

VOCAL COMMUNICATION IN THE PALE-WINGED TRUMPETER (*PSOPHIA LEUCOPTERA*): REPERTOIRE, CONTEXT AND FUNCTIONAL REFERENCE

by

NATHALIE SEDDON¹ , JOSEPH A. TOBIAS and ADRIANA ALVAREZ²

(Department of Zoology, University of Cambridge, UK)

(Acc. 6-IX-2002)

Summary

Adult pale-winged trumpeters produce a varied repertoire of vocalizations: apart from one loud 'tremolo song' we recorded 11 structurally discrete close-range calls, one of which (the 'mew') was individually distinct. There was significant variation across vocalization type with respect to the identity and behaviour of the caller and the response of the receiver(s). It was possible to group vocalizations into six broad contextual classes: alarm, recruitment, social, contact, feeding and territory defence. On detection of danger, trumpeters gave two acoustically different calls, one for aerial predators, and another for terrestrial predators or conspecific intruders. They also produced distinct calls on detection of large prey items such as snakes. These (alarm and snake-finding) call types seemed to evoke different responses by receivers and therefore appeared to be functionally referent. Vocal behaviour was positively correlated with dominance rank and at least two other calls had important roles in mediating social interactions within the group. Finally, the 'mew' call was only given when a trumpeter was separated from, and usually out of visual contact with the rest of the group. This call was functionally referent, eliciting a vocal response from receivers: they produced a loud 'grunt' call, which was also unique to this situation. This is the first experimental demonstration in a bird of the proximate factors motivating production of an individually distinct contact call.

Keywords: alarm calls, contact calls, dominance hierarchy, functional reference, pale-winged trumpeter, individual distinctness.

¹ Correspondence to: N. Seddon, Department of Zoology, Downing Street, Cambridge CB2 3EJ; e-mail: ns10003@hermes.cam.ac.uk

² We are grateful to INRENA for granting us permission to conduct research at Cocha Cashu Biological Station, Manu National Park, Peru. We also thank Renate Leite and Carmen Chavez for logistical help, John Terborgh for advice and Pete Sherman for comments on this manuscript. This research was supported by a Phyllis and Eileen Gibbs Travelling Research Fellowship from Newnham College, Cambridge, U.K.

Introduction

The structure and function of passerine bird vocalizations has been the subject of intensive research since the 1970s (see reviews in Catchpole & Slater, 1995; Kroodsma & Miller, 1996). Relatively few studies have focused on the vocal behaviour of non-passerines. The loud calls of some non-passerine groups such as seabirds (Bretagnolle, 1996), flamingos (Mathevon, 1997) and gruiforms (Seddon, 2002) have received recent attention, but the function of close-range calls used by group-living non-passerine birds is not known. In primates, there has been some research into what role these quiet calls might play in coordinating behaviour within groups (Harcourt & Stewart, 1996; Uster & Zuberbuhler, 2001), but birds have been greatly neglected in this respect.

As emphasized by Markl (1985), close-range communication is likely to be 'at the very heart of complex and highly organized animal societies'. For example, in numerous mammal species, vocalizations labelled 'alarm calls' have been shown to coordinate group vigilance (*e.g.* Suricate *Suricata suricata*, Manser, 2001) while those labelled 'contact calls' appear to play a role in maintaining group cohesion (*e.g.* Chacma baboon *Papio cyanocephalus ursinus*, Rendall *et al.*, 2000). Importantly, the alarm calls of some mammal species living in relatively stable social groups are functionally referent: they signal predator-specific information (*i.e.* they show production specificity) and are alone sufficient to evoke adaptive anti-predator responses in receivers (*i.e.* they show perception specificity; see Evans *et al.*, 1993). Although alarm calls are widespread among social birds, evidence that they use vocalizations in this way has only received detailed investigation in domestic fowl *Gallus domesticus* (Gyger *et al.*, 1987), and the cooperatively breeding Arabian babbler *Turdoides squamiceps* (Naguib *et al.*, 1999). Domestic fowl were shown to produce predator-specific calls, but there was no evidence that the calls alone elicited anti-predator behaviour, and whilst babbler alarm calls were shown to signal degree of risk in predator-induced situations, they were not specific to predator type. Although these studies demonstrated the potential of avian alarm calls to be semantic, they were inconclusive about the extent to which they could be functionally referent and it was clear that further studies of alarm calling in other group-living birds were needed.

Similarly, although so-called 'contact calls' are ubiquitous among birds they have received scant attention compared to the substantial literature on

the structure and function of contact calls in primates (reviewed in Snowdon, 1986). Instead, studies of avian contact calls have mainly focused either on the costs of calling (*e.g.* Krams, 2001) or the extent to which contact calls are individually distinct (Mammen & Nowicki, 1981; Mathevon, 1997; Lefevre *et al.*, 2001). No study has investigated the proximate factors affecting the production of avian contact calls.

We studied the vocal behaviour of the pale-winged trumpeter *Psophia leucoptera*, a group-living, terrestrial frugivorous bird endemic to the lowland moist forest of SE Amazonia (Sherman, 1996). A five-year study of this species' breeding biology found it to be cooperatively polyandrous with a complex social system wherein dominance hierarchies are maintained by various stereotyped visual and vocal cues (Sherman, 1995a, b). The species was also reported to have a large vocal repertoire, including various alarm calls (Sherman, 1996), but no quantitative study was undertaken.

Our study had four objectives. First, we described the acoustic structure and behavioural context of pale-winged trumpeter vocalizations (Catchpole & Slater, 1995; Horn & Falls, 1996). Second, we assessed the extent to which some of the calls are individually distinct and functionally referent. Third, we examined the social correlates of vocal behaviour. And finally, we experimentally investigated the proximate factors motivating contact call production.

Materials and methods

Study site and species

This study was conducted at Cocha Cashu Biological Station in Manu National Park, Peru (71°19'W, 11°51'S) in August-October 2001. The site covers *ca* 200 ha of pristine lowland tropical moist forest (see Terborgh, 1983 for full description); it is accessed by an extensive grid of trails encompassing the territories of seven groups of pale-winged trumpeters (see Sherman 1995a). Although three groups were fully habituated in 1987, only one group remained habituated in 2001. The remaining six were encountered infrequently and were extremely wary, usually running away from observers as soon as they were detected. The brief duration of the study precluded the habituation of other groups (a process usually taking several weeks, P. Sherman pers. comm.). We gathered high quality data from the habituated group, which occupied a large territory (*ca* 70 ha) bordering the cocha (ox-bow lake) and could be followed continuously at a distance of <3 m.

Behavioural observations

The white hind-wing of each bird was individually marked with a squirt of water-diluted black paint dispensed from a water pistol at 2 m range. This enabled the identification of group members without catching them or causing any undue stress. Behavioural observations indicated that this group comprised one adult female, four adult males (all of which copulated with the female) and one juvenile bird of unknown sex (which always stayed close to the female and gave 45% of all subordinate displays recorded, see below). The dominant male was estimated to be at least 15 years old, on the grounds that it possessed a single blue ring, which it can only have acquired during Sherman's study in 1983-1987. These trumpeters were followed from their descent from the roost at dawn (*ca* 06h00) to their ascent to the roost at dusk (*ca* 18h00), and their vocal behaviour was recorded by at least two observers (see below). This study is based on a total of 195 diurnal hours of observations.

We attempted to rank dominance by analyzing stereotyped aggressive and submission displays given in dyadic interactions. A submissive display was characterized by the subordinate bird crouching in front of the dominant bird opening its wings (Sherman, 1995b). An aggressive display involved the dominant individual standing tall and rapidly flicking its folded wings 1-3 times in the direction of the subordinate bird, which it then occasionally pecked on the head or chased for a distance of <3 m. In contrast to Sherman (1995b), we found no clear-cut linear hierarchy: all members of the group gave and received submissive displays, and all but one member of the group (D) gave aggressive displays to all other group members. We therefore calculated the hierarchy by scoring each submissive display as -1 and each aggressive display as $+1$. For each pair-wise comparison, whichever bird had the highest score was assumed to be the dominant. In all but one pairing (B and C), one bird had a 'dominance score' at least twice as high as the other. As B and C scored equally, whilst scoring more highly in comparisons with D, E and F, they were placed equal second in the hierarchy (see Table 5).

Acoustic structure of vocalizations

A Sennheiser ME80-K3U directional gun-microphone and a Sony TCM-5000EV cassette recorder were used to record trumpeter vocalizations onto 60 min TDK metal tapes, and behavioural observations were recorded onto a Sanyo Dictaphone. Vocalizations were sampled from 240 mins of recordings made *ca* 2 m from vocalizing birds during continuous focal watches on one group of six trumpeters in August and September 2001. Using Avisoft SASLabPro Version 4.0c with a 16-bit acquisition sound card (0 VIA [Wave] 5.10), taped vocalizations were automatically filtered at half the Nyquist frequency to prevent aliasing and then digitized at sampling rates of 4000-11025 Hz depending on the maximum frequency of the call. Digitized calls were subsequently high-pass FIR filtered to remove some background noise at 50-150 Hz depending on the minimum frequency of the call. To maximize the frequency resolution of the spectrograms then generated, we used the narrow-band (55 Hz) filter settings in Avisoft (FFT = 512, Frame = 100%, Window = Hamming, Overlap = 88%; see Fig. 1). A call was defined as a single, simple stereotyped vocalization represented by a continuous trace on a spectrogram. Different call types were distinguished by their visual appearance as spectrograms, *i.e.* by the way their frequency changed with time. We applied names to calls on the basis of renditions of their distinctive sounds and qualitatively classified calls as one type or another both by ear and the similarity of their 'shape'. A bout of calling

was defined as a series of two or more identical calls wherein the intervals between calls were relatively constant within the bout while the inter-bout interval varied between renditions and was greater than that between calls. To describe the calls quantitatively a variety of time (in s) and frequency (in Hz) measurements were then made. Call duration was measured from the time signal and minimum frequency, maximum frequency and call bandwidth were measured from the sound spectrograms using cursors that moved in increments of 2 ms and 8 Hz. The way in which maximum frequency was measured depended on the acoustic properties of the call. For a call with no or only one faint harmonic (*e.g.* twangs, chirps and squeaks) where peak frequency was close to the minimum frequency, maximum frequency refers to the maximum of the time-frequency contour of the minimum frequency. For a call with two or more distinct harmonics (*e.g.* mews, growls and chacks) where peak frequency greatly exceeded minimum frequency, maximum frequency refers to the highest frequency component in the call's spectrogram. Peak frequency (the frequency in the call with the most energy) was automatically measured by the software from amplitude spectra. As part of the more in-depth acoustic analysis of the individual distinctness of the 'mew' calls (see below), the lower, mean and upper quartile frequencies (the frequencies below which 25%, 50% and 75% of the energy in the call is found) were also measured automatically from amplitude spectra.

Individuality of 'mew' calls

Trumpeter 'mew' calls appeared to vary between individuals. Given their probable function as contact calls (see below), there may be some advantage of 'mews' encoding identity information, as has been found for the contact calls of other non-passerine birds (*e.g.* Brännich's guillemot [=thick-billed murre] *Uria lomvia*, Lefevre *et al.*, 2001). Having standardized the time and frequency characteristics of 67 'mew' calls (9-15 per trumpeter), we produced a Pearson correlation matrix. Forty-three percent of the correlation coefficients were >0.5, no single variable had low coefficients with most other measures and the matrix was significantly different from an identity matrix wherein all variables were completely unrelated (Bartlett's test of sphericity: $\chi^2_{21} = 362$, $p < 0.0001$). It was therefore appropriate to use principal components analysis (PCA, using SPSS 11.01), to examine inter-individual differences in 'mew' call structure. We used a Kruskal-Wallis test to investigate if the mean scores of the first principal component differed significantly between individuals. To further examine the extent to which the frequency characteristics of 'mew' calls were individually distinct we cross-correlated spectrograms of all 67 'mew' calls using the Avisoft Correlator. Spectrograms of all calls were generated from recordings that were sampled at 8000 Hz and then digitally filtered using FIR filters (high pass = 250 Hz, low pass = 4000 Hz). Narrow-band filter settings (see above) were then used for all 'mews' to produce the spectrograms. By sliding each spectrogram over each other, the correlator calculated a coefficient of similarity, wherein a correlation of 0 indicated that the two calls were orthogonal to each other, and a correlation of 1 indicated that the calls were identical; see Charif *et al.* (1995) for a detailed description of this method.

Pattern and context of vocalizations

During focal watches of the study group, the time of almost every vocal event was noted. The exception was the 'soft grunt', which was emitted sporadically throughout the day whenever

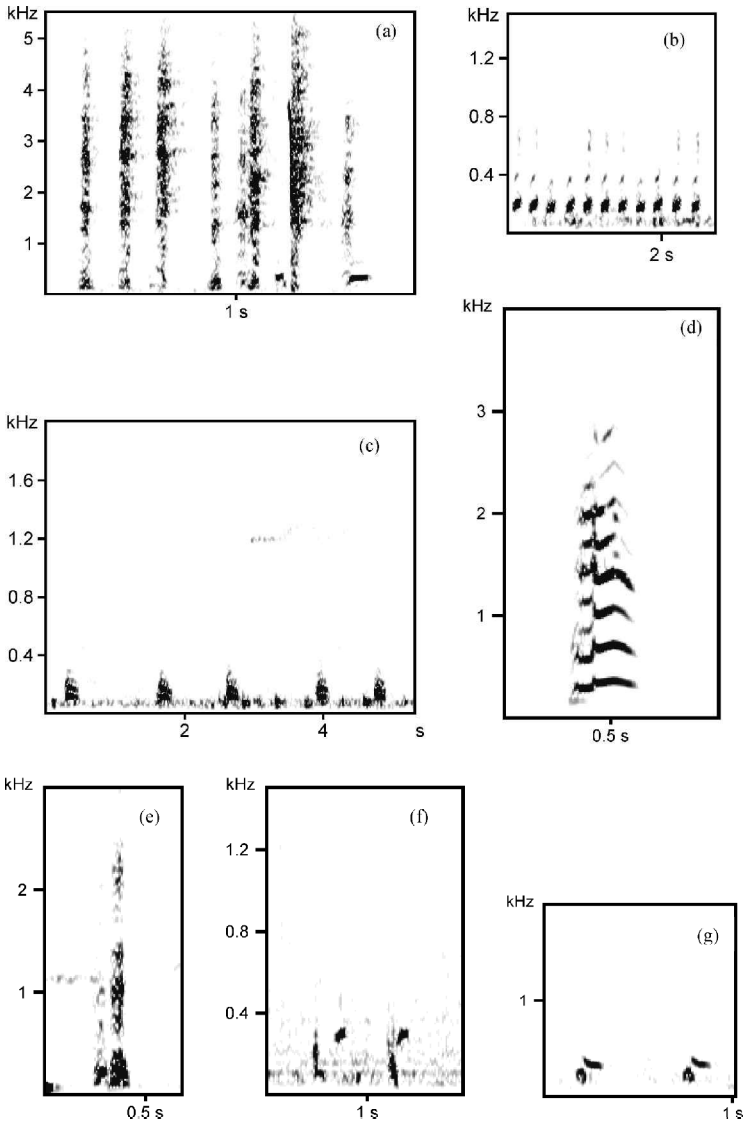
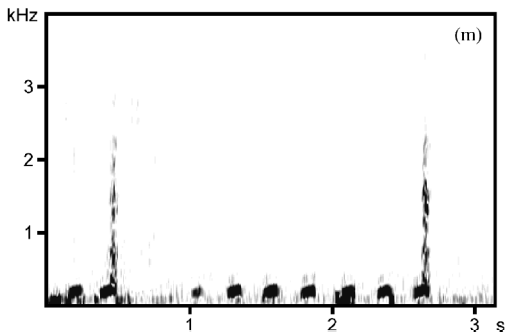
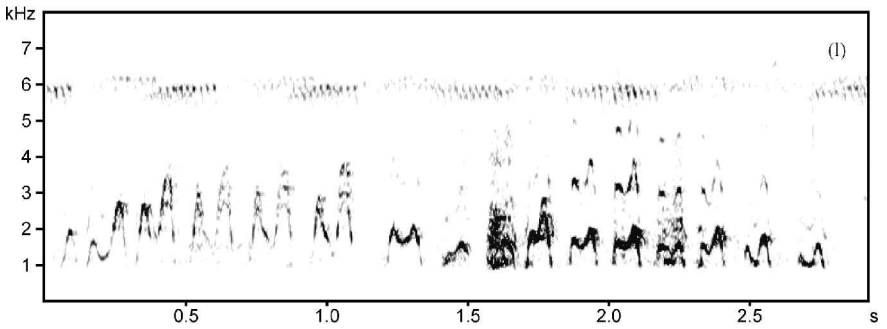
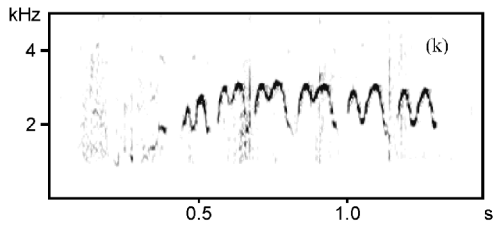
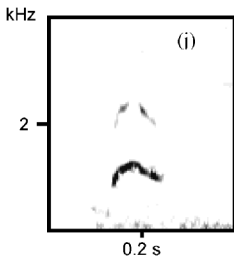
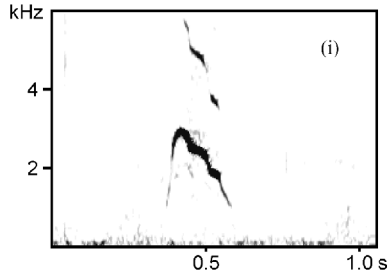
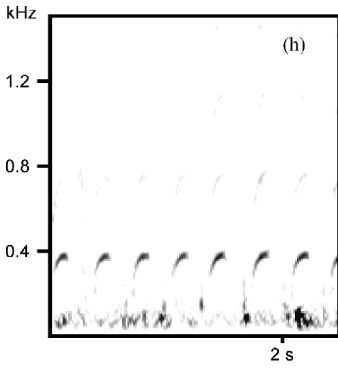


Fig. 1. Sound spectrograms of pale-winged trumpeter calls or bouts of calling: (a) Chack, (b) Drum, (c) Growl, (d) Mew, (e) Grunt, (f) Disyllabic drum, (g) Soft grunt, (h) Twang, (i) Squeak, (j) Chirp, (k) Twitter, (l) prolonged twitter given during copulation and (m) Drum-chack. Sampling rate for call (a) was 11025 Hz, for calls (b), (c), (e), (f), (g) and (h) was 4000 Hz, for calls (d) and (m) was 8000 Hz, and for calls (i)-(l) was 16000 Hz. Spectrogram (a) had frequency resolution (FR) = 21 Hz and bandwidth (BW) = 28 Hz; (b)-(h) had FR = 7 Hz and BW = 10 Hz; (i)-(l) had FR = 31 Hz and BW = 41 Hz; and (m) had FR = 15 Hz and BW = 117 Hz. Spectrograms (d), (i)-(l) are of single calls, whilst the remainder are of bouts of calling.



the birds were foraging and which was so low in pitch and amplitude it was barely discernable above the ambient din of the forest. Separate vocal events were classified as such if an interval of silence lasting 60 s elapsed between them. For each event we recorded the identity of the calling bird and the distance between it and the nearest and furthest group member. Each vocal event was also assigned to one of 15 different behavioural categories: *i.e.* those given by a trumpeter when it was: (i) alert (*i.e.* had a highly-erect 'vigilant' posture) and scanning horizontally (AH); (ii) alert, motionless with its head tilted upwards (AU); (iii) being aggressive towards another group member (AD); (iv) apparently 'requesting' to be preened by another group member (AP); (v) feeding at an ant swarm (AS); (vi) begging for food (FB); (vii) 'parading' around with an item of food (FF); (viii) foraging under a fruiting tree (FT); (ix) playing (P); (x) descending from or ascending to a roost site (R); (xi) resting and preening (RP); (xii) directing attention towards a snake or frog (S); (xiii) being submissive towards another group member (SD); (xiv) singing during a territorial interaction with intruder(s) (T); (xv) walking whilst sporadically foraging on invertebrates or small vertebrates (WF). For each vocal event, we quantified the response of the rest of the group as either: (i) 'no response' if within 5 s of the vocal event at least three birds continued whatever they were doing before the event (NR); (ii) an 'alert response' if within 5 s at least three birds stopped what they were doing, looked up and remained motionless (AR); or (iii) a 'movement response' if within 5 s at least three birds moved >0.5 m towards the vocalising bird (MR). A full description of all the aforementioned behaviours are provided by Sherman (1996).

Investigation of the function of 'mew' calls

Behavioural observations suggested that 'mew' and 'grunt' calls function in maintaining acoustic contact between group members when they become separated when moving through the understorey (*e.g.* Fig. 5). We tested this experimentally as follows. The six trumpeters often became scattered over an area of 5-10 m²; when an individual lagged behind and became separated from the group naturally (*e.g.* when delayed by a food item found in the leaf litter) one observer stayed close (<3 m) to this bird. It was discouraged from rejoining the group by gentle shepherding. Meanwhile, by following at a distance of *ca* 2 m, a second observer encouraged the rest of the group to walk away from the separated bird. When the separated bird was *ca* 15 m from the nearest group member, both its vocal behaviour and that of the rest of the group was recorded for 2 mins before the bird rejoined the group. This procedure was repeated 3-6 times per trumpeter (24 trials in total), and we calculated the mean number of 'mews' and 'grunts' given per bird in the 2 mins before, during and after the separation. To determine if these vocalizations were alarm calls given in response to the presence of the observers, we performed one control trial per bird. In each trial we repeated the above procedure, but separated each subject by 3-5 m only. In this way we attempted to subject each trumpeter to a comparable degree of disturbance as during the full separation, but allowed it to maintain visual contact with the rest of the group.

Anecdotal tests of the referentiality of 'growl' and 'mew' calls

Observations suggested that the 'growl' call was specific to potential danger overhead (see Table 5). To examine this further, we conducted two simple tests. To simulate a raptor in low-level flight, a plastic Frisbee was skimmed at a height of *ca* 3 m over the group as it walked across a clearing. Vocalizations made before, during and after the event by any

member of the group were tape-recorded. We repeated this on four separate occasions at 3-4 day intervals, in different areas in the group's territory and at different times of day. To test whether acoustic clues to overhead danger could be used by trumpeters, we conducted a simple playback experiment. We broadcast one 20-s recording of the calls of an ornate hawk-eagle *Spizaetus ornatus* from a Sony SRS-58 loudspeaker held by one observer at head height from 10 m behind the group as it walked through the understorey. A second observer tape-recorded the vocal behaviour of the group for a minute before, during and after the playback. This anecdotal test was repeated using two different hawk-eagle recordings on two separate occasions a month apart.

To investigate whether the 'mew' calls alone were sufficient to evoke the appropriate response in receivers, we played single 'mew' calls to the group on six separate occasions. Each repeat involved broadcasting a single 'mew' belonging to a different individual at a realistic amplitude (*ca* 40 dB (A) SPL) at *ca* 3 m behind the group as it walked through the understorey. The group's vocal and non-vocal behaviour was noted during the minute before and after playback. Each anecdotal playback was repeated at an interval of 2-4 days.

Statistics

For each call type, we analyzed alternate calls from all vocal events given by as many different individuals as possible from our sample of clear recordings. Tests were done using SPSS 11.01 and StatView, with reference to Siegel & Castellan (1988) and Rohlf & Sokal (1995). To test whether there were significant associations between call and (i) the identity of the caller, (ii) its behaviour, or (iii) the response of the group to the call, we performed Fisher's exact tests rather than chi-square tests as over half the cells in each of the contingency tables had expected values of <5 . For these tests, Monte Carlo significance levels (which were based on 10,000 sampled contingency tables) are provided, the data set being too large to compute exact significance. Tables of the post-hoc cell contributions of each combination of nominal variables were then generated using StatView. The numbers in the tables are standardized residuals that indicate what each cell in the contingency table contributes to the chi-square statistic (see StatView Reference, 1998). As some group members gave a significant proportion of certain calls, it is possible that significant associations in analyses (ii) and (iii) were determined by the behaviour of particular individuals. To investigate this, for each of those calls that were significantly associated with a specific context or group response, we performed Fisher's exact tests of identity versus behavioural context and identity versus group response. For anecdotal tests of call referentiality, we simply present the results without further statistical analysis. Means \pm SD are given throughout; all statistical tests are two-tailed and are corrected for ties where appropriate.

Results

Call structure

We identified 11 distinct close-range calls (Fig. 1a-k), the acoustic structures of which are given in Tables 1 and 2. The calls range from high-pitched, frequency-modulated 'twitters', simple 'squeaks' and 'chirps', to broadband,

TABLE 1. *Temporal and frequency characteristics of pale-winged trumpeter vocalizations*

Vocalization	Duration (s)	Min. frequency (Hz)	Max. frequency (Hz)	Bandwidth (Hz)	Peak frequency (Hz)	N (calls)	Rate of calling (s ⁻¹)	N (bouts)
Chack	0.08 ± 0.01	252 ± 243	4047 ± 814	3795 ± 760	1914 ± 712	30	2.92 ± 1.01	6
Drum	0.14 ± 0.02	162 ± 23	217 ± 15	55 ± 21	199 ± 47	73	3.6 ± 0.78	9
Growl	0.28 ± 0.18	99 ± 21	295 ± 38	195 ± 28	135 ± 29	15	0.84 ± 0.02	4
Mew	0.38 ± 0.06	173 ± 63	2436 ± 426	2264 ± 416	1266 ± 544	67	0.21 ± 0.06	10
Grunt	0.15 ± 0.04	94 ± 15	2152 ± 600	2059 ± 551	1940 ± 46	20	0.45 ± 0.22	5
Disyllabic drum	0.37 ± 0.09	79 ± 20	308 ± 18	230 ± 23	111 ± 76	20	0.78 ± 0.27	5
Soft grunt	0.17 ± 0.02	143 ± 12	435 ± 21	292 ± 26	194 ± 49	9	0.46 ± 0.23	9
Twang	0.20 ± 0.05	126 ± 51	385 ± 52	259 ± 54	267 ± 117	30	3.0 ± 0.36	5
Squeak	0.18 ± 0.05	1242 ± 444	2679 ± 601	1437 ± 422	1953 ± 154	8	*	*
Chirp	0.13 ± 0.03	859 ± 44	1200 ± 103	340 ± 101	1077 ± 50	8	*	*
Twitter	0.82 ± 0.27	825 ± 379	3414 ± 621	2590 ± 768	2141 ± 467	15	*	*
Tremolo song	3.84 ± 1.49	94 ± 32	381 ± 61	287 ± 80	220 ± 25	25	0.16 ± 0.04	7

* Calls not delivered in bouts, but given singly and irregularly.

Means ± SD are given.

TABLE 2. *Temporal and frequency characteristics of trumpeter 'mew' calls*

Identity (<i>N</i>)	Duration (s)	Min. frequency (Hz)	Max. frequency (Hz)	Bandwidth (Hz)	Peak frequency (Hz)	Lower quartile (Hz)	Mean frequency (Hz)	Upper quartile (Hz)
B (15)	0.41 ±0.06	154 ±13	2404 ±329	2250 ±329	1294 ±496	920 ±270	1399 ±201	1735 ±232
L (11)	0.34 ±0.09	249 ±118	2241 ±447	2557 ±307	1728 ±525	1150 ±239	1627 ±254	2115 ±256
M (13)	0.36 ±0.06	153 ±14	2806 ±348	2089 ±450	1163 ±471	877 ±113	1306 ±68	1649 ±83
C (9)	0.41 ±0.05	144 ±13	2423 ±536	2444 ±354	1548 ±290	1079 ±161	1508 ±104	1941 ±196
I (9)	0.36 ±0.05	178 ±53	2207 ±307	2245 ±56	1190 ±318	860 ±233	1363 ±220	1752 ±229
R (10)	0.40 ±0.03	164 ±28	2588 ±348	2044 ±311	663 ±499	733 ±311	1237 ±179	1622 ±253
χ^2_5	13.7	18.3	17.5	14.5	26.8	16.8	23.9	24.5
<i>p</i>	0.017	0.03	0.004	0.013	0.0001	0.005	0.0001	0.0001

PCA revealed that the overall structure of the mew calls differed significantly between individuals (see text). Values for χ^2_5 derive from post-hoc Kruskal-Wallis tests comparing the mean values for each call parameter. *N* refers to number of mew calls sampled per individual.

harsh and abrupt 'chacks', low-pitched harmonically rich, tonal 'mews' and rhythmic, nasal 'drums' and 'twangs'. In addition, we identified two variants: a prolonged 'twitter' produced by a female during copulation (Fig. 1l) and a composite of two calls, the 'drum-chack' (Fig. 1m). The copulation call may well qualify as a twelfth distinct call as playback elicited a strong aggressive response from the female. Trumpeters also produce a loud, long-range vocalization, the 'tremolo song', which is usually given at night. This consists of a series of 2-16 rapidly descending staccato 'bu' notes followed by a long, low-pitched, rapidly frequency-modulated resonant tremolo note (Fig. 2). When given during the day, these songs were often preceded by a series of 2-8 'chacks' (19/25 'songs' recorded). These 'chacks' had a significantly lower minimum frequency (Mann-Whitney *U*-test: $z = -4.28$, $N_1 = 30$, $N_2 = 14$, $p < 0.0001$) and broader bandwidth ($z = -2.94$, $p = 0.03$) than those produced in contexts of alarm, but were otherwise structurally identical to alarm 'chacks' (*p* values ranged from 0.07 to 0.12).

There was great variation between vocalization types in the frequency with which they were produced, with 'twitters' accounting for the majority

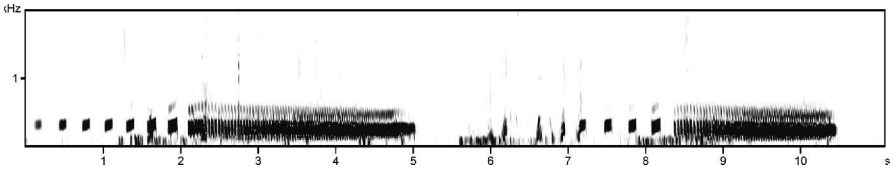


Fig. 2. Spectrogram of two bursts of trumpeter ‘tremolo song’ given by the dominant female (C). The song was sampled at 8000 Hz and the spectrogram was produced with a frequency resolution of 15 Hz and a bandwidth of 117 Hz.

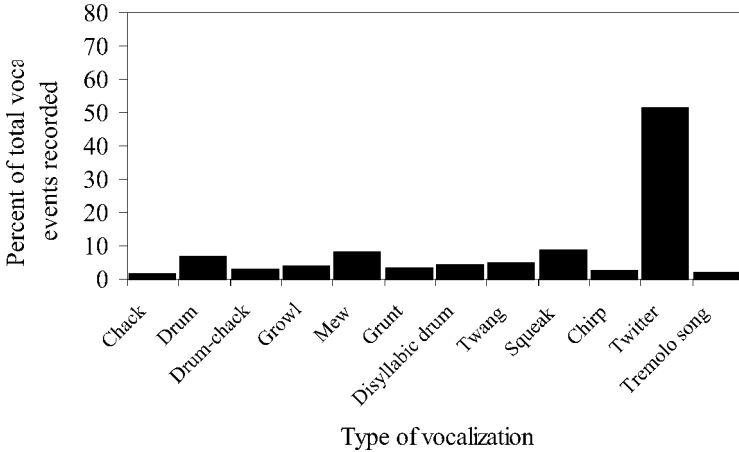


Fig. 3. Percentage of the different types of vocalization given by the study group.

of all diurnal vocal events recorded and ‘chacks’ and ‘tremolo songs’ accounting for the minority (Fig. 3).

Individuality of ‘mew’ calls

PCA identified four factors that explained 93.6% of the total variation in the data set. As the first factor accounted for a high proportion of the total variance and had an eigenvalue that was much larger than that of the next factor (Table 3), it was used to compare calls between individuals. We found that there was significantly greater variation in the PC1 scores between individuals than within individuals (Kruskal-Wallis test: $\chi_5^2 = 24.7$, $p < 0.0001$). The cross-correlation analysis also revealed that each trumpeter produced ‘mew’ calls that were significantly more similar to each other than they were to those produced by other trumpeters (Table 4). In all cases, the mean coefficient of similarity was greater in within-group comparisons than

TABLE 3. *Factor loadings for the first two principal components of trumpeter 'mew' call measurements*

	PC1	PC2
Proportion of variance	60.7	17.1
Eigenvalue	4.86	1.37
Factor loadings		
Duration	-0.169	0.827
Minimum frequency	0.386	-0.774
Maximum frequency	0.884	0.095
Bandwidth	0.847	0.214
Peak frequency	0.779	-0.061
Lower quartile	0.893	0.133
Mean frequency	0.951	0.104
Upper quartile	0.933	0.009

TABLE 4. *Coefficients of mew call similarity within and between individual trumpeters*

Identity	Coefficients of similarity				
	Within individuals	Between individuals	<i>t</i>	df	<i>p</i>
A	0.41 ± 0.14	0.38 ± 0.12	-2.08	700	0.038
B	0.50 ± 0.12	0.34 ± 0.12	-9.53	556	<0.0001
C	0.50 ± 0.14	0.41 ± 0.13	-3.69	442	<0.0001
D	0.42 ± 0.10	0.38 ± 0.10	-1.79	502	0.074
E	0.44 ± 0.11	0.34 ± 0.09	-6.25	413	<0.0001
F	0.68 ± 0.17	0.34 ± 0.12	-16.9	553	<0.0001

Mean ± SD are given for the coefficients of similarity of each trumpeter's mew call compared within and between individuals. Values of *t* and *p* derive from unpaired *t*-tests in which coefficients in the within-individual cross-correlation are compared with those generated in the between-individual cross-correlation.

between-group comparisons, and this difference was significant in all but one individual (D). Together these analyses suggest individual trumpeters can be discriminated by means of their 'mew' calls.

Pattern and frequency of calling

The group vocalized at a rate of 11.9 ± 2.2 vocal events h^{-1} , calling throughout the day from dawn at *ca* 06h00 until dusk at *ca* 18h00. Vocal

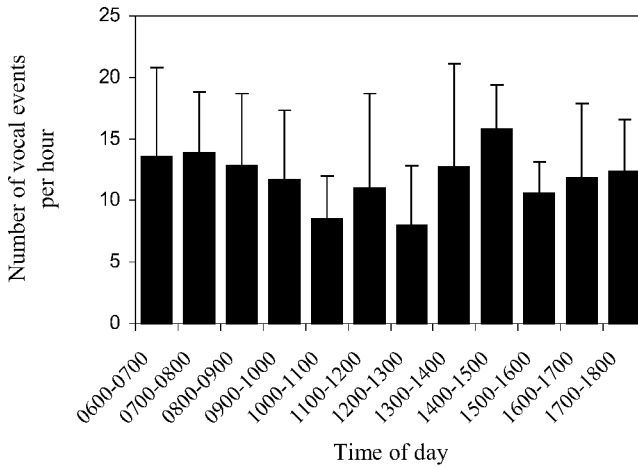


Fig. 4. The study group vocalized throughout the day and there was no significant difference between sampling periods in the number of vocal events recorded (Friedman test: $\chi^2_{12} = 12.2$, $p = 0.43$). Bars show mean \pm SD; $N = 7$ hours per sampling period.

activity remained fairly high and constant during this period (Fig. 4). Trumpeters also produced ‘tremolo songs’ from their roosts after dark, several group members apparently vocalizing simultaneously for a duration of 20–180 s. Continuous data were gathered on the vocal behaviour of the study group from 18h30 to 06h00 on five dates only. On 19–20/08/01 songs were given at 18h40, 22h15 and 00h05; on 27–28/08/01 at 24h10 and 03h05; on 17/09/01 at 20h48 and 21h05; on 21–22/09/01 at 19h10, 04h30 and 04h50; and on 1–2/10/01 at 20h45, 22h40 and 04h35.

Social correlates of vocal behaviour

There was significant variation across vocalization type with respect to identity of the caller (Fisher’s exact test: $\chi^2_{55} = 364$, $p < 0.0001$; Table 5). The dominant individual (A) produced a significant proportion of the alarm (‘chack’ and ‘growl’), recruitment (‘drum’) and contact (‘grunt’) calls. In particular, this individual almost exclusively produced the food-related ‘twang’ call. Meanwhile, the most subordinate individual (F) produced the majority (40%) of the ‘twitter’ calls. If all vocal events were considered, there was no relationship between the dominance rank and number of vocal events (Spearman rank correlation: $\rho = 0.09$, $N = 6$, $p = 0.87$). However, when vocal events were partitioned into those that were associated with

TABLE 5. *Total number of each type of vocal event given by the six trumpeters*

Dominance rank	Identity of caller						Total
	A	B	C	D	E	F	
	1	2	2	3	4	5	
Vocalisation:	5*	1	–	4*	1	–	11
Chack	34*	1	4	–	2	1	42
Drum	6	5*	2	6*	–	–	19
Drum-chack	8*	1	2	6*	–	1	18
Growl	9	6	11	3	18*	10	57
Mew	8*	2	3	1	–	2	16
Grunt	12*	2	2	2	3	1	22
Disyllabic drum	25*	1	2	–	4	5	37
Twang	11	4	13*	4	4	4	40
Squeak	6*	5*	1	–	–	–	12
Chirp	20	22	84*	23	62*	141*	352
Twitter	–	15*	–	–	–	1	16
Tremolo song	144	65	124	49	94	166	642
Total	5*	1	–	4*	1	–	11

* Combinations of call type and trumpeter identity, the occurrence of which differed significantly from that which would be expected under the hypothesis of independence (post-hoc cell contributions > 1.96 , $p < 0.05$).

submissive displays (*i.e.* ‘twitters’) and those that were not, we found a weak positive relationship between dominance rank and total number of vocal events, and a weak negative relationship between rank and total number of ‘twitter’ events recorded (Fig. 5).

Context of calling and responses to anecdotal tests

There was significant variation across vocalization type with respect to the behavioural context of vocalizing birds (Fisher’s exact test: $\chi^2_{154} = 1007$, $p < 0.0001$), and an analysis of post-hoc cell contributions revealed significant associations between vocalization type and behavioural context (Table 6). For most of these calls, we found no significant effect of caller-identity on context (χ^2 -values: 1.62-3.99, p -values: 0.43-1.0), the exception being the ‘twitter’ (see below). There was also significant variation across call type with respect to response of the group to the calls ($\chi^2_{55} = 729$, $p < 0.0001$; Table 7). For all calls except the ‘growl’ (see below), we

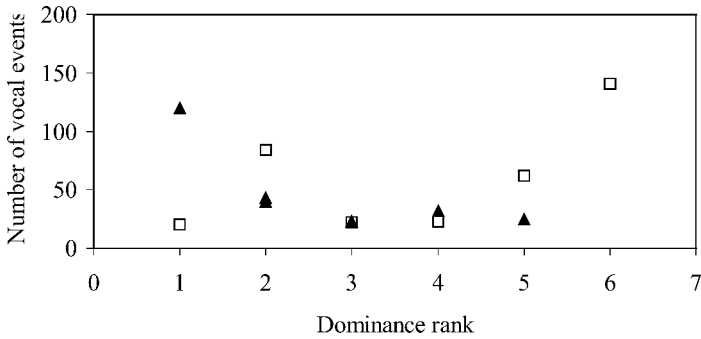


Fig. 5. Dominance rank was positively correlated with the total number of vocal events, excluding 'twitters' (solid triangles; Spearman-rank correlation: $\rho = 0.81$, $N = 6$, $p = 0.05$), whilst the number of 'twitters' produced (open squares) tended to be inversely related to dominance ($\rho = 0.75$, $p = 0.08$).

found no significant effect of caller-identity on context (χ^2 -values: 2.6-5.5, p -values: 0.19-1.0).

Specifically, 'chacks' were usually given by stationary birds that were scanning horizontally, and they almost invariably resulted in at least three group members also stopping and looking alert. Six 'chack' events coincided with the appearance of a mammal moving through the undergrowth within 15 m of the group (identified once as a green acouchi *Myoprocta pratti*, twice as a brown agouti *Dasyprocta variegata*, twice as a white-lipped peccary *Tayassu pecari* and once unidentified).

Similarly, 'growls' were almost entirely given by birds that had frozen still and were looking up into the canopy. Of the 32 'growl' events, 20 coincided with over-head disturbances: primates (*i.e.* black spider monkeys *Ateles paniscus* and brown capuchins *Cebus apella*) moving through the canopy on seven occasions, a large branch or leaf falling through the canopy on five occasions, raptors taking off on two occasions, and macaws *Ara* spp. landing or taking off from the canopy on two occasions. In 69% of the 'growl' events recorded, at least three other group members stopped what they were doing and looked up. However, this may have been determined by the behaviour of the dominant individual (A) who gave the majority of these calls, as there was significant effect of caller-identity on group response for this call (Fisher's exact test comparing across individuals the proportions of 'growls' that elicited an alert versus a non-alert response from the rest of the group: $\chi^2_5 = 7.7$, $p = 0.05$). When a Frisbee was thrown over the group, a series of five, two and three 'growls' respectively were given by the dominant

TABLE 6. *Occurrence of trumpeter vocal events with respect to 15 categories of behavioural context*

	Behavioural context ¹															Total
	AH	AU	AD	AP	AS	FB	FF	FT	P	R	RP	S	SD	T	WF	
Chack	9*	-	1	-	-	-	-	1	-	-	1	-	-	-	3	15
Drum	19*	-	2	-	2	-	-	3	1	3	10	7*	-	-	6	53
Drum-chack	6*	-	-	-	3	-	-	1	-	-	3	-	-	-	9	22
Growl	2	20*	-	-	1	-	-	3	-	-	2	-	-	-	4	32
Mew	47*	-	-	-	1	-	-	-	-	-	3	-	-	-	16	67
Grunt	18*	-	-	-	1	-	-	-	-	-	2	-	-	-	6	27
Disyllabic drum	2	-	1	-	-	-	-	5	1	-	6	-	-	-	20*	35
Twang	-	-	-	-	1	-	34*	1	1	-	-	-	-	-	1	38
Squeak	4	-	1	2	19*	1	1	2	-	-	14	-	-	-	24*	68
Chirp	1	-	1	-	6*	-	-	2	-	-	5	-	-	-	5	20
Twitter	14	-	1	28*	15	35*	-	18	4	-	62	-	191*	-	48	416
Tremolo song	4	-	-	-	-	-	-	-	-	-	-	-	-	10*	2	16
Total	122	20	7	30	49	36	35	36	7	3	108	7	191	10	144	807

¹ Calls given by trumpeters when they were AH: alert and scanning horizontally; AU: alert and looking up; AD: showing aggression towards another group member; AP: apparently requesting another group member to allopreen them; AS: feeding at an ant swarm; FB: begging for food; FF: parading around carrying an item of food; FT: foraging under a fruiting tree; P: playing; R: descending from or ascending to a roost site; RP: resting and preening; S: aggressing a snake or large frog; SD: showing submissive behaviour to another group member; T: singing during a territorial interaction with another group or intruder; WF: walking and foraging.

* Combinations of call type and behavioural context, the occurrence of which differed significantly from that which would be expected under the hypothesis of independence (post-hoc cell contributions > 1.96, $p < 0.05$).

individual (A) in the minute following each of the first three trials and at least three group members froze and looked up; there was no obvious response to the fourth appearance of the Frisbee. No 'growls' were given in the minute before the throw in any repeat.

Similarly, on both occasions when ornate hawk-eagle calls were played to the group, within 3 s of the start of playback, individual (A) gave a series of 'growls' (three in the first trial and five in the repeat), all members of the group froze and looked-up. In the first trial, they then fluffed themselves up and approached the speaker nervously to within *ca* 5 m, before turning and

TABLE 7. *Occurrence of trumpeter vocal events with respect to three categories of group response*

Vocalization	Response of group ¹			Total
	NR	AR	MR	
Chack	2	11*	0	13
Chirp	20*	0	0	20
Growl	10	22*	0	32
Disyllabic drum	35*	0	0	35
Drum	17	15	21*	53
Drum-chack	6	16*	0	22
Grunt	12	15*	0	27
Mew	28	39*	0	67
Squeak	67*	1	0	68
Tremolo	0	16*	0	16
Twang	9	0	29	38
Twitter	416*	0	0	416
Total	622	135	50	807

¹ Response of group to a vocal event was scored as NR (no response) if within 5 s of the vocal event at least three birds did not appear to change their behaviour; AR (alert response) if within 5 s at least three birds stopped what they were doing, looked up and looked alert; or MR (movement response) if within 5 s at least three birds moved >0.5 m towards the vocalizing bird.

* Combinations of call type and trumpeter identity, the occurrence of which differed significantly from that which would be expected under the hypothesis of independence (post-hoc cell contributions > 1.96, $p < 0.05$).

running, heads down, in the opposite direction. In the repeat, all members of the group merely remained alert for *ca* 3 mins before continuing walking. No 'growls' were given in the minute prior to either playback.

'Drums' were significantly associated with contexts of alarm, and 41.5% of 'drum' events resulted in at least three group members moving towards the vocalizing bird. On six occasions when a snake and one occasion when a large frog (*ca* 10 cm long) was encountered, this call was given first by the bird that had found the animal, and then by all other group members as they surrounded and 'peered' at it. All snakes (apart from one brightly coloured juvenile snake) <50 cm in length and <2 cm in diameter were killed and consumed, a process taking up to 50 mins, the 'drum' call being emitted by all birds throughout. The association of 'drums' with snakes is corroborated by Sherman's observations of several trumpeter groups. He

reports anecdotally that ‘the longest “drumming” bouts were elicited by the largest snakes’ (P. Sherman, pers. comm., 2002), and states that ‘...larger snakes are investigated for several minutes or longer, throughout which time all of the birds investigating the snake produce this unmistakable [drum] call’ (Sherman, 1996).

‘Titters’ were strongly associated with submissive displays and were most frequently given by a trumpeter as it crouched and opened its wings before another individual. However, this association is likely to have been the result of the behaviour of the individual giving the majority of these calls (F), there being a significant effect of caller-identity on context (Fisher’s exact test comparing across individuals the proportion of ‘titters’ given in subordinate versus non-subordinate display contexts: $\chi^2_5 = 17.4$, $p = 0.004$). Birds begging for food items or ‘requesting’ to be allopreened by another group member also gave these distinctive high-pitched calls. The female was recorded giving a prolonged and emphatic ‘twitter’ whilst copulating (Fig. 11). No other call was directly associated with submissive or dominance displays. ‘Titters’ were seemingly directed at one receiver only, and never elicited any change in the behaviour of the rest of the group (Table 7).

‘Twang’ calls were almost entirely given by birds as they ‘paraded’ with an item of food. However, the dominant bird (A) also gave the call on two occasions during ‘play’ behaviour when it instead carried a twig. Of the 38 ‘twang’ events recorded, 76.3% resulted in at least three other trumpeters moving towards the caller.

‘Mews’ and ‘grunts’ were almost always given by birds that had stopped walking or foraging and were looking alert. Following over half the ‘mew’ events, at least three group members stopped and also looked alert, and 81.5% (22/27) of the ‘grunts’ recorded occurred <5 s after a ‘mew’. There was no obvious source of alarm when these calls were given, however compared to other calls, the group was more scattered when ‘mews’ were given (Fig. 6). To investigate this further, we analyzed the ‘mewing’ behaviour of individuals rather than of the group as a whole. We found that trumpeters were a significantly greater distance from their nearest (4.7 ± 2.3 m) and furthest (19.8 ± 4.5 m) group members when giving ‘mew’ calls ($N = 6$ birds) than when giving other calls (nearest = 2.7 ± 2.1 m, furthest = 8.3 ± 2.3 m; Wilcoxon signed-rank tests comparing ‘mew’ calls with ‘other’ calls for both nearest and furthest group member distances: $T = 0$, $N = 6$, $p = 0.02$

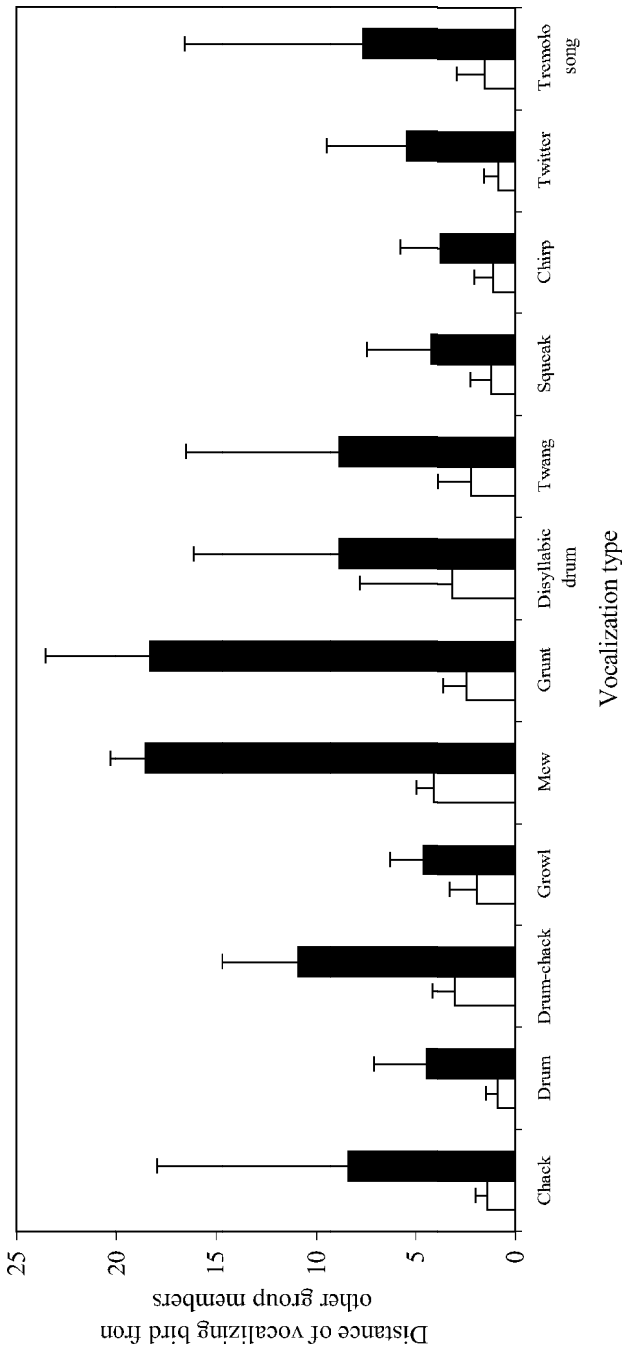


Fig. 6. There was significant variation across vocalization types in the mean distance vocalizing trumpeters were from their nearest and furthest fellow group member (Kruskal-Wallis tests: nearest: $\chi^2_{11} = 68.8$, $p < 0.0001$; furthest: $\chi^2_{11} = 109$, $p < 0.0001$). Bars show mean \pm SD distance of calling birds from their nearest (open bars) and furthest (solid bars) group members, with sample sizes given above.

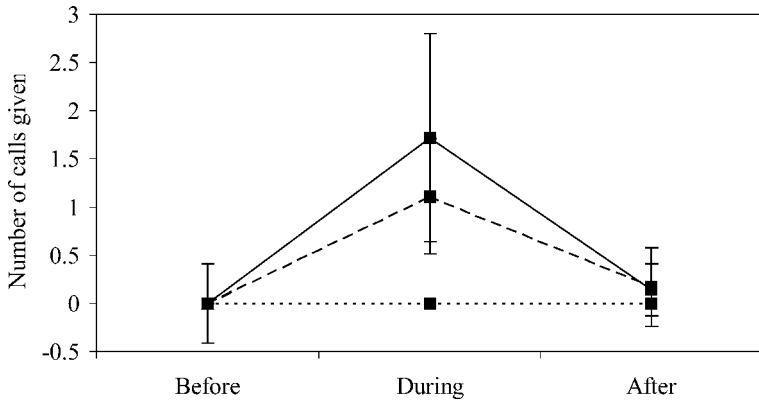


Fig. 7. Trumpeters produced significantly more mew calls (solid line) when separated from the rest of the group than before or after (Friedman test: $\chi^2_2 = 11.2$, $N = 6$, $p = 0.004$). And significantly more grunt calls (thick dashed line) were produced by member(s) of the separated group during separation than either before or after ($\chi^2_2 = 8.32$, $p = 0.016$). No mews were given during the control (fine dashed line). Means \pm SD are shown.

in both comparisons). On each of the six occasions when a single different 'mew' call was played to the group, a 'grunt' was given by one group member (the dominant individual on four of the six repeats) within five seconds of the playback and at least three group members immediately stopped walking and looked alert. No 'grunts' were given in the minute before playback.

No obvious context other than 'walking and foraging' could be assigned to the 'disyllabic drum' and it did not appear to elicit a response from other group members. 'Squeaks' and 'chirps' were associated with ant swarms (Table 6); they also did not appear to elicit any response from the rest of the group.

Finally, diurnal 'tremolo songs' were associated with territorial events. They were produced either during encounters with groups of intruders (six events), during border disputes with neighbouring groups (three events), or given at a territory boundary at dawn the morning after a bout of nocturnal counter-singing with a neighbouring group (seven events).

Separation experiment

Isolated trumpeters gave significantly more 'mew' calls, and members of the separated group gave significantly more 'grunt' calls during the period of separation than before or after (Fig. 7). No 'mews' or 'grunts' were

given during the control trial on any bird. Of the 50 'mew' calls given by separated birds during the experiment, a mean (\pm SD) of $69.7 \pm 38\%$ ($N = 6$ trumpeters) were within 5 s followed by a 'grunt' call given by a member of the separated group. In 15 of 24 trials, at least three group members stopped walking after the separated bird had 'mewed' and remained stationary until the isolated bird had come within 3-5 m. The total lack of 'mewing' or 'grunting' during controls suggested that these calls are not alarm calls.

Discussion

The pale-winged trumpeter has a rich vocal repertoire, producing at least 12 structurally distinct and largely context-specific vocalizations. This repertoire sets the species apart from other non-passerine birds for which much fewer call types are usually recorded: *e.g.* five have been recorded from Bulwer's petrels *Bulweria bulwerii* (Bretagnolle, 1996) and six from adult Brünnich's guillemots (=thick-billed murre) (Lefevre *et al.*, 2001). It has perhaps the most complex vocabulary amongst the varied gruiform families: two within-group adult calls have been recorded in the subdesert mesite *Monias benschi* (Seddon, 2002); four are noted for the great bustard *Otis tarda* (Cramp, 1980); and up to ten are identifiable from cranes Gruidae (Archibald & Meine, 1996).

Trumpeter vocalizations can be grouped into six broad contextual classes: alarm, recruitment, social, contact, feeding and territory defence. Table 8 summarizes the contexts and possible functions of these calls.

Production-specificity of alarm and recruitment calls

To demonstrate that structurally different calls are functionally referent, it is necessary to show that they have 'production specificity', *i.e.* they are given in response to specific stimuli, and 'perception specificity', *i.e.* that the calls alone evokes appropriate responses by the receivers (Marler *et al.*, 1992; Macedonia & Evans, 1993).

Contextual data and anecdotal tests showed that aerial alarm calls ('growls') are produced in response to objects moving overhead, or to the calls of an aerial predator; that ground alarm calls ('chacks') are evoked principally by mammals moving through the understorey or conspecific intruders; and that recruitment calls ('drums') are elicited by potentially dangerous prey items that might require group-effort to kill, such as snakes and

TABLE 8. Summary of pale-winged trumpeter vocalizations, their contexts and putative functions

Broad class of vocalization	Specific type of vocalization	Main vocalizer	Main response of receivers	Primary contexts	Putative function
1. Alarm	Growl	Dominant	Freeze, look up	Over head disturbance	Signals aerial predator
	Chack + Drum-chack	All	Look alert and scan horizontally	Disturbance at ground level; intruder(s)	Signals terrestrial predator and intruder(s)
2. Recruitment	Drum	Dominant	Move towards caller	Large prey item	Enlisting help
3. Food	Squeak	All	No obvious response	Ant swarm	?
	Chirp	All	No obvious response	Ant swarm	?
4. Contact	Mew	All	Stop and look alert	Group scattered	Signals identity and separation from group
5. Social	Grunt	All	No obvious response	Group scattered	Signals location of group
	Disyllabic drum	All	No obvious response	Walking and foraging	Group cohesion?
	Twitter	Subordinates	No obvious response	Submission; food begging	Appeasement
6. Territorial	Twang	Dominant	Move towards caller	Parading with food in bill	Food offer; reinforcement of hierarchy
	Tremolo song	Female	Look alert	Interactions with intruders	Territory defence

amphibians. All these calls therefore meet the first criterion for functional referentiality.

These calls were almost always immediately followed by appropriate behaviour in the other members of the group, *i.e.* to freeze and look up following 'growls', to look alert and scan horizontally following 'chacks', or to approach the caller and investigate the prey item following 'drums'. These observations are all consistent with perception specificity. However, playback experiments are needed to show that vocal signals, rather than the behaviour of the caller, influences the behaviour of receivers.

Such a dichotomy between alarm vocalizations given in response to aerial predators, and alerting vocalizations given to terrestrial predators and/or intruding conspecifics is common to a number of different birds and mammals (Bradbury & Vehrencamp, 1998). However, unlike other bird species whose aerial predator alarm calls are usually above the sensitive hearing range of raptors (Catchpole & Slater, 1995), trumpeter aerial alarm calls are likely to be well below raptor auditory sensitivity. In this regard, trumpeters resemble primates such as the forest guenon *Cercopithecus cephus*, whose aerial predator alarms are also soft, low in pitch and thus difficult to hear and localize (Gautier, 1978).

Interestingly, not all group members gave alarm calls. The dominant male (A) produced the majority of 'chack' and 'growl' events, and was almost exclusively responsible for initiating bouts of 'drumming'. This situation contrasts with that found in other social vertebrates such as capybaras *Hydrochoerus hydrochaeris* in which subordinate males do all the alarm calling (Yber & Herrera, 1994) and other cooperatively breeding birds (*e.g.* Arabian babblers) in which all group members give alarm calls at similar rates (Wright *et al.*, 2001). A more active role in defence by the dominant male may simply reflect the dominant bird's greater ability to detect danger: vigilance may improve with experience and individual A was at least 15 years of age and probably the oldest bird in the group. Alternatively, it may reflect a disparity between dominant and subordinates in the cost-benefit ratio of alarm calling. For the dominant male, the benefits of protecting the group (on all members of which he is dependent for care of his offspring, Sherman 1995a, b) may outweigh the costs of attracting a predator's attention. For the subordinates, who have much less chance of breeding, the immediate costs to survival are likely to outweigh any benefits to reproduction. Sherman (1995b) found that the dominant male in all his

study groups played the most active role in chick defence, suggesting that the foregoing observations reflect a general behavioural trait of trumpeters, rather than a situation unique to our study group.

Functional referentiality and individuality of contact calls

Although 'contact' calls are prevalent in many species of bird and mammal, 'the proximate factors that motivate [contact] call production and mediate their contact function remain poorly specified' (Rendall *et al.*, 2000). Here we provide observational and experimental evidence that two contact calls ('mews' and 'grunts') are motivated by the separation of a bird from the group. Specifically, 'mews' appear to signal that the vocalizing bird has been separated from and may have lost visual contact with the group, while 'grunts' appear to signal the location of the group to the separated 'mewing' bird. Whilst similar findings exist for primates (Rendall *et al.*, 2000), to our knowledge this is the first time the proximate motivating factor of a contact call has been clearly demonstrated in a bird. Furthermore, all playbacks of 'mew' calls caused at least three group members to stop and one group member (the dominant in 4/6 cases) to 'grunt', even though all group members were present when playbacks were conducted. Our data indicate, therefore, that the 'mew' call shows both production and perception specificity, and could thus be described as functionally referent.

Interestingly, spectrograms of 'mews' strongly resemble those representing the tonal barks produced by Chacma baboons when they are at risk of losing contact with the group (Fischer *et al.*, 2001). In common with these baboon barks, and the contact calls of a wide variety of other non-passerine birds (Mammen & Nowicki, 1981; Mathevon, 1997; Lefevre *et al.*, 2001), trumpeter 'mew' calls were found to be individually distinct. This raises the likelihood that these calls not only communicate that a signaller is 'lost', but who that signaller is. Indeed, a prerequisite for maintaining a complex social system is that interacting individuals can recognize each other (Falls, 1982). For groups of terrestrial birds having to coordinate their movements in dense undergrowth, where separation events are frequent, vocal cues might supplement or even replace visual cues. Although no tests were carried out to investigate whether the individuality of 'mew' calls could be perceived by the trumpeters themselves, given the ability of other cooperatively breeding birds to use vocal cues to recognize individuals (Payne *et al.*, 1991; Cooney & Cockburn, 1995) it is conceivable that trumpeters can recognize different group members' 'mew' calls.

Social role of vocalizations in trumpeters

The most obviously social vocalization was the 'twitter'. The juvenile bird produced the majority of 'twitters', and frequency of 'twitter' production was inversely related to dominance rank. These calls resemble chick begging calls (Sherman, 1996) and seem to be retained by adults for use as appeasement signals: they form part of the submissive display, were often given by birds that had been aggressed and were used to stimulate feeding and allopreening, behaviours known to be important in mediating dominance interactions (Bradbury & Vehrencamp, 1998). The use of high-pitched juvenile-like calls as appeasement signals is also found in many other social animals (Bradbury & Vehrencamp, 1998); the observation that 'twitters' are occasionally given by dominant birds does not contradict this interpretation as dominant animals are known to appease in numerous species (Harcourt & Stewart, 1996).

The 'twang' call was almost exclusively produced by the dominant male as it paraded around carrying an item of food. The call frequently evoked bouts of 'twittering' amongst subordinates, who appeared to beg and compete for the food item. Interestingly, during his five-year study of trumpeters, Sherman noted that all group members give this call when chick-feeding and that the call stimulated 'twittering' and begging behaviour in the chicks (P. Sherman, pers. comm., 2002). Together these observations hinted that, at least outside the breeding season, the 'twang' call might have been used by the dominant bird to reinforce his status and maintain the hierarchy.

Conclusion

The pale-winged trumpeter was found to have an unusually complex system of within-group vocal communication, including an individually distinct and functionally referent contact call and two acoustically different predator-specific alarm calls. This preliminary study indicated that close-range calls play an important role in coordinating group vigilance, group cohesion and dominance interactions in this species and hinted that vocal communication in group-living birds can exhibit a level of sophistication once thought unique to primates. However, a long-term study of the vocal behaviour of the pale-winged trumpeter is required before firm conclusions can be drawn.

The findings of this study have opened up many interesting avenues for further work. In particular, playback experiments on a number of different study groups could be used to establish whether trumpeters: (1) give alarm and recruitment calls that alone stimulate appropriate anti-predator behaviour in receivers (and thereby be classified as functionally referent); (2) vary their alarm calling behaviour with respect to social context and/or the degree of threat to related group members; (3) recognize and respond differently to different group members' contact calls; and (4) are able to use vocal as well as visual cues to identify potential predators, a cognitive ability not yet reported in birds.

References

- Archibald, G.W. & Meine, C.D. (1996). Family Gruidae (cranes). — In: Handbook of the birds of the world. Volume 3 (J. del Hoyo, A. Elliott & J. Sargatal, eds). Lynx Edicions, Barcelona, p. 60-89.
- Bradbury, J.W. & Vehrencamp, S.L. (1998). Principles of animal communication. — Sinauer Associates, Sunderland, Massachusetts.
- Bretagnolle, V. (1996). Acoustic communication in a group of non-passerine birds, the petrels. — In: Ecology and evolution of acoustic communication in birds (D.E. Kroodsma & E.H. Miller, eds). Cornell University Press, New York, p. 160-177.
- Catchpole, C.K. & Slater, P.J.B. (1995). Bird song: biological themes and variations. — Cambridge University Press, Cambridge, U.K.
- Charif, R.A., Mitchell, S. & Clark, C.W. (1995). Canary 1.2 User's Manual. — Cornell Library of Ornithology, New York.
- Cooney, R. & Cockburn, A. (1995). Territorial defence is the major function of female song in the superb fairy-wren, *Malurus cyaneus*. — *Anim. Behav.* 49, p. 1635-1647.
- Cramp, S. (1980). Handbook of the birds of Europe, the Middle East and North Africa. Volume 2: hawks to bustards. — Oxford University Press, Oxford.
- Evans, C.S., Evans, L. & Marler, P. (1993). On the meaning of alarm calls: functional reference in an avian vocal system. — *Anim. Behav.* 46, p. 23-38.
- Falls, J.B. (1982). Individual voice recognition by sounds in birds. — In: Acoustic communication in birds, Volume 2. Song learning and its consequences (D.E. Kroodsma, E.H. Miller & H. Quillet, eds). Plenum Press, New York, p. 237-278.
- Fischer, J., Hammerschmidt, K., Cheney, D.L. & Seyfarth, R.M. (2001). Acoustic features of female chacma baboon barks. — *Ethology* 107, p. 33-54.
- Gautier, J.-P. (1978). Repertoire sonore de *Cercopithecus cephus*. — *Z. Tierpsychol.* 46, p. 113-169.
- Gyger, M., Marler, P. & Pickert, R. (1987). Semantics of an avian alarm call system — the male domestic-fowl, *Gallus domesticus*. — *Behaviour* 102, p. 15-40.
- Harcourt, A.H. & Stewart, K.J. (1996). Function and meaning of wild gorilla 'close' calls 2. correlations with rank and relatedness. — *Behaviour* 133, p. 827-845.

- Horn, A.G. & Falls, J.B. (1996). Categorisation and the design of signals: the case of song repertoires. — In: *The ecology and evolution of acoustic communication in birds* (D.E. Kroodsma & E.H. Miller, eds). Comstock, Ithaca, New York, p. 121-135.
- Krams, I. (2001). Communication in crested tits and the risk of predation. — *Anim. Behav.* **61**, p. 1065-1068.
- Kroodsma, D.E. & Miller, E.H. (1996). *Ecology and evolution of acoustic communication in birds*. — Cornell University Press, New York.
- Lefevre, K., Gaston, A.J. & Montgomerie, R. (2001). Repertoire, structure and individual distinctness of thick-billed murre calls. — *Auk* **103**, p. 134-142.
- Macedonia, J.M. & Evans, C.S. (1993). Variation among mammalian alarm call systems and the problem of meaning in animal signals. — *Ethology* **93**, p. 177-197.
- Mammen, D. & Nowicki, S. (1981). Individual differences and within-flock convergence in chickadee calls. — *Behav. Ecol. Sociobiol.* **9**, p. 179-186.
- Manser, M.B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of urgency. — *Proc. Roy. Soc. London, B* **268**, p. 2315-2324.
- Markl, H. (1985). Manipulation, modulation, information, cognition: some of the riddles of communication. — In: *Experimental behavioural ecology and sociobiology* (B. Holldobler & M. Lindauer, eds). Gustav Fischer Verlag, Stuttgart, p. 163-194.
- Marler, P., Evans, C.S. & Hauser, M.D. (1992). Animal signals: motivational, referential or both? — In: *Nonverbal vocal communication: comparative and developmental approaches* (H. Papoušek, U. Jürgens & M. Papoušek, eds). Cambridge University Press, Cambridge, p. 66-86.
- Mathevon, N. (1997). Individuality of contact calls in the greater flamingo *Phoenicopterus ruber* and the problem of background noise in a colony. — *Ibis* **139**, p. 513-517.
- Naguib, M., Mundry, R., Ostreiher, R., Hultsch, H., Schrader, L. & Todt, D. (1999). Cooperatively breeding Arabian babblers call differently when mobbing in different predator-induced situations. — *Behav. Ecol.* **10**, p. 636-640.
- Payne, R.B., Payne, L.L., Rowley, I. & Russell, E.M. (1991). Social recognition and response to song in cooperative red-winged fairy wrens. — *Auk* **108**, p. 811-819.
- Rendall, D., Cheney, D.L. & Seyfarth, R.M. (2000). Proximate factors mediating 'contact' calls in adult female chacma baboons (*Papio cynocephalus ursinus*) and their infants. — *J. Comp. Psychol.* **114**, p. 36-46.
- Rohlf, F.J. & Sokal, R.R. (1995). *Statistical tables*. — W.H. Freeman & Company, New York.
- Seddon, N. (2002). The structure, context and possible function of solos, duets and choruses in the subdesert mesite (*Monias benschi*). — *Behaviour* **139**, p. 645-676.
- Sherman, P.T. (1995a). Breeding biology of white-winged trumpeters (*Psophia leucoptera*) in Peru. — *Auk* **112**, p. 285-295.
- (1995b). Social organisation of cooperatively polyandrous white-winged trumpeters (*Psophia leucoptera*). — *Auk* **112**, p. 296-309.
- (1996). Family Psophiidae (trumpeters). — In: *Handbook of the birds of the world. Volume 3* (J. del Hoyo, A. Elliott & J. Sargatal, eds). Lynx Edicions, Barcelona, p. 96-107.
- Siegel, S. & Castellan, N.J. (1988). *Nonparametric statistics for the behavioral sciences*. — McGraw-Hill Book Company, New York.
- Snowdon, C.T. (1986). Vocal communication. — In: *Comparative primate biology, volume 2A: behavior, conservation and ecology* (G. Mitchell & J. Erwin, eds). Liss, New York, p. 495-530.

- Terborgh, J. (1983). Five New World primates. — Princeton University Press, New Jersey.
- Uster, D. & Zuberbuhler, K. (2001). The functional significance of Diana monkey 'clear' calls. — *Behaviour* 138, p. 741-756.
- Wright, J., Berg, E., de Kort, S.R., Khazin, V. & Maklakov, A.A. (2001). Cooperative sentinel behaviour in the Arabian babbler. — *Anim. Behav.* 62, p. 973-979.
- Yber, M.C. & Herrera, E.A. (1994). Vigilance, group size and social status in capybaras. — *Anim. Behav.* 48, p. 1301-1307.
-