pushing or tugging the recipient's fur with an inhibited bite.
Fur bite	The actor tugs the recipient's fur by an inhibited bite.
Play chase	The actor follows in fast pursuit of the recipient, who tries to escape by abruptly changing the direction. The roles of follow and escape may change.

Play wrestle	This behaviour involves all play situations, in which the actor shows inhibited bite movements towards the recipient, while he keeps the recipient in constant eye contact. May also include playful embraces, where the actor embraces the neck of the recipient from the front, the recipient can stand on four or two hind legs, roles may switch back and forth.
Social play	All other forms of play.
Feeding behaviour	
Solitary feeding	Individual is feeding with no other group members within a body's length.
Group feeding	Individual is feeding from the same carcass as other individuals or within body's length from other group members
Food steal	Individual quickly takes food which other group members are feeding from and retreats, monopolising that food.
Attempted food steal	Individual attempts to perform a food steal, but does not succeed in taking the food, resulting either in retreating or both / all individuals maintaining a grip on food for a period.
Re-ingesting vomit	Individual eats their own regurgitations.
Resting behaviour	
Resting alone	Resting with no other group members within one body's length.
Resting group	Resting within a body's length from another group member.
Readjusting for rest	Individual readjusts body either by rolling over or moving a few steps and returning to rest.
Vigilance	Individual pops up head, might be propped on elbows, watching surroundings for no less than 5 seconds.
Miscellaneous behaviours	
Scent mark	Individual rolls face and neck in or against object or substance including vehicles, trees, or vomit.
Investigative sniff	One or more pack members are engaged in extensive sniffing at an object or some particle on the ground, can be in direct contact.
Travelling	Animals on the move, walking to another part of the enclosure or feeding site, alone or as a group.
Misc.	Behaviour not otherwise described in ethogram, to be described in notes.