Long- and short-range jackal (*Canis aureus* L.) vocalizations: a new approach based on stationary observations of a non-captive family group

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Abstract. By consensus, jackal howling is considered a vocal means through which a resident family group demarcates its foraging territory so that other groups refrain from intrusion and, consequently, inter-group conflicts are avoided. Alongside this primary meaning of howling, its collective nature is considered to enhance intra-group cohesion. In this article, we argue that the groupcohesion meaning of howling is to be regarded as functionally primary. We also indicate that demarcating 'own' foraging territory seems to be of low functional value since it does not serve to preclude core-territorial intrusion and consequent inter-group conflicts. These occur on a regular basis but are resolved in a non-aggressive way. The data supporting these findings comes from longitudinal field-based research (2017- ongoing) at a stationary bait-site on the Bulgarian bank of the River Danube. Results from the field study of 2021, on which this article is based, suggested that advertising group presence did not deter competing jackal groups from entering the core territory of the bait site 'hosts'. Neither did it deter 'hosting' and 'trespassing' groups from agonistic behaviour and conflict. Our records showed that while conflicts occurred all the time, they resulted only in the hosts chasing away the trespassers, without any aggressive fight. Our results have confirmed our hypothetical assumption that long-range vocalization ('howling') does not preclude core-territorial trespassing and, consequently, does not avert conflicts with a competing group. Their resolution is accompanied by short-range vocalizations (shouting, growling, etc). In the final account, long-range chorus vocalizations, particularly their last ('yip') phase, can be interpreted as a vocal manifestation of a group's numerical strength and unity. The fact that such a manifestation does not, by itself, deter inter-group conflicts, supports our view that group mobilization constitutes the principal functional meaning of long-range vocalization ('howling').

Keywords: Canis aureus, jackal behavior, jackal vocalization repertoire, social meaning of howling, Lower Danube, NW Bulgaria.

Introduction

Referred to generally as 'howling', a broad consensus exists concerning the meaning and function of this golden jackal (Canis aureus) form of sound production. According to the prevailing opinion, jackal howling functions as a partnerseeking and conflict-evasive means of inter- and in-group communication (Jaeger et al. 1996, Jhala & Moehlman 2004, Comazzi et al. 2016, Kershenbaum et al. 2016, Graf & Hatlauf 2021). It is thus considered to signal marking of territorial borders, as well as of family group identification, both in the African 'jackal' (actually the African golden wolf, Canis lupaster), and the Eurasian golden jackal (Canis aureus L.) (Van Lawick-Goodall & Goodall 1970, Golani & Keller 1975, Nikolskii & Poiarkov 1981, Acosta-Pankov et al. 2018). By advertising presence in a foraging territory, howling is assumed to deter potentially competing groups from trespassing into each other's foraging ranges. Ultimately, an important functional meaning of the activity is avoiding antagonistic conflicts leading to unnecessary injuries and fatal outcomes.

At the same time, it has been noted that at present, 'there is no direct evidence that howling acts as a passive means of territory maintenance' (Jaeger et al. 1996). In this article, we show that howling does not deter competitors from entering another group's core territory and attempting to use the resource/ resources situated therein. We hypothesize that the principal function of jackal howling is to sustain in-group cohesion, rather than maintain territorial borders. As regards the term 'territory' itself, we argue that it needs a bi-partite qualification. We propose that a resident group's efforts are

focused on controlling their core territory, rather than their entire foraging territory. During the denning period, the core territory will include the den itself with, ideally, a watering point and a stable food resource situated in close proximity. The defense of the food resource against conspecific and/or allospecific intrusion involves types of vocalizing different from what in the literature is referred to by the blanket term 'howling'. We subsume such vocalizing types under the category 'short-range vocalization'.

Materials and methods

To test this hypothesis, we have created a stable food-resource point as a bait site. We aimed to see whether long-range vocalization ('howling'), broadcast by a resident jackal group controlling the resource, served to deter competitors' intrusions.

Location and schedule

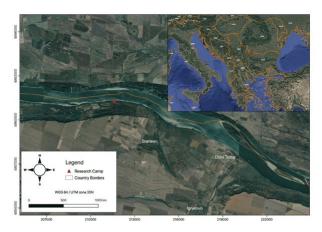
In the spring of 2017, the bait site was created at a remote location on the Bulgarian bank of the Lower Danube. The habitat of this area in the north-western part of the country is suitable for jackals, whose expansion has been well noted during the last 20-30 years. Previous to this period, they were unknown in this part of the country (Spassov 1989, Stoyanov 2013, Spassov & Acosta-Pankov 2019).

The design of the bait-site followed a methodological position, according to which it should replicate organic waste-dumps by anglers'/recreational camps, dotting the riverside during the summer. Accordingly, the bait consisted of leftovers from the researcher's tent-camp table (vegetable peelings, fish heads and innards, fresh fish when in abundance, etc.). For bulk, 1 kg of soaked oat flakes and half a loaf of sliced bread would be added. The nightly food subsidy would average out to some 4-5 kg. The bait would be

dumped in the centre of the bait-site opening at 18:00 hrs.

The observations were made by positioning the stationary bait site close to a single researcher's tent camp. This article analyses the data from the study period of spring-early autumn 2021 (henceforth: Season '21).

The location of the stationary camp and adjacent bait-site was River Km 727 (43°50′54″ N, 23°24′48″ E), on the right bank of the Danube (16 km downstream from the Port City of Lom). The nearest village was Stanevo (150 inhabitants) at 3 km SE (Figs. 1a, b; 2). The site was located in a part well-represented for the current density of the golden jackal population in the country (Spassov & Acosta-Pankov 2019). A specific reason for the choice of the site followed the choice of a stationary bait-site as a principal field-based research tool. In the particular location, the bait-site at River Km 727 was between the two nearest summer recreational camps, at Km 726 and 728, respectively. In this way, we minimized artificiality of intrusion, allowing golden jackal behaviour in respect of the bait-site not to deviate from the manner resident groups behaved regarding organic waste associated with recreational camping.



(a)



(b)

Figure 1. Location of the camp (a); a view of the camp location in a Google Earth image (b). (1) camp and bait-site; (2) den; (3) cowherd grazing range; (4) southern wooded cover; (5) plateau with cornfields; (6) industrial vineyard; (7) Village of Stanevo.

In Season '21, day-to-day monitoring registered a variety of patterns of vocal behaviour, elicited during jackal presence at the bait-site and in the foraging territory around it. The whole vocal repertoire included both intra-family interactions, as well as inter-group ones. In this article, we examine how the family group 'hosting' the resource maintained their resource-ownership status in the face of continuous conspecific trespassing.

The Season '21 field study lasted for 149 days, from 22 April to 17 September. 132 nights were recorded, totaling 3,388 min (56.46 hrs.) of 554 visually recorded jackal visits. A total of 132 long- and short-range vocalizations were registered.



Figure 2. The camp and bait-site at low water: (1) bait-site, (2) main tent, (3) birthing den.

Camera trap recording

The single camera used was a Victure Trail Game Camera 1080P. It was set to record a still photo, followed by a 30-second video clip. The trigger was set to work at 5-second intervals. The camera was turned on simultaneously with serving food at the bait site. In the morning, an hour after sunrise, the data from the camera's memory card was transferred into the visual database of the field study. Subsequent processing of this data followed.

Processing of visual data

The first step of processing consisted of segmenting the material into separate visits. A visit would include the arrival of the animal(s) at the bait site, their use of it for a certain amount of time, and their departure.

The overwhelming majority of visits were by members of a jackal family group who had established themselves as 'hosts' or 'owners' of the bait site. A second place was held by a badger who appeared alone, or, more often, in a commensal association with the jackals (Konstantinov et al. 2022). In addition, a few visits were registered from foxes and stray cats. Smaller animals were visiting alone, or simultaneously with the jackals (hedgehogs, rats, mice, squirrels, snakes, birds, etc.). They would use scraps of food remaining in the bait site in the absence of jackals (in daylight hours or between jackals' visits).

Processing of audio data

A sound recorder (Sony ICD-UX570B) was strapped side-by-side with the camera trap. Both devices were activated at food-serving time (~18:00 hrs). Recording was continuous, the sound-recorded material coming up to approximately 10 hours and resulting in a file of 500-600 MB. When retrieved, it was converted to a sonogram form using a WMA-to-WAV AVS file converter. The resulting Audacity hertz sonogram was manually processed to select the total number of jackal vocalizations for a given night. The events were archived in a Sound Protocol. The type of auditory event (distant chorus, close chorus, shouting, barking, 'cackling', clicking, hissing, 'twigging') would be noted. In addition, the final protocol for the entire field season included a diary of textual notes. The total amount of data has been archived and made accessible for sharing with interested researchers.

Method

The underlying research principle consisted of allowing sufficiently long periods for field-based observations of non-captive jackals. As previously stated, the observations were based on creating a bait site as a stable resource point. In this way, the method used came closest to monitoring stable anthropogenic-resource points (Raichev et al. 2013, Tsunoda et al. 2017), as also to methods that have been employed in urban-based patch-use studies (Newsome et al. 2015,

Dorning & Harris 2017).

The following modifications have been applied as regards the method used. In the first place, only a single 'patch' (in the form of a stationary bait-site) was set up, with statistical verification relying on a finely-detailed longitudinal study of a single resident family group. The investment of considerable research time paid off in gaining qualitative depth for the study.

As a result, a resident jackal family group was attracted as a regular site user, turning the latter into a defining feature of their core territory. During Season '21, the birthing-den was found in the immediate vicinity, 15-30 m from the bait-site, and 35 m from the tent camp. A third core territory defining locus was the watering point: the river's water-edge. That stood at a variable distance from the bait-site, relative to water-level: from a meter to over 50 m.

The two monitoring devices (camera trap and sound recorder) were strapped to a tree at a distance of 3 m from the centre of the bait site, standing 1.5 m above ground. The camera thus covered the open space of the site, as well as the Amorfa (*Amorfa fruticosa*) bushes forming its circular periphery. The sound recorder covered a much larger area on all sides. It can be judged to pick up sounds from an average distance of 1 km, while, as will be shown further on, this distance can be considerably exceeded, reaching up to 4 km (cf. Graf & Hatlauf 2021).

Semantic bias

A principal difference with existing jackal research methods, specifically in studying jackal howling, was what can be called a semantic bias of the study (for a typology of current methods see Hatlauf et al. (2016)). The method of existing studies can be summarized as one that has used the propensity of resident jackal groups to respond to broadcasts of pre-recorded howling (Giannatos et al. 2005, Acosta-Pankov et al. 2018). The general aim has been to elicit responding vocalization and thus judge jackal density and distribution in a given area, group composition by individuation of

separate group members, or, more broadly, to test the dominant 'conflict-evasion' thesis, mentioned at the beginning.

The method of the present field research offers to add to such programs by rearranging the focus. In the first place, it asked a question which, for all its obviousness, has not been adequately addressed so far. Namely, what stimulates jackal groups to respond to broadcasted recordings by howling and advancing to the point of the broadcast? Existing explanations point to similarities with wolf behavior: that neighboring packs advertise their presence by responding to broadcast recordings (Harrington & Mech 1978, 1982), and are thus faithful, as it were, to the conflict-evasive thesis.

The way a principal focus has been rearranged in the method used is that it does not rest on broadcasts, but on passive monitoring of spontaneous jackal vocalization. This operational feature is in answer to the basic thrust of the method: to examine the meaning and function of the various parts of the rich jackal vocal repertoire, or to add to existing research through a deeper semantic engagement.

Consequently, the principal focus in this quest becomes the baitsite and how the group that has assumed the position of its exclusive user (its 'owner' or 'host') is maintaining ownership. This direction has been inspired by longitudinal field-studies in East Africa, relying on close engagement with *Canis lupaster* groups (Van Lawick-Goodall & Goodall 1970, Moehlman 1981, 1987).

Statistical analysis

The dataset for the jackal vocalizations was collected into 15 independent variables related to the type of vocalization (Table 1), and one categorical dependent variable (unit) for each of the actors performing the vocalization (Table 2). Using R 4.3.2 (R Core Team, 2023), a Spearman's correlation test was made to show correlation coefficients between the variables, and subsequently, a Principal Component Analysis (PCA) was conducted as exploratory data analysis (the different types of vocalizations are described further down in Results).

Table 1. Vocalization types: Independent variables defined

Inter-group communication / Inter-Gr Com (long-range vocalization)	Vocalization type
	wailing
Challenging (offensive) sequence of the incoming neighboring group	ua-ua (aua-aua) howling
	chorus howling
	wailing
Defensive sequence of the bait-site hosting group	ua-ua (aua-aua) howling
Defensive sequence of the ban-site nosting group	chorus howling
	chorus yip-ending
Inter-group communication / Inter-Gr Com (short-range vocalization)	shouting
	shouting
	cackling
	clicking
In-group communication / In-Gr Com (short-range vocalization)	growling
	hissing
	snorting
	squealing
Inter-species communication / Inter-S Com (short-range vocalization) (in jackal/badger interactions)	growling
Inter-species communication / Inter-S Com (short-range non-vocal sound production)	twigging

Table 2. Vocalizing actors to whom the units (dependent variables) correspond

Units	Vocalizing actors ID	Description
(Dependent Variable)		
NA	NA	Not applicable (the event doesn't occur)
1	NGr	Neighbouring Group
2	NGr-HGr	Neighbouring Group vs. Host Group
3	BM	Big Man
4	Wh	Whiskers
5	WB	White Back
6	S-D	Sub-dominant (1+ yr.)
7	HGr	Host group
8	HGrC	Host group + Cubs
9	С	Cubs

Results

Family group members

In Season '21, seven members were identified, as well as two cubs born in late May. Identification relied on constitutional, as well as on behavioural features (Table 3). (Custers et al. 2024) Three of the adult members had been monitored during the previous field season of 2020, with a possibility for them also being present during the one of 2019. These were the male ('Big Man', Fig. 3), and female of the breeding pair ('Whiskers', Fig. 4), as well as another adult male, consistently appearing in a bait-site supervising/den-helping ('avuncular') role in respect of the younger members of the group ('White Back').

The younger part of the group was represented by a sub-dominant male of possibly 2+ years.+ ('Pretender'), as well as by three 1+yr.+ sub-adults ('Black Tail', 'Boldy', and 'Skinny'). Two newborn cubs were registered securely.

Long-range (Type a) vocalizations

In the course of long-range (henceforth: Type a) observations, a recurring howling pattern was noted. It was characterized by a dynamic linear movement of what began as distant, solitary wailing. The initial (introductory) wails were recorded from as far as the sound-recorder could pick them

up (possibly, up to 4 km away). The following vocal phases developed then in a gradual movement towards the bait-site/den/camp complex.

A characteristic feature of the pattern was that it invariably began to the east of the complex. Progressing in a linear trajectory westward, it culminated in a group chorus directly above the resident group's core territory. An abrupt or a trailing off end followed.

The sound-recorder picked up after-sunset jackal vocalisations as starting far downstream, coming closer, and ending directly above the bait-site/ core territory location. Solitary wailing followed by group howling would move along the brink of the first terrace above the bank, following an E-to-W linear trajectory. The group-phase of a howling event, in the form of a group chorus of all members, would culminate in a 'yip' phase directly overhead. The details of this long-range vocal activity are presented below.

The structure of the howling pattern neatly fell into classical partitioning, as described in early coyote (*Canis latrans*) studies. Namely, into 'solitary wails', 'group howling', and 'group yip-howling' (Lehner 1976, 1978a, b). Yip-howling itself has been described as 'a high intensity vocalization with several individuals howling and yipping together in seemingly distinct patterns.' (Bender et al. 1996, Lehner 1978a, b, Giannatos et al. 2005).

Table 3. Description of resident family group members

No	Name	Sex	Age	Social role/position	Observed in previous years	Prominent identification features
1	Big Man	m	Ad. (3+)	Male of the breeding pair	2021; '20 (?)	Biggest in group; very massive constitution, thick neck, often stands profile-to-camera, male urine- marking; bristling neck and spine hairs; very long (wolf-like) legs.
2	Whiskers	f	Ad. (3+)	Breeding female	2021; '20 (?)	Characteristic 'whiskers', active nipples, visible bond with breeding male
3	White Back	m	Ad. (3+)	Non-breeding male (Supervising/helping role)	2021; '20 (?)	Light hue, short S-shaped tail, often stands back-to- camera, male urine-marking, fecal-marking of the bait-site
4	Pretender	m	Ad. (2+)	Sub-dominant, but aspiring for a higher position	2021	Slender constitution, male marking, short straight drooping tail, faces the camera.
5	Black Tail	m	Yearling (1+)	'Supervised' when present in a 'supervisor-supervised' pair	2021	Dark hue, long, completely black tail, timid, crouching, always facing camera; head up for wind sniffing; daylight and early night visits; male urine- marking
6	Boldy	m	Yearling (1+)	Rarely present in a 'supervisor- supervised' pair	2021	Light hue, short tail, bold entry of stage, male urine- marking, upright walking (not crouching), entering of bait-site
7	Skinny	? f	Yearling (1+)	Rarely present in a 'supervisor- supervised' pair	2021	Light hue, long tail, female urine-marking, slender, upright approach of the bait site
8	Two cubs	?	0	Cubs	2021	Characteristic vocalism, slender and undeveloped outer appearance, long thin 'rat' tails, visibly smaller



Figure 3. The male of the breeding pair ('Big Man').



Figure 4. The female of the breeding pair ('Whiskers') in late July (birth of pups in late May). The milk-bag is still hanging

On average, one to three wails would come from far downstream. After these initial solitary wails, more individuals would join in, the wailing developing into a 'uaua' (or 'aua-aua') phase. In its two stages, the wailing sequence would last for 20-40 sec., as a rule, the amplitude of the sound being low and not perceptibly rising. This indicated its distance from the bait-site/ core territory complex and a comparatively slow advance towards it.

What is well seen in the sonograms (and being clearly perceived by ear) would be a second - and much louder series of three single wails, followed by others emitted by joining in individuals. This second wailing sequence would also develop into a 'ua-ua' ('aua-aua') phase. At a rapidly amplifying pace, the sequence would further develop into a group 'chorus' howling. At maximum amplification, perceived as occurring directly above the bait-site, the 'chorus' howling would further culminate into a yip-phase. At this point, the high-pitch vocalization ('yipping') would strongly suggest that the whole family group was involved i.e., not only the breeding pair and the sub-dominant male ('White Back'), but also the 2+ yr. 'Pretender', and the three 1+ year olds. In the post-denning months (i.e., after late July), the cubs could also be heard in the yipping ending of the full chorus phase. A typical illustration of the whole vocal process is presented in a sonogram form (Fig. 5).

A slight variation of this pattern is shown by linear vocal events occurring not directly above the bait-site complex, but at some distance to the east (or downstream) from it. Fig. 6, below, illustrates such an event.

The sonogram of that particular instance showed a longer distant wailing phase (a-b) of 1.01 min before the break-off (c)

occurred. By ear, the 'break-off voice' was recognizable as that of the breeding male of the host group ('Big Man'). To his voice, those of the sub-dominant adult members of the group were added (d) – individuation again being based on earlier records, as well as on 'by ear' knowledge of the 'voices' of the bait-site host family members. Finally, the yip-phase (e) again mobilized vocalization of the adults, the 2+ sub-dominant ('Pretender), and the three 1+-year-olds. This younger cohort (and later in the summer, with the cubs joining in) yip-vocalized at a high pitch and very distinctly. By the end of the yip phase, the sound quickly fell and trailed off in the western (upstream) direction.

Core territory trespassing by a competing neighbouring group

Short-range vocalizations: Shouting.

While the audio record of linear howling patterns suggested advertising the host family group's full presence, the visual record spoke of that last not deterring an advancing competing group. In other words, trespassing was still a regular occurrence despite all the Type (a) long-range howling. This assertion is thus consonant with findings in coyote studies of trespassing (Gese 2001). Or, as this author states: 'While indirect means of territory maintenance (i.e., howling and scent-marking) were utilized by resident packs, trespassing still occurred (our emphasis) and direct confrontation was needed to enforce boundaries and assert occupancy against other resident packs, as well as against lone intruders seeking territory vacancies' (Gese 2001). A trespassing event of this type is illustrated by the sonogram in Fig. 7, below.

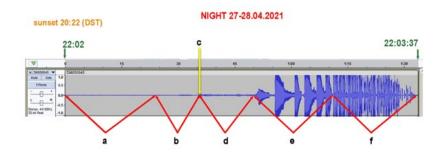


Figure 5. Sonogram of a wailing-howling progression (27-28.04.21): (a) distant incoming wails; (b) closer wailing, louder; (c) break-off point (new voice – 'Big Man'); (d) wailing; (e) wailing and 'uaua' chorus, high amplitude; (f) all-group 'yip'-chorus, maximum amplitude.

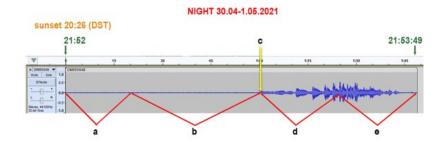


Figure 6. Sonogram of a variant of the wailing-howling progression (30.04-01.05.21): (a) distant wailing, dogs; (b) louder group wailing, closer; (c) break-off point (new voice – 'Big Man'); (d) group wailing/'ua-ua' chorus, high amplitude; (e) 'yip' all-group chorus, overhead, maximum amplitude, trailing off at the end.

Long/short-range jackal voclizations 55

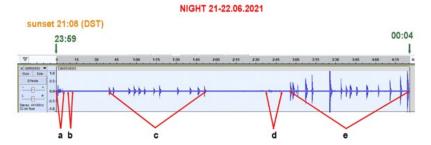


Figure 7. Sonogram of trespassing and related shouting (21-22.06.2021: (a) intruder chases away 'host' breeding female; (b) breeding female growling, rushing at intruder, and chasing him away; (c) breeding male shouting at intruder (12 shouts); (d) breeding male growling at intruder; (e) breeding male goes on shouting (15 shouts).

Cackling.

Another type of vocalization associated with short-range altercations and scuffles between 'hosts' and 'trespassers' resembled cackling. This vocal type consists of short, highpitch bursts, enunciated with a wide-open mouth (Fig. 8a, b), without teeth baring. Cackling would often be followed by sharp, click-like sounds ('clicks'). A good illustration of both vocalizations was provided in a video clip from the night of 19-20 June (4th visit). A 9-sec segment from the sonogram for that night is given on Fig. 9. It represents a series of cackling bursts, enunciated by two sub-adult members of the 'host' family, and directed at an intruder, also a sub-adult, judging from the visual material, capturing the event.

Hissing and snorting

It belonged to short-range in-group vocalizations in bait-use contexts. As a rule, they would be enunciated by an older animal (typically the breeding female) in respect of either yearlings or cubs. The meaning of these low-frequency (> 1 kHz), brief utterances could be interpreted as signs of displeasure with younger animals.

This interpretation was borne out by simultaneously rushing upon youngsters on such occasions. This would be followed by head-butting and final removal from contact with food, so the older animal could finish eating unperturbed. In response, juniors would emit short sequences of high-pitched sounds ('squealing').





Figure 8 (a). A sub-dominant 'trespasser' intruding at the bait-site and 'cackling' at two sub-dominant 'hosts' (unseen behind the bait-site periphery wall of amorfa-bushes). In a following scene, the two 'hosts' rush upon the trespasser and a brief scuffle ensues. It ends in the trespasser being chased away. (b). Same in 'cackling' enunciation/posture contours. Note raised ears and upward-raised posture. This is to be compared with the flat-back ears and curved downward posture in a more intensely confrontational growling bout between 'trespassing' vs. 'host' alpha contenders (further down, Fig. 15a, b).



Figure 9. Sonogram of cackling bursts interspersed with clicking.

Short-range non-vocal signaling: 'twigging'

A special case was presented by non-vocal sound production of short-range broadcasting power, which we called 'twigging'. The technique consisted of an animal taking hold of an Amorfa-bush twig, bending it halfway to the ground, and then violently shaking it from side to side. A swishing noise was produced, or a crashing one in case the twig broke or hit against dry vegetable matter (Fig. 10a, b, c). The aim of this form of sound production is unclear.

Summing up

Two general groups of vocalizations have been illustrated in the material presented above. These are (i) Type (a) wailing, chorus howling, and chorus yipping, and (ii) Type (b) vocalizations: shouting, cackling, clicking, growling, snorting, hissing, etc. A non-vocal sound production was also noted, using overhanging twigs ('twigging'). In topographical terms, Type (a) developed along a straight line from E to W, meant to be heard over the entire foraging territory. It was initiated by a potentially intruding group from a distant location downstream, moving with varying speed along the edge of the bluff overhanging the riverbank.

Type (b) vocalization has been recorded at the cameracovered space of the bait-site (the 'stage'), or around its amorfa bush periphery. Characteristically of this type, contenders emitted vocalizations in a threatening or 'quarrelling' manner. A special case was the instrumental sound production of 'twigging'.

The correlation test between variables showed, in general, a low correlation between them as shown in the Spearman's correlation test plot (Fig. 11). However, strong correlation was found between growling, shouting, etc., and inter-species communication (Inter.S.Com).

We have used a Heatmap plot (Fig. 12) to represent the values from the matrix, where each cell color corresponds to the magnitude of the value in the dataset. That means that in the present study, it represents magnitude (or relative 'weight') in terms of counts or frequencies of the number of times each type of vocalization was made by each vocalizing actor. As can be seen in the figure, it was found that the type of vocalization that was most frequently heard was chorus and wailing produced by the neighboring group (NGr), as well as in-group communication (InGrCom), with subdominants (S-D) and White Back (WB) as prominent actors. Similar 'weight' was attributed to shouting by White Back (WB) and growling by Big Man (BM).

A relatively high magnitude score (of 10 to 15) was marked for the sub-dominant group (S-D) in their intergroup (InterGr) participation. Predictably, neighboring vs. host group communication showed the same magnitude score regarding intergroup interaction and challenge-defense sequences (CDS).

Insofar as CDSs occur only in a long-range context, while InterGr can occur in both long- and short-range ones, the two types reflect a partial synonymy (visualized as a double rectangle on the NGr-HGr line).

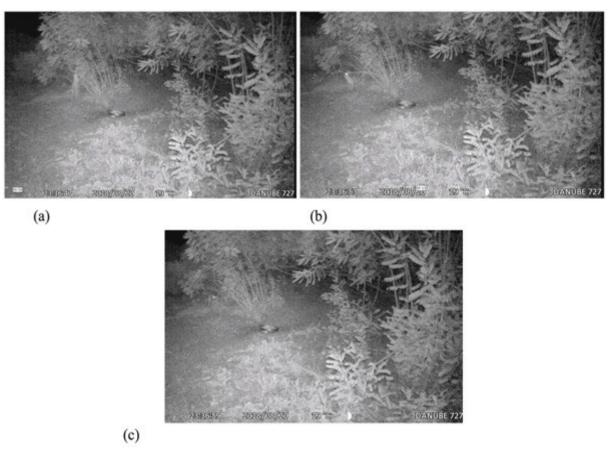


Figure 10. 'Twigging': (a) reaching up to catch a twig; (b) bending the twig; (c) shaking it from side to side to produce a swishing sound.

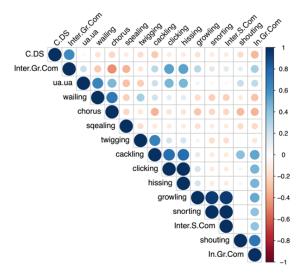


Figure 11. Visualization of the correlation between the variables (types of vocal events).

For the Principal Component Analysis (henceforth PCA, Fig. 13), 27.3% of the total variance in the data is accounted for by the first principal component, Dimension 1 (Dim1). An additional 22.7% of the total variance is accounted for by the second principal component, Dimension 2 (Dim2). Together, the two dimensions explain 50% of the total variance in the data.

The observations (data points or vocalizing actors) close together in the space defined by the first few principal components are based on the variables (types of vocalization) used in the PCA. This similarity is in the original features as they contribute to these principal components. Consequently, the clusters reveal natural groupings within our data. In the present study, the PCA for the data set shows five different clusters for the variables separating the vocalizing actors Big Man (BM), White Back (WB), Neighboring Group (NGr), and

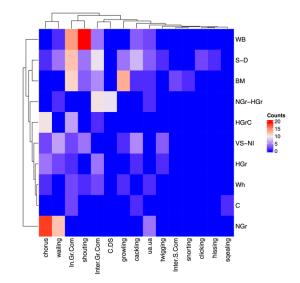


Figure 12. Heatmap plot.

Sub-dominants (S-D) from the rest.

In Table 4, it is possible to appreciate the p-value with significance (95 %) for most of the variables forming the five clusters.

In the PCA biplot (Fig. 14), the variables are represented as vectors (arrows). These vectors indicate how each variable contributes to the plotted principal components (PC1 and PC2). The length of the vector indicates the strength of the contribution of the variable to the principal components being displayed. Longer vectors mean that the variable has a stronger effect on the variance explained by the plotted principal components. This shows that vocalization type (cackling, hissing, clicking, growling, snorting, intergroup communication (Inter-Gr.Com), and interspecies communication (Inter-S Com)) has a strong effect on PC1 and PC2.

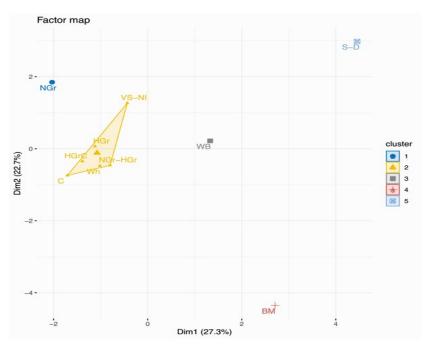


Figure 13. Factor map plot for the PCA

Table 4. *p*-values for the variables in the PCA.

Vocalization type	p-value (PCA)	PCA Cluster
wailing	0.01	
chorus	0.01	1
ua.ua	0.03	
In.Gr.Com	0.04	2
shouting	0.004	3
Inter.S.Com	0.002	
snorting	0.002	4
growling	0.004	
hissing	0.002	
clicking	0.002	5
cackling	0.02	

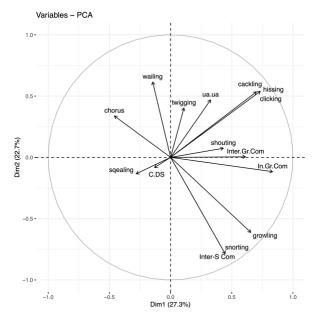


Figure 14. Biplot or vectorial representation of variables (type of vocalization) for PC1 and PC2.

Discussion

The current consensus is that a principal function of jackal howling is to advertise territorial presence and thus deter competing groups from intrusion into their territory. Jackal howling is therefore considered as an evolutionary technique for avoiding costly, violent confrontations. This 'confrontation-avoiding' thesis seeks empirical validation by studying responses to broadcast howling. As a rule, broadcast howling is based on recording group howling sessions, emitted by jackals living in captivity. Each broadcasting session's location is usually chosen to reach all groups within the auditory range of the broadcasting source.

In the passive monitoring method presented here, the long-range Type (a) resembles the above technique in the sense that vocalization by jackal groups is being recorded. At the same time, there are substantial differences. First, we rely on spontaneous vocal activity by the jackals, rather than stimulation of a response to howling, pre-recorded in an entirely different context. In our case, vocal interaction between competing groups has been registered from the point of view of how a jackal family group responds to intruders

from a competing group or advertises its presence without such provocation. The overall context in this case is one of competition for using an attractive resource placed in the core territory of the 'resource-hosting' family group. In this situation, our objective has been to monitor the vocalization repertoire from the perspective of how events occurred at the core territory, rather than from an arbitrarily chosen broadcasting/ recording point in a wide open space.

It is to be stressed that auditory observations were much assisted by the linear geography of the terrain. In this location (River Km 727), the river flows from due west to east in a nearly straight line (Figs. 1, 2). A 10-15 m high bluff rises above the thin strip of the bank. A natural linear boundary is thus formed, separating terraced land on the southern (Bulgarian) bank from the river itself, 800 m-1 km wide at this location. This riparian terrain has been found to predetermine jackal movements and the distribution of resident jackal groups. As shown in Fig. 1 b, the line between salient human presence (Stanevo Port and Hotel) at one end and the bait-site/den/camp complex at the other is nearly a straight E-to-W one. The Village of Stanevo bends this line to the SE. Consequently, movement between food-resource points (waste dumps) and day hiding-cover was either in a straight W-to-E line from the core territory to Port/Hotel resource points or along a SE vector to the village (and its waste dumps). These major orientations of movement have been well evidenced by tracks left, as also by after-sunset vocalization.

This suggests an answer to why jackals respond to stimulated howling and even come up close to the emitting actors. Our answer to this is surprise and curiosity as regards a vocalizing group appearing at an unusual location and, probably, not recognizable as an actor in previous challenge-defense interactions.

A prominent vocal event in this connection, and described as Challenge-Defense Sequence (C-DS), has been explained in Figs. 6-7. The finding that the yipping phase of the Defense part signals to the approaching 'trespassers' the presence of a fully mobilized defending 'host' group resonates well with Hallberg's (2007) analysis of coyote (Canis latrans) yiphowling. Of particular salience is her statement that 'acoustic analyses conducted in the present study support the hypothesis that group size information (our emphasis) is potentially available in the group yip-howl vocalization of the coyote' (Hallberg 2007).

Maximum mobilization of the host group, vocally expressed by choral 'howling', and particularly in its final 'yip '- chorus phase, has been shown to find a homology with Kolar et al.'s (2005) 'warble howl' and 'yip'-calls. At the same time, some critical differences exist. In Kolar et al.'s case, researchers position themselves at some location during the night and record all available jackal vocal activities. In our case, vocal activities have been recorded from the vantage point of a family-group core territory, which coincides with the bait site/research camp. As a result, we can record the linear progression of 'howling' phases and their culmination at the core territory.

It has been shown in the Results section that Type (b) vocalizations, shouting, and cackling in particular, typically followed the appearance of 'trespassers' at the bait-site, and their ultimate repulsion and chasing away by the 'hosts'.

Long-range 'host' vocalizations did not deter intrusion as regarded as a focal resource, nor did they prevent conflict between 'trespassers' and 'hosts' in and around the bait-site itself (Fig. 15a, b).

This was particularly evident in those instances in which Type (a) vocalization was followed by chase-away scuffles at the bait-site, effected through Type (b) vocalization. A prominent expression of the type was repeated shouting by the breeding male, up to 27 successive shouts in one instance.

It is to be stressed here that Type (b) vocalizations: growling, shouting, cackling, etc., occur not only in 'hosts vs. trespassers' encounters, but also in altercations between members of the resident 'host' group. Shouting in particular has been observed to be a constant vocal expression of enmity between the breeding male ('Big Man') on the one hand, and the principal 'bait-site supervisor/ helper' ('White Back'), on the other.

The fact that twigging invariably occurred either at the bait-site or along the amorfa bush line that separated the jackal core territory from the open space of the researcher's camp could suggest a food-related message (more food?), addressed to the food-provider, i.e., the camp-inhabitant. More work on this instrumental form of sound production with jackals is required before any firmer conclusion is reached.

As shown in Fig. 14, Type (b) SRVs are represented to a prevailing extent over Type (a) LRVs. Considering that Spearman's correlation coefficient ranges from -1 to 1, a coefficient close to 1 implies a strong positive monotonic relationship (as one variable increases, the other tends to increase). A coefficient close to -1 implies a strong negative monotonic relationship (as one variable increases, the other tends to decrease). A coefficient around 0 implies no monotonic relationship.

Several factors can be seen to be contributing to this. In the first place, Type (a) vocalizations are subject to weather conditions to a greater degree than Type (b) ones. In this study, Type (a) vocalizations predominantly occurred in dry, windless nights (Acosta-Pankov et al. 2018). They have not been observed in conditions of strong winds, rainy nights, as well as during thunderstorms. Association of long-range (Type (a)) vocalizations with weather conditions facilitating broadcasting to an optimal-to-maximum range (1-4 km) can be connected with a functional meaning of Type (a). Namely, to advertise the mobilized presence of the core-territory

defending group, to far-positioned competitors.

Short-range interactions around the bait site are not subject to such limitations. This applies to the three interaction types occurring there: between members of the host-group (In-Group Communication, InGrCom), in host vs. trespasser's events (Inter-Group Communication, Inter-GrCom), and in jackal/badger interactions (Inter-Species Communication, InterSCom). In the final account, Type (b) vocalizations are both more frequent, of greater addressee range, and virtually unconstrained by weather conditions.

The evidence presented here suggests that both Type (a) and Type (b) vocalizations in the defending group function as signals of mobilized presence. At the same time, this, by itself, is not capable of deterring conflict. It is another matter what makes conflict not escalate from a bloodless stage of 'quarrelling', vocalization, and scuffles into aggressive fights. What may be surmised at this point is that while 'howling' (to put it most generally) does not achieve deterrence and conflict-evasion (and is probably not geared for such tasks at all), it does achieve mobilization of a resident group. As regards the actual defence of that resident group's core territory, it is typically a single senior adult (predominantly the breeding male) who engages in chasing out an intruder, not the group as a whole.

The data presented above bears out such a conclusion. It thus confirms our initial hypothesis that the primary function of Type (a) vocalization ('howling'), principally in its groupchorus and yipping phases, is to sustain intra-group cohesion. Our data do not support a defense-of-territory function of Type (a) vocalization. The latter shows that competing group members regularly intrude into the defending group's core territory. Subsequent conflicts get resolved by bloodless scuffles, accompanied by Type (b) vocalization (growling, shouting, cackling, clicking, etc.). Growling, concurrent with ridge-bristling and a horizontally extended tail, clearly intends intimidating and repulsing an adversary, with the latter adopting a similar posture and vocalization. When the adversary is sensed to be near, but not directly confronting the defender, the latter can be seen 'earth-throwing' with hind legs, again as a gesture of intimidation. Shouting has also been registered as being evinced by the sub-dominant senior male ('White Back'), standing at a distance. It is unclear whether that is another intimidating device, directed at an intruder, or part of recurrent 'quarrels' with the breeding dominant male ('Big Man').

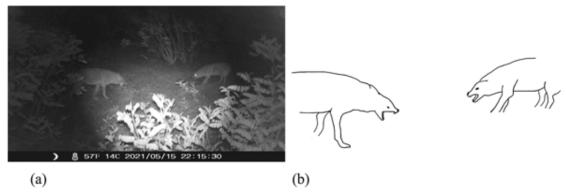


Figure 15. A growling bout between 'trespasser' (right) and dominant 'host' ('Big Man', left) in a confrontation at the bait-site (a); same in enunciation/ posture contours (b).

Conclusions

Against this background, several conclusions are to be made. In the first place, 'howling' is to be used as a blanket term covering only long-range vocalization. Thus qualified, its various parts need to be segmented, with special attention given to the high amplitude concluding ones, referred to above as 'group chorus', and 'yipping'. As stated, these two phases ideally engage all group members, thereby vocally manifesting the group's inner cohesion. This can be considered to be the main role of the howling. Secondly, howling could have a "show of muscle" significance to neighboring groups representing potential invaders, but this is, possibly, a secondary role. Defense of the core-territory, and a key focal point in the form of a stable food resource, elicits another vocal register that cannot be referred to as 'howling'. The term we have suggested is 'short-range vocalization' (Type b). In its various forms (growling, shouting, cackling, clicking, etc.), it has been shown to be part of non-aggressive conflict resolution around a contested resource. Alongside the bipartite division of vocalization, a parallel one needs to be made concerning the blanket term 'territory'. We have shown that long-range vocalization is associated with vocal interaction between competing groups. On the other hand, short-range vocalization is to be associated with an attractive contested resource which, ideally, may be positioned within the core territory of a resident group. Control over it is maintained in respect of conspecific and allospecific competition. Finally, short-range vocalization in this space constitutes aspects of intra-group communication.

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