



Vocal labelling of family members in spectacled parrotlets, *Forpus conspicillatus*

RALF WANKER, YASUKO SUGAMA & SABINE PRINAGE

Biozentrum Grindel, Universität Hamburg

(Received 30 January 2004; initial acceptance 5 April 2004;
final acceptance 30 September 2004; published online 23 May 2005; MS. number: 7985R)

Although there is increasing evidence that signalling animals can refer to objects external to themselves, only weak evidence exists that nonhuman animals use referential signals for different social companions. We tested whether spectacled parrotlets use different acoustic signals for different family members. We recorded two parrotlets interacting with one another during spatial but not visual separation. Discriminant function analysis of the acoustic cues of calls revealed high similarities between calls when both the individual and the interacting partner were loaded together as grouping variables. In playback experiments, the parrotlets were tested with contact calls of a family member recorded during interaction with the tested bird and with calls of the same stimulus bird recorded during interaction with another family member. The birds responded more often to calls uttered in their presence than to calls uttered in the presence of another family member. This suggests that spectacled parrotlets use contact calls to refer to a social companion and thus are labelling or naming their conspecifics. Spectacled parrotlets may thus have mental representations of their social companions, an important ability to live within their complex social system.

© 2005 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

There is increasing evidence that many animal species use signals in which the sender provides the receiver with referential information about objects external to itself (reviewed in Evans 1997; Bradbury & Vehrencamp 1998; Hauser 1998). These external objects include resources, predators and conspecifics. Since the classical experiments of von Frisch (1967), it is known that honeybees, *Apis mellifera*, inform their colony members about the location of food patches. The transfer of information about food patches has also been reported in several birds (Brown et al. 1991; Heinrich & Marzluff 1991; Evans & Marler 1994) and mammals (Dittus 1984; Elowson et al. 1991; Benz et al. 1992; Clark & Wrangham 1993; Hauser & Marler 1993b; Judd & Sherman 1996; Janik 2000). In some species, signals contain further information about the quality of food encountered (Dittus 1984; Elowson et al. 1991; Benz et al. 1992; Benz 1993; Hauser & Marler 1993a, b). Cheney & Seyfarth (1981, 1985) reported that vervet monkeys, *Chlorocebus aethiops*, have a referential alarm call system, using different alarm calls for terrestrial and aerial predators, a phenomenon also found in other mammals (Macedonia

1991; Pereira & Macedonia 1991; Macedonia & Evans 1993; Manser 2001; Manser et al. 2001, 2002; Zuberbühler 2001, 2002; Fichtel & Kappeler 2002) and in domestic chickens, *Gallus gallus domesticus* (Gyger et al. 1986, 1987; Gyger & Marler 1988; Evans & Marler 1991, 1992). The presence of conspecifics often alters the number of signals given in a certain context. Domestic chickens make more food calls when they are with females than when they are alone or with other males (Marler et al. 1986). In some cases, the presence of a certain conspecific can alter the structure of a given signal. Neighbouring song sparrows, *Melospiza melodia*, match their song repertoire and type (Beecher et al. 1996, 2000; Burt et al. 2002) and wild bottlenose dolphins, *Tursiops truncatus*, match their signature whistles during social interactions (Janik 2002). However, there is only weak evidence that nonhuman animals use referential signals for different social companions (Masataka 1983).

In the wild and in captivity, spectacled parrotlets use a specific call, the contact call, when they are out of sight or when they need to reach each other. Contact calls last 36–159 ms and have a frequency bandwidth of 438–946 Hz (Wanker & Fischer 2001). In a series of playback experiments, Wanker et al. (1998) found that parrotlets responded in a different manner to the contact calls of their mates, siblings and other group members. These data strongly suggest that these birds have the ability to

Correspondence: R. Wanker, Biozentrum Grindel, Universität Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg (email: wanker@zoologie.uni-hamburg.de).

identify individuals and social classes by using acoustic cues. Social class recognition requires that the birds are able to categorize their conspecifics into social classes and to identify them according to different characteristics of these classes (Payne et al. 1991; Gheusi et al. 1997). Individual recognition means that the receiver of a signal is able to perceive the individually distinctive characteristics of a known individual and to match this individual signature to a memorized template of the phenotype of this particular individual (Sherman et al. 1997). Contact calls of spectacled parrotlets contain information about both the individual identity and the social status of the caller (Wanker & Fischer 2001). They also vary between individuals in some acoustic features (Wanker et al. 1998; Wanker & Fischer 2001; Wanker 2002).

We investigated whether spectacled parrotlets use contact calls with a different acoustic structure for different social conspecifics, thus using referential signals for their social companions. We hypothesized that the acoustic structure of contact calls may vary depending on the identity of the interacting partner. We also predicted that an individual should discriminate between contact calls of a family member recorded during interaction with that individual and calls of the same stimulus bird recorded during interaction with another family member. To test our first hypothesis, we analysed, by discriminant function analysis, contact calls from birds separated spatially but with visual and acoustic contact. Our second hypothesis was tested with playback experiments.

METHODS

Animal Housing

Our parrotlets were captive bred and had been housed together with other conspecifics in two groups of variable size for 1–9 years. At the beginning of the study, the group sizes were 30 and 16 individuals. They were ringed with permission of the Vereinigung für Artenschutz, Vogelhaltung und Vogelhaltung AZ. Permission to breed the birds was given by Bezirksamt Eimsbüttel, Veterinäramt Hamburg. The parrotlets were held in two indoor aviaries of 20 m² and 5 m², respectively. To simulate natural conditions, rooms were illuminated by fluorescent tubes on a 12:12 h schedule and by natural light (i.e. windows in the room with automatic blinds). Room temperature was 20–25 °C. A large tree trunk with twigs was located in the centre of each aviary serving as a 'grouptree' (Wanker et al. 1996). Some more twigs and rotten trunks were provided as perches near the nestboxes. As in the wild (Wanker 1997), the birds could breed twice a year. We initiated two breeding seasons by attaching wooden nestboxes (standard boxes for budgerigars, upright version 24 × 13 × 13 cm) to the walls and increasing the relative humidity to 80%. The first breeding season extended from March to July and the second from October to January. Outside the breeding seasons, the nestboxes were replaced by trunks of approximately the same size and relative humidity was reduced to 70% (Wanker & Fischer 2001).

Our group sizes resembled the natural group sizes of 10–25 individuals (Wanker 1997; Wanker et al. 1996). The groups contained old, established pairs, recently paired younger adults and unpaired individuals of different ages, including subadults and juveniles. To simulate dispersal, death and immigration and to maintain genetic variation, we gave some subadult individuals and some adult pairs to aviculturists in return for some juvenile or subadult individuals once a year. The new birds were whole sibling groups unrelated to the rest of our breeding stock. From time to time, unpaired and paired individuals were interchanged between the aviaries (Wanker & Fischer 2001).

Birds received sunflower seeds (once a week, freshly germinated), a seed mixture for seed-eating passerines, fruits, berries, wild seed-bearing plants and water ad libitum and, once a week, a multivitamin and amino acid supplement (Korvimin) and a mixture of dried insects. Fresh twigs were introduced every few weeks.

All birds were individually marked with coloured celluloid and numbered aluminium bands and, if necessary, with Igora-Brillant-Blond hair dye made by Schwarzkopf, Hamburg, Germany (Wanker & Fischer 2001). The dye has no obvious effect on the birds (Wanker et al. 1996).

We recorded contact calls of 17 individuals from five families (Table 1). Two families could not be used for the playback experiments: in the family of Moses, Sven, Sveda and Quinquin, the mother died and the male re-paired, and in Frodo's family the pair had only one offspring, whereas all other pairs were tested with two offspring. Playback experiments were done with the remaining 12 individuals.

To assess the social status of each parrotlet tested we observed its social interactions once a week between 14 September 1999 and 10 February 2000. Every 10 min, the behaviour of each individual was recorded. Observation periods generally lasted 90 min and occasionally 60 min, depending on how active the parrotlets were.

Recording Methods

During September and November 1999, all birds were recorded in a room with a sound-deadening layer on the walls and the ceiling. Before being recorded, birds were made familiar with the room and the recording conditions. They were taken from the initial groups and kept with their family members in a third group of up to 10 individuals in an aviary (2 × 0.45 m and 1 m high) inside the recording room for 2 weeks. They were then returned to their original groups. Every parrotlet was put into a recording cage for 1–3 h during these 2 weeks. We used two recording cages (35 × 35 × 35 cm and 30 × 32 × 30 cm), 40 cm apart with a blind between them. We put another blind 20 cm from the other end of each cage, so the birds could not see the experimenter. This recording chamber was on a table, 70 cm high, with the blinds attached to the wall. A microphone was placed 20 cm in front of each cage.

At the beginning of each recording session we placed two parrotlets into the two recording cages without visual

Table 1. List of recorded individuals and their interacting partners

Calling individual	Fledging month	Interacting partner	Social category of interacting partner
Eddi	August 1993	Renee Ustinov Uvo	Pair mate Offspring Offspring
Renee	February 1993	Eddi Ustinov Uvo	Pair mate Offspring Offspring
Ustinov	August 1999	Eddi Renee Uvo	Parent Parent Sibling
Uvo	August 1999	Eddi Renee Ustinov	Parent Parent Sibling
Timothy	November 1995	Inka Vico Vanni	Pair mate Offspring Offspring
Inka	July 1994	Timothy Vico Vanni	Pair mate Offspring Offspring
Vico	August 1999	Timothy Inka Vanni	Parent Parent Sibling
Vanni	August 1999	Timothy Inka Vico	Parent Parent Sibling
Luke	April 1998	Emily Olivia Theo	Pair mate Offspring Offspring
Emily	August 1993	Luke Oskar Olivia Theo	Pair mate Offspring Offspring Offspring
Olivia	April 1999	Luke Emily Ottilie Oskar	Parent Parent Sibling Sibling
Theo	July 1999	Luke Emily Svewa Sven	Parent Parent Sibling Sibling
Frodo	January 1993	Kira Nina	Pair mate Offspring
Moses	December 1999	Kes Quinquin Svewa Sven	Pair mate Offspring Offspring Offspring
Quinquin	May 1999	Moses Quark Quinyi	Parent Sibling Sibling
Svewa	July 1999	Moses Sven Theo	Parent Sibling Same sibling group*
Sven	July 1999	Moses Svewa Theo	Parent Sibling Same sibling group*

Females are indicated in bold.

*Birds that were not related but grew up in the same group (see Wanker 1999 for further details).

contact. After 30 min we removed the central blind and inserted it again after another 30 min to give the birds a new stimulus. A recording session lasted up to 1.5 h. We recorded at least 20 contact calls for each bird, on metal tapes, using a Sennheiser ME80 microphone with K3-U module connected to a Sony TC-D5 M tape recorder.

Acoustic Analysis

Contact calls were digitized using a 486 personal computer with a Data Translation A/D-board model DT-2821 and the RTS 2.0 software (Engineering Design, Belmont, MA, U.S.A.) at a sample rate of 40 000 Hz. For each bird, 20–140 contact calls per recording session were stored as RTS-files on disk resulting in a total of 4094 sound files. We used only calls of high quality, that is, without overlapping with the calls of the other individual and with a low level of background noise during situations when the two birds were calling alternately.

For further analysis of the calls we used routines within the Signal 3.0 software (Engineering Design) programmed with the Microsoft DOS-editor. All routines are available from the authors upon request. For each interacting partner of each individual (Table 1) we chose 15 calls using a randomization routine resulting in a total of 810 analysed calls. Because calls with periods of silence (gaps) over 5 ms were treated as two different calls by our routines, we used only calls with gaps less than 5 ms. We restarted randomization until 15 calls were chosen. For comparison of call parameters we set each call to a maximum amplitude of 10 volt units and the time axis to the same scale as for the longest contact call by padding with trailing zeroes; background noise under 1000 Hz was eliminated with high-pass filtering. With our routines, we measured call duration (time between onset and offset of the call), minimum and maximum frequency (the lowest and the highest frequency of the entire call) and bandwidth (maximum frequency minus minimum frequency). The values were stored to disk. With a special routine, we measured the maximum peak frequency (the frequency with the maximum amplitude in the power spectrum). To evaluate the performance of the routines, we compared the values obtained with values measured on screen during each step of the programming. We also measured the start and end frequency and the number of frequency modulations on screen. A frequency modulation was defined as an up- or down-sweep in the frequency–time contour.

All power spectra were generated with a sample rate of 32 000 Hz and a Fast Fourier Transform window size of 8192 points (frequency resolution: 3.9 Hz; time resolution: 256 ms).

Playback Experiment

For each dyad of a calling individual and interaction partner we chose five calls out of our sample used for the acoustic analysis, with a randomization routine. We set all calls to equal length by cutting out each call with 20 ms of background noise before the beginning and 20 ms after

the end of the call. We then inserted 50 ms of 0 dB before and after these sections. On both 20-ms sections with background noise we set a ramp function, so that the amplitude increased from 0 to the amplitude of the beginning of the call and decreased from the end of the call back to 0. We thus avoided an abrupt start and end of the call.

For each bird tested we played back calls from the computer to the playback tape with the same parameter settings as for digitizing. The playback sequence for each bird started with 15 s of sound of the whole parrotlet group, followed by a pause of 10 s. For each bird, we used calls from three different calling individual-interacting partner dyads arranged in the same way (Table 2). The sequence comprised five calls of the first dyad followed by a pause of 10 s, then five calls of the same calling individual but with another interacting partner, followed by a pause of 10 s, then five calls of the same calling individual with a third interacting partner. After a pause of 20 s, the calling individual-interacting partner dyad was changed. After the calls of the third calling individual-interacting partner dyad, we inserted a pause of 60 s and then recorded the same calls as above but in the reverse order.

Playback took place in the same cage where the birds were recorded. The central blind was inserted and on its other side an amplifier (Grundig V 301) and a loudspeaker (Canton LE 250) were placed. The same tape recorder used for recordings was used for the playback experiments.

Each playback sequence was played twice to each bird, and there were at least 1 or 2 days between test sessions. To assess the behavioural response we counted the calls of

the bird during the 15 s for which each five calls lasted and the following 10 s of each pause.

Statistical Analysis

We performed a discriminant function analysis on the 810 calls to assign the correct classification of calls to the caller and the interacting partner on the basis of their acoustic measures. Statistical analyses were done with SPSS (for Windows v. 10.0, SPSS Inc., Chicago, U.S.A.). As grouping variables we used (1) the identity of the calling individual (e.g. Eddi calling with Renee, Eddi calling with Ustinov and Eddi calling with Uvo were assigned to group 1), (2) the identity of the interacting individual (e.g. Eddi calling with Renee, Ustinov calling with Renee and Uvo calling with Renee were assigned to group 1), (3) the social category of the interacting individual (e.g. Eddi calling with Renee, Renee calling with Eddi were assigned to group 1 as were Timothy calling with Inka and all other calls when the interacting individual was a pair mate), (4) the identity of the calling individual combined with the identity of the interacting individual (e.g. Eddi calling with Renee was assigned to group 1, Eddi calling with Ustinov to group 2, Eddi calling with Uvo to group 3 and so on) and (5) same social category of the calling and interacting individuals (e.g. Ustinov calling with Uvo, and Uvo calling with Ustinov were assigned to group 1 as well as Vico calling with Vanni and all other calls where the calling and the interacting partner were siblings). The acoustic variables were used as the predictor variables which were entered simultaneously with each grouping variable.

The a priori probability, i.e. the probability that a call is classified to the correct group by chance, was used to indicate the significance of the classification. The discriminant functions are valuable only when the classification results are higher than the a priori probabilities (Backhaus et al. 2000). A priori probabilities were calculated from group size.

To test for the call parameters with the highest variability between the grouping variables, we performed an equality test of group means and calculated Wilk's λ (Backhaus et al. 2000). A low value for Wilk's λ indicates a high difference in group means.

We tested samples for normality with a Kolmogorov-Smirnov goodness-of-fit test (Lozán & Kausch 1998). To test for differences in the number of response calls given to the calls elicited with the tested bird and calls elicited with another family member, we used a paired *t* test (Lozán & Kausch 1998).

RESULTS

Visual inspection of the sonograms showed that spectacled parrotlets used different contact calls for specific social companions (Fig. 1). Discriminant function analysis could assign the contact calls to the correct caller, but was not successful in classifying the calls of the calling individuals according to the identity of the interacting individuals (Table 3). The analysis did slightly better when the calls

Table 2. Example of the arrangement of a playback sequence (to bird A)

No. of calls	Calling individual	Interacting partner	Pause (s)
5	B	A	10
5	B	C	10
5	B	D	20
5	C	A	10
5	C	B	10
5	C	D	20
5	D	A	10
5	D	B	10
5	D	C	60
5	D	A	10
5	D	B	10
5	D	C	20
5	C	A	10
5	C	B	10
5	C	D	20
5	B	A	10
5	B	C	10
5	B	D	60

The playback sequence for bird A (e.g. Eddie) contained calls from his pair mate B (e.g. Renee) and family members C and D (e.g. offspring Uvo and Ustinov) in various dyads of a calling bird and an interacting partner.

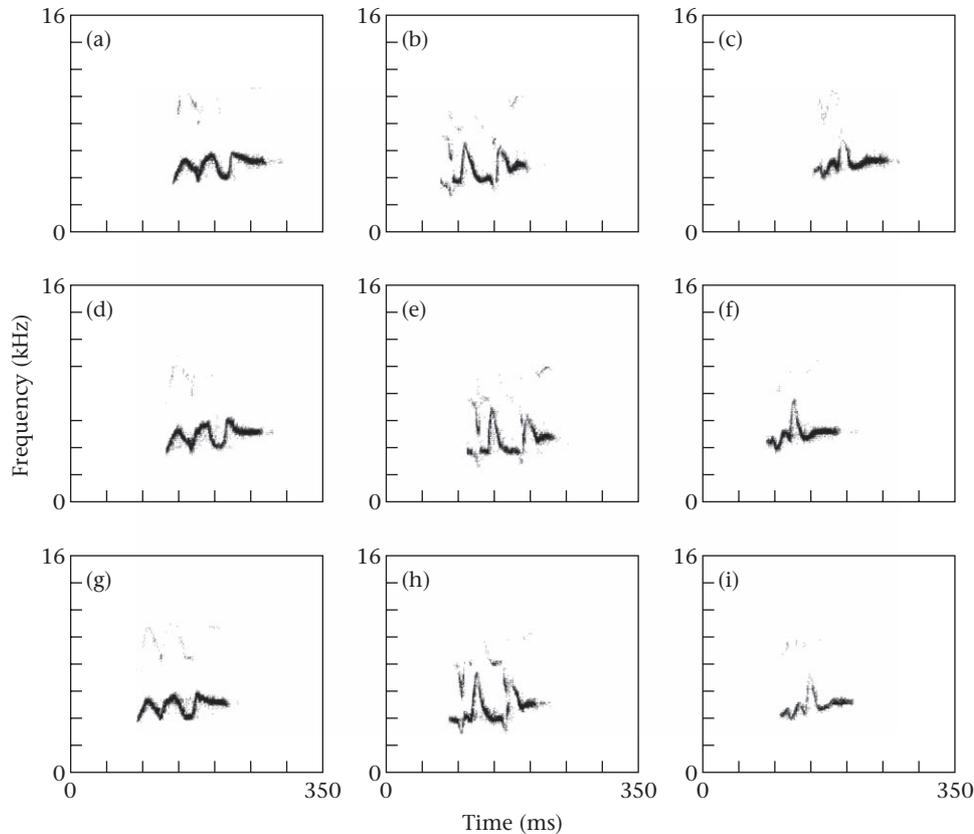


Figure 1. Spectrograms of contact calls from the male Eddi interacting with different partners. (a, d, g) Eddi interacting with his pair mate Renee, (b, e, h) Eddi interacting with his offspring Ustinov and (c, f, i) Eddi interacting with his offspring Uvo. (Fast Fourier Transformation (FFT) window size: 256 pts; frequency resolution: 125 Hz; time resolution: 8.0 ms; number of FFTs: 500 steps).

were classified according to the social category of the interacting individual (Table 3), thus indicating that individuals of the same social category shared some parameters in their contact calls. This was also indicated by the high percentage of correctly classified calls when the calling individual and the interacting individual shared the same social category. Discriminant function analysis did best when the calls were assigned to the combination

Table 3. A priori probabilities and percentages of correctly classified calls for different grouping variables of the discriminant function analysis of contact calls

Grouping variable	A priori probability	% Correctly classified
Identity of calling individual	0.037–0.074	54.4
Identity of interacting individual	0.019–0.074	20.2
Social category of interacting individual	0.148–0.315	44.2
Identity of calling individual combined with identity of interacting individual	0.019	64.7
Same social category of calling and interacting individual	0.429–0.571	86.7

of the identity of the calling individual and the identity of the interacting individual. Here the difference between the a priori probability and the percentage of correctly classified calls was largest (Table 3). Thus, the birds used different contact calls for different interacting individuals. For example, Eddi's call to his pair mate Renee differed from those he used when interacting with his sons Ustinov and Uvo (Fig. 1). This is evidence that spectacled parrotlets use different contact calls for specific social companions. The differences in the calls for specific individuals could be caused by differences in duration, peak frequency and minimum frequency (Table 4). The group means of the call parameters showed the highest variability between the grouping categories (Table 4).

In the playback experiment, the parrotlets answered calls significantly more often when they were uttered during interactions with themselves than with another family member (mean calls per session \pm SD: tested bird: 10.85 ± 4.38 ; family member: 10.26 ± 2.42 ; $t_{11} = 2.997$, $P < 0.05$). When the data set was divided by maturity of the tested birds, adults did better in discriminating between calls uttered in their presence and calls uttered in the presence of a family member (mean calls per session \pm SD: tested bird: 11.22 ± 6.05 ; family member: 10.6 ± 2.68 ; $t_5 = 3.544$, $P < 0.05$) than did juveniles (mean calls per session \pm SD: tested bird: 10.47 ± 2.28 ; family member: 9.92 ± 2.34 ; $t_5 = 1.184$, $P > 0.29$).

Table 4. Equality test of group means for different call parameters of different social categories

Call parameter	Calling individuals			Interacting individuals			Social category			Calling individual with interacting individual			Same social category of calling and interacting individual		
	Wilk's λ	F	P	Wilk's λ	F	P	Wilk's λ	F	P	Wilk's λ	F	P	Wilk's λ	F	P
Start frequency	0.697	21.586	<0.001	0.861	5.759	<0.001	0.906	27.893	<0.001	0.551	11.597	<0.001	0.828	21.448	<0.001
End frequency	0.750	16.530	<0.001	0.775	10.401	<0.001	0.984	4.331	0.005	0.619	8.753	<0.001	0.957	4.643	0.034
Minimum frequency	0.649	0.762	<0.001	0.777	10.284	<0.001	0.914	25.229	<0.001	0.510	13.685	<0.001	0.535	89.681	<0.001
Maximum frequency	0.676	23.771	<0.001	0.819	7.892	<0.001	0.980	5.577	<0.001	0.525	12.857	<0.001	1.000	0.012	0.914
Peak frequency	0.737	17.732	<0.001	0.764	11.074	<0.001	0.968	8.906	<0.001	0.623	8.630	<0.001	0.927	8.148	0.005
Modulations	0.809	11.723	<0.001	0.900	3.997	<0.001	0.991	2.552	0.054	0.689	6.430	<0.001	0.985	1.574	0.213
Bandwidth	0.776	14.308	<0.001	0.828	7.413	<0.001	0.941	16.798	<0.001	0.585	10.103	<0.001	0.961	4.207	0.043
Duration	0.559	39.087	<0.001	0.894	4.244	<0.001	0.850	47.348	<0.001	0.433	18.641	<0.001	0.988	1.237	0.269

A low value for Wilk's λ and a high F value indicate that here the differences in the measured parameter were largest between the groups tested.

DISCUSSION

Our results show that spectacled parrotlets use different contact calls for different social companions and that they respond differently to calls uttered in interactions with themselves or with other family members. This suggests that they use a referential signalling system in which they label their conspecifics.

Macedonia & Evans (1993) pointed out that functional reference of a signal requires at least production and perceptual specificity combined with acoustic distinctiveness of the respective call. With regard to production, referential signals should be structurally discrete and should have a high degree of stimulus specificity (Evans 1997; Bradbury & Vehrencamp 1998; Hauser 1998). Thus, there should be a tight connection between the acoustic structure of the signal and the context in which it is produced. The signals should be preferentially produced during interactions with a particular type of eliciting stimulus (Evans 1997). The perceptual criterion is that responses of receivers should be elicited by the signals in the absence of contextual information (Evans 1997; Bradbury & Vehrencamp 1998; Hauser 1998).

Given these criteria, the contact call of the spectacled parrotlet could be considered to be referential. Our study shows that the acoustic structure depends on the stimuli that elicit this call, in our case the individual identity of conspecifics. The high similarity of calls used for one individual suggests that the contact call is individual specific. Thus, spectacled parrotlets use specific contact calls for different family members.

On the perceptual side, there is further evidence that the contact call of spectacled parrotlets is referential. At least in adult, experienced parrotlets, the calls elicited the appropriate behavioural response. The birds being tested responded more often to contact calls that were elicited during interactions with themselves even in the absence of the interacting partner. The difference in the reactions of adult and juvenile parrotlets to calls that were directed towards themselves or towards another family member could be the result of young birds being more likely to answer every call of a conspecific. Furthermore, it seems that young spectacled parrotlets have to learn their contact calls from their parents (C. Crassel & R. Wanker, unpublished data). Thus, they might not be able to detect slight differences in the calls.

Schusterman et al. (2001) suggested that the main function of the vocalizations of pinnipeds is to capture the attention of other individuals in the group. The loud contact call of other New World parrots elicits the same response from conspecifics and its supposed function is to establish a vocal connection between specific birds (Bradbury 2003). We think that this is also true for spectacled parrotlets except that parrotlets also signal their own identity and social category (Wanker et al. 1998; Wanker & Fischer 2001). Furthermore, our results support the hypothesis that spectacled parrotlets name the conspecific with whom they want to get in vocal contact, and thus label their social companions.

Labelling or 'naming' has been suggested to occur when two individuals match their vocalizations (Janik 2002;

Tyack 2003). Janik (2002) has shown that in wild bottlenose dolphins, individuals match their signature whistles to other dolphins. The imitation of signature signals in whistle-matching dolphins and duetting birds is thought to serve as a signal to initiate contact with a specific individual (Tyack 2003).

Call matching or call convergence is known from another parrot species, the budgerigar, *Melopsittacus undulatus* (Farabaugh & Dooling 1996; Bartlett & Slater 1999), in which males imitate the calls of their mates (Hile & Striedter 2000; Hile et al. 2000; Striedter et al. 2003). This could also be a mechanism for the effect of labelling found in our study, indicated by the high percentage of correct classifications when a calling individual and its interaction partner were loaded in the discriminant function analysis. The fact that the birds responded more to calls elicited by other birds during interactions with themselves suggests that the birds have a special call for their social companion.

Studies on individual-specific social interactions suggest that each actor has an internal model of different individuals, along with the ability to memorize the interactions with these individuals (Seyfarth & Cheney 2003). If an animal refers to something external to itself with a signal, it should have an abstract or mental representation of the referent apart from the structural properties of the signal (Tyack 2003). We conclude that spectacled parrotlets have a mental representation of at least their family members because they use different labels for them.

What are the benefits of labelling conspecifics in spectacled parrotlets? These birds live in groups and spend much of the day and the whole night with conspecifics (Wanker et al. 1996; Wanker 1997, 2002). In these groups, contact calls are uttered by many birds and in this babbling it might be useful to communicate only with the intended receiver of the call. Further studies are needed to understand the function of labelling of conspecifics in spectacled parrotlets.

Acknowledgments

We thank Eckhard Kirschning, Ingo Schlupp and Frank Thomsen for helpful comments on the manuscript and Cord Crasselt, Karin Teege, Angelika Taebel-Hellwig and Inga Diekmann for fruitful discussions and assistance in animal care.

References

- Backhaus, K., Erichson, B., Plinke, W. & Weiber, R. 2000. *Multivariate Analysemethoden*. Berlin: Springer-Verlag.
- Bartlett, P. & Slater, P. J. B. 1999. The effect of new recruits on the flock specific call of budgerigars (*Melopsittacus undulatus*). *Ethology Ecology and Evolution*, **11**, 139–147.
- Beecher, M. D., Stoddard, P. K., Campbell, S. E. & Horning, C. L. 1996. Repertoire matching between neighbouring song sparrows. *Animal Behaviour*, **51**, 917–923.
- Beecher, M. D., Campbell, S. E., Burt, J. M., Hill, C. E. & Nordby, J. C. 2000. Song type matching between neighbouring song sparrows. *Animal Behaviour*, **59**, 21–27.
- Benz, J. J. 1993. Food-elicited vocalizations in golden lion tamarins: design features for representational communication. *Animal Behaviour*, **45**, 443–455.
- Benz, J. J., Leger, D. W. & French, J. A. 1992. Relation between food preference and food-elicited vocalizations in golden lion tamarins (*Leontopithecus rosalia*). *Journal of Comparative Psychology*, **106**, 142–149.
- Bradbury, J. W. 2003. Vocal communication in wild parrots. In: *Animal Social Complexity, Intelligence, Culture, and Individualized Societies* (Ed. by F. S. B. M. De Waal & P. L. Tyack), pp. 293–316. Cambridge, Massachusetts: Harvard University Press.
- Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer.
- Brown, C. R., Bomberger Brown, M. & Shaffer, M. L. 1991. Food-sharing signals among socially foraging cliff swallows. *Animal Behaviour*, **42**, 551–564.
- Burt, J. M., Bard, S. C., Campbell, S. E. & Beecher, M. D. 2002. Alternative forms of song matching in song sparrows. *Animal Behaviour*, **63**, 1143–1151.
- Cheney, D. L. & Seyfarth, R. M. 1981. Selective forces affecting the predator alarm calls of vervet monkeys. *Behaviour*, **76**, 25–61.
- Cheney, D. L. & Seyfarth, R. M. 1985. Vervet monkey alarm calls: manipulation through shared information? *Behaviour*, **94**, 150–166.
- Clark, A. P. & Wrangham, R. W. 1993. Acoustic analysis of wild chimpanzee pant hoots: do Kibale Forest chimpanzees have an acoustically distinct food arrival pant hoot? *American Journal of Primatology*, **31**, 99–109.
- Dittus, W. P. 1984. Toque macaque food calls: semantic communication concerning food distribution in the environment. *Animal Behaviour*, **32**, 470–477.
- Elowson, A. M., Tannenbaum, P. L. & Snowdon, C. T. 1991. Food-associated calls correlate with food preference in cotton-top tamarins. *Animal Behaviour*, **42**, 931–937.
- Evans, C. S. 1997. Referential signals. In: *Communication, Perspectives in Ethology*. Vol. 12 (Ed. by D. H. Owings, M. D. Beecher & N. S. Thompson), pp. 99–143. New York: Plenum.
- Evans, C. S. & Marler, P. 1991. On the use of video images as social stimuli in birds: audience effects on alarm calling. *Animal Behaviour*, **41**, 17–26.
- Evans, C. S. & Marler, P. 1992. Female appearance as a factor in the responsiveness of male chickens during anti-predator behaviour and courtship. *Animal Behaviour*, **43**, 137–143.
- Evans, C. S. & Marler, P. 1994. Food-calling and audience effects in male chickens (*Gallus gallus*): their relationships to food availability, courtship and social facilitation. *Animal Behaviour*, **47**, 1159–1170.
- Farabaugh, S. M. & Dooling, R. J. 1996. Acoustic communication in parrots: laboratory and field studies of budgerigars, *Melopsittacus undulatus*. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsmaa & E. H. Miller), pp. 97–117. Ithaca, New York: Cornell University Press.
- Fichtel, C. & Kappeler, P. M. 2002. Anti-predator behavior of group-living Malagasy primates: mixed evidence for a referential alarm call system. *Behavioral Ecology and Sociobiology*, **51**, 262–275.
- von Frisch, K. 1967. Honeybees: do they use direction and distance information provided by their dancers? *Science*, **158**, 1073–1076.
- Gheusi, G., Goodall, G. & Dantzer, R. 1997. Individually distinctive odours represent individual conspecifics in rats. *Animal Behaviour*, **53**, 935–944.
- Gyger, M. & Marler, P. 1988. Food calling in the domestic fowl, *Gallus gallus*: the role of external referents and deception. *Animal Behaviour*, **36**, 358–365.

- Gyger, M., Karakashian, S. J. & Marler, P. M. 1986. Avian alarm calling: is there an audience effect? *Animal Behaviour*, **34**, 1570–1572.
- Gyger, M., Marler, P. & Pickert, R. 1987. Semantics of an avian alarm call system: the male domestic fowl, *Gallus domesticus*. *Behaviour*, **102**, 15–40.
- Hauser, M. D. 1998. *The Evolution of Communication*. 3rd edn. Cambridge, Massachusetts: MIT Press.
- Hauser, M. D. & Marler, P. 1993a. Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors influencing call production. *Behavioral Ecology*, **4**, 104–205.
- Hauser, M. D. & Marler, P. 1993b. Food-associated calls in rhesus macaques (*Macaca mulatta*): II. Costs and benefits of call production and suppression. *Behavioral Ecology*, **4**, 206–212.
- Heinrich, B. & Marzluff, J. M. 1991. Do common ravens yell because they want to attract others? *Behavioral Ecology and Sociobiology*, **28**, 13–21.
- Hile, A. G. & Striedter, G. F. 2000. Call convergence within groups of female budgerigars (*Melospittacus undulatus*). *Ethology*, **106**, 1105–1114.
- Hile, A. G., Plummer, T. K. & Striedter, G. F. 2000. Male vocal imitation produces call convergence during pair bonding in budgerigars, *Melospittacus undulatus*. *Animal Behaviour*, **59**, 1209–1218.
- Janik, V. M. 2000. Food-related bray calls in wild bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society of London, Series B*, **267**, 923–927.
- Janik, V. M. 2002. Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science*, **289**, 1355–1357.
- Judd, T. M. & Sherman, P. W. 1996. Naked mole-rats direct colony mates to food sources. *Animal Behaviour*, **51**, 957–969.
- Lozán, J. L. & Kausch, H. 1998. *Angewandte Statistik für Naturwissenschaftler*. Berlin: Parey.
- Macedonia, J. M. 1991. What is communicated in the antipredator calls of lemurs: evidence from antipredator call playbacks to ringtailed and ruffed lemurs. *Ethology*, **86**, 177–190.
- Macedonia, J. M. & Evans, C. S. 1993. Variation among mammalian alarm call systems and the problem of meaning in animal signals. *Ethology*, **93**, 177–197.
- Manser, M. B. 2001. The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society of London, Series B*, **268**, 2315–2324.
- Manser, M. B., Bell, M. B. & Fletcher, L. B. 2001. The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society of London, Series B*, **268**, 2485–2491.
- Manser, M. B., Seyfarth, R. M. & Cheney, D. L. 2002. Suricate alarm calls signal predator class and urgency. *Trends in Cognitive Sciences*, **6**, 55–57.
- Marler, P., Dufty, A. & Pickert, R. 1986. Vocal communication in the domestic chicken: II. Is a sender sensitive to the presence and nature of a receiver? *Animal Behaviour*, **34**, 194–198.
- Masataka, N. 1983. Categorical responses to natural and synthesized alarm calls in Goeldi's monkeys (*Callimico goeldi*). *Primates*, **24**, 40–51.
- 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**, 811–819.
- Pereira, M. E. & Macedonia, J. M. 1991. Response urgency does not determine antipredator call selection by ringtailed lemurs. *Animal Behaviour*, **41**, 543–544.
- Schusterman, R. J., Southall, B. L., Kastak, D. & Reichmuth Kastak, C. 2001. Pinniped vocal communication: form and function. In: *Proceedings of the 17th International Congress on Acoustics*. Vol. 4 (Ed. by E. Alippi), Rome.
- Seyfarth, R. M. & Cheney, D. L. 2003. The structure of social knowledge in monkeys. In: *Animal Social Complexity, Intelligence, Culture, and Individualized Societies* (Ed. by F. S. B. M. De Waal & P. L. Tyack), pp. 207–229. Cambridge, Massachusetts: Harvard University Press.
- Sherman, P. W., Reeve, H. K. & Pfennig, D. W. 1997. Recognition systems. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 69–96. Oxford: Blackwell Science.
- Striedter, G. F., Freibott, L., Hile, A. G. & Burley, N. T. 2003. For whom the male calls: an effect of audience on contact call rate and repertoire in budgerigars, *Melospittacus undulatus*. *Animal Behaviour*, **65**, 875–882.
- Tyack, P. L. 2003. Dolphins communicate about individual-specific social relationships. In: *Animal Social Complexity, Intelligence, Culture, and Individualized Societies* (Ed. by F. S. B. M. De Waal & P. L. Tyack), pp. 342–361. Cambridge, Massachusetts: Harvard University Press.
- Wanker, R. 1997. Der Einfluß unterschiedlicher Sozialisationsbedingungen auf die Paarbindungsfähigkeit bei Augenring-Sperlingspapageien, *Forpus conspicillatus* (LAFRESNAYE, 1848): Untersuchungen zum sozialen System unter seminaturalen Bedingungen und im Freiland. *Papageienkunde-Parrot Biology*, **1**, 3–100.
- Wanker, R. 1999. Socialization in spectacled parrotlet (*Forpus conspicillatus*): how juveniles compensate for the lack of siblings. *Acta Ethologica*, **2**, 23–28.
- Wanker, R. 2002. Social system and acoustic communication of spectacled parrotlets (*Forpus conspicillatus*): research in captivity and in the wild. In: *Bird Research and Breeding* (Ed. by C. Mettke-Hofmann & U. Gansloßer), pp. 83–109. Fürth: Filander Verlag.
- Wanker, R. & Fischer, J. 2001. Intra- and interindividual variation in the contact calls of spectacled parrotlets (*Forpus conspicillatus*). *Behaviour*, **138**, 709–726.
- Wanker, R., Cruz Bernate, L. & Franck, D. 1996. Socialization of spectacled parrotlets *Forpus conspicillatus*: the role of parents, crèches and sibling groups in nature. *Journal für Ornithologie*, **137**, 447–461.
- Wanker, R., Apcin, J., Jennerjahn, B. & Waibel, B. 1998. Discrimination of different social companions in spectacled parrotlets (*Forpus conspicillatus*): evidence for individual vocal recognition. *Behavioral Ecology and Sociobiology*, **43**, 197–202.
- Zuberbühler, K. 2001. Predator-specific alarm calls in Campbell's monkeys, *Cercopithecus campbelli*. *Behavioral Ecology and Sociobiology*, **50**, 414–422.
- Zuberbühler, K. 2002. A syntactic rule in forest monkey communication. *Animal Behaviour*, **63**, 293–299.