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# Program

**31 July, 2008**

<b>12:00 – 17:00</b>	<b>Registration</b>
<b>17:00 – 17:20</b>	<b>Conference Opening</b>
<b>17:20 – 18:00</b>	<i>50 years on!</i> A. Manning
<b>18:00 – 19:30</b>	<b>Wine Reception</b>

**1 August, 2008 - morning**

- 9:00 – 10:00**      *Bird song and sexual selection*  
C. K. Catchpole
- 10:00 – 10:30**      **Coffee break**
- 10:30 – 10:45**      *Female voices as cues to fertility?*  
J. Fischer
- 10:45 – 11:00**      *What's love got to do with it? - Conflict and cooperation in duets of the gray-breasted wood-wren (*Henicorhina leucophrys*)*  
C. Dingle & H. Slabbekoorn
- 11:00 – 11:15**      *Limits on the independent vocal behavior of the right and left syrinx during two-voice phenomena*  
S. Zollinger & R. A. Suthers
- 11:15 – 11:30**      *Two sides of the call: vocal tract modelling and vocalizations in lemurs*  
M. Gamba
- 11:30 – 11:45**      *Vocal processing in the left and right hemispheres*  
L.J. Rogers & M. Siniscalchi
- 11:45 – 12:00**      *Inter- and uni-modal discrimination by chimpanzees based on auditory and visual information*  
L. Martinez & T. Matsuzawa
- 12:00 – 12:15**      *Can songbirds detect recursive syntax patterns?*  
C. ten Cate, J. de Visser, J. Zuidema & C. van Heijningen
- 12:15 – 12:30**      *Wild chimpanzees distinguish between different scream types: evidence from a playback study*  
S.W. Townsend, K.E. Slocombe & K. Zuberbuhler
- 12:30 – 14:00**      **Lunch Break**

**1 August, 2008 - afternoon**

- 14:00 – 15:00**      *Performance limits on bird song: timing and consequences*  
J. Podos
- 15:00 – 15:15**      *Geographic variation of signature whistle types from Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in coastal Zanzibar*  
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- 15:15 – 15:30**      *Vocal communication in a hybrid zone between two African dove species*  
P.M. den Hartog & C. ten Cate
- 15:30 – 15:45**      *Sperm whale codas at the individual level: repertoires, overlapping interactions and spatial scales*  
L. Rendell, T. Schulz & H. Whitehead
- 15:45 – 16:00**      *Sex role convergence, territoriality and vocal behaviour in Australian magpies*  
G. Kaplan
- 16:00 – 17:00**      **Poster Session with Coffee**
- 17:00 – 18:00**      *Vocal duetting in neotropical wrens: acoustic communication in the animal kingdom's most coordinated singers*  
D. Mennill

**2 August 2008 - morning**

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P. Tyack
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H. Slabbekoorn
- 10:45 – 11:00**      *Causes and consequences of urban song divergence in the European blackbird*  
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- 11:00 – 11:15**      *Seismic noise induces increase in blue whale call production*  
L. Di Iorio & C. W. Clark
- 11:15 – 11:30**      *Mechanisms of song adaptation to urban noise in the house finch: syllable pitch plasticity or differential syllable use?*  
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T. Götz & V.M. Janik
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- 15:30 – 15:45**      *Social mechanisms of vocal learning in songbirds and human infants*  
M. Goldstein
- 15:45 – 16:00**      *Neural signature of tutor song in pre-singing zebra finches: an emerging birdsong memory*  
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S. de Kort, E. Bohman, S. Valderrama, C. Botero & S. Vehrencamp
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- 19:30 –**              **Banquet & Ceilidh**

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# **ABSTRACTS**

**(in alphabetical order)**

## **Neural signature of tutor song in pre-singing zebra finches: an emerging birdsong memory**

P. Adret & D. Margoliash

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The auditory template theory of songbird vocal learning invokes a two-step process in which song memorization precedes rehearsal, and subsequent adjustment of singing occurs by referencing vocal feedback to the song memory. This particular memory (template) may reside within the forebrain auditory and/or song systems, but its localization and mode of action remain unresolved. Here we report on recordings in forebrain nuclei from urethane-anesthetized zebra finches (*Taeniopygia guttata*) raised by both parents with the father serving as a tutor, and tested at 21-24 days of age, prior to the onset of singing. In a first study, using a large set of both natural and artificial stimuli, many neurons were effectively stimulated by the amplitude modulation found in juvenile subsong, including subsong of Bengalese finch and white-backed munia (*Lonchura striata*), closely related species. Remarkably, for approximately half of the subjects, few neurons exhibited a strong preference for tutor songs over all other stimuli. In a second study, using a smaller stimulus set with a more rigorous sampling strategy, a small fraction of neurons were tutor song selective whereas no site was selective for other adult songs, either familiar or unfamiliar. Such cells also strongly preferred tutor song played forward over the same song played in reverse. Reconstruction from fiduciary lesions confirmed that the recording sites selective for tutor song originated from HVC, one of its efferent targets, the paraHVC and deeper in the caudal nidopallium, to the exclusion of the auditory shelf region apposed to HVC. Our data support an instructional model of birdsong learning and point to an emerging neural network well suited to encode together with other parts of the brain the memory (“acquired template”) that guides a young zebra finch in the process of vocal imitation.

## **Neural patterns of pre-motor activity associated with production of subsong and plastic song in juvenile zebra finches**

P. Adret & D. Margoliash

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Understanding the neural mechanisms that underlie imitative learning in oscine songbirds requires observation from both auditory areas and song system nuclei in freely moving juveniles exposed to a song model. To gain insight into such mechanisms we recorded from the HVC of the nidopallium, a sensorimotor nucleus critical for song production and perception. Juveniles were implanted with fixed recording electrodes on day 32 post-hatch and then housed with their father with whom they could interact both visually and vocally through a clear partition. Early in the subsong stage (days 43-45), HVC neurons often fired a sequence of long bursts of spikes that was predictive of imminent singing. Unlike the short phasic bursts of premotor activity associated with stereotyped calls, tonic bursting started up to ~900 ms prior to onset of vocalization and terminated ~200 ms after song ended. Remarkably, on few occasions, sustained but modulated bursting of up to ~1.6 s preceded production of brief (< 50 ms) song-like vocalizations. These observations, together with a recent report of subvocal events recorded during production of early plastic song (Cooper et al., Soc. for Neurosci. abstract, 2006) suggest that juveniles may engage in “silent singing” whereby synchronized, but insufficient excitation in HVC fails to drive downstream motor programs. In one juvenile, HVC multiunit activity was monitored continuously over a 3-week period during which the young bird learned to copy his father’s song. In parallel with song development, we observed a gradual reduction of tonic bursting prior to song onset such that, following emergence of introductory notes, HVC premotor activity was more tightly locked to sound onset. These changes presumably reflect local inhibitory mechanisms and stronger coupling between forebrain and brainstem respiratory and vocal circuitry that help shape motor output during the sensorimotor phase of song learning.

## **Different acoustics method analyses yield to different results**

S. Alain <sup>1</sup>, N. Giret <sup>1</sup>, P. Roy <sup>2</sup>, F. Pachet <sup>2</sup>, M. Kreutzer <sup>1</sup> & D. Bovet <sup>1</sup>

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The installation of efficient method analysis is necessary to establish a reliable vocal directory. So, the classification of vocalizations is slow and is subjected to the experimenter's subjectivity. Therefore, automated acoustics method analysis supplies a powerful help to categorize. In the present study, we compared four acoustic methods: a human analysis, an automated graphic analysis (Software ANA), a mi-human mi-automated analysis (Music Browser software) and an analysis in supervised learning (EDS software). Vocal recordings of five African grey parrots (*Psittacus erithacus*) rose in captivity have been used. We observed that for human analysis, the categorization of vocalizations varied by three persons according to their experience. Among the different automated acoustic methods of analysis that we tested, the analysis in supervised learning seems to be the most successful. Moreover, the results of the mi-human mi-automated analysis allows a first sorting of analysis. To conclude, these new methods are promising to conduct powerful and faster categorization of acoustics signals.

## **Copulation solicitation calls of female canaries (*Serinus canaria*) and their effect on males**

M. Amy

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In songbirds, female preferences are often assessed by copulation solicitation displays (CSD) assay. During these displays a female crouch, arch her back and simultaneously brings her tail forward and her head back, the wings move away from the body and vibrate. For the first time we describe the typical calls emitted by female canaries (*Serinus canaria*) during these displays. To our knowledge, these calls have never been studied. In a first experiment, female canaries were allowed to hear male songs containing slightly attractive phrases. We noted Copulation Solicitation Displays (CSD) and Copulation Solicitation Calls (CSC). We also recorded CSC and analyzed their parameters. Copulation Solicitation Calls are composed of high-pitched notes with a small bandwidth, repeated at a relatively high rate. We observed a positive significant correlation between CSD and CSC. We conclude that CSC seems to be a sexual signal directed towards males. We are presently testing whether these calls influence vocalisations of male canaries.

## **The role of bioacoustics in the reproduction of the African cheetah (*Acinonyx jubatus*)**

M. Anderson

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Systematic behavioral observations have revealed that the African cheetah (*Acinonyx jubatus*) possesses a wide vocal repertoire. Both males and females use a variety of calls during social interactions which can be readily recorded and analyzed in respect to behavioral context. In direct contrast to frequently heard high pitched fear chirps and associated growls which relate to increased levels of aggression between conspecifics, the male stutter-bark call is uttered more sporadically and has an unknown function. Pilot data highlighted that the stutter-bark may be important in cheetah reproduction. Previously published information appertaining to cheetah breeding has suggested that this species may be an induced ovulator and that females do not cycle regularly as in most other large carnivores. Further, females from other mammalian species with induced ovulation appear to rely upon certain cues to initiate increases in reproductive hormone levels and thereby ovulation. This study examined levels of both oestrodiol and progesterone in relation to the timing and frequency of the male stutter-bark in order to ascertain whether the call represents one such reproductive stimulus. Observation of behavioral interactions between adult male and female cheetahs held at San Diego Zoo's Wild Animal Park revealed that both oestradiol and progesterone levels increased significantly following extended bouts of stutter-barking. This was observed not only in females who were paired with stutter-barking males but also seen in females held within close auditory proximity of the calling male. Such findings are valuable in relation to increasing reproductive success in this endangered species especially in relation to the possibility of playbacks of stutter-bark calls as part of a captive breeding protocol. The findings also suggest that induced ovulation in cheetahs may depend upon receipt of male stutter-barks.

## **Vocal repertoire of Asian elephants (*Elephas maximus*) in captivity: a current project**

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Elephants are well known for their complex acoustic communication system. So far all major reports about elephant communication focused on African elephants (*Loxodonta africana*) and next to nothing is known about the vocal repertoire and the communicative behaviour of Asian elephants (*Elephas maximus*). The only published study addressing the acoustic repertoire of Asian elephants was published in 1973 by McKay who found and described 10 call types and divided them into three major categories. Artelt (2006) characterized and defined further call types in her diploma thesis. Therefore the aims of the presented study are to extend the knowledge on the acoustic repertoire of Asian elephants and to set the categorized call types in a behavioural context. In the course of the project, we are recording and analysing the vocalizations of four Asian elephant groups in captivity (Germany and Netherlands). We started in March 2008 at the Zoo in Cologne. Recordings are made at 48 kHz sampling rate on a HDD Sound Devices 722 recorder with an AKG condenser microphone. For the analysis of the recorded signals we are using S\_TOOLS-STX from the "Acoustic Research Institute of the Austrian Academy of Science, Vienna". In our poster we will present preliminary results on the vocal repertoire, the varieties between the calls and the behavioural context in which calls occur. Moreover, information on call repertoire and variations between individuals or elephant groups will be useful for the development of planned acoustic monitoring or early warning systems in Asia to reduce the human-elephant conflict.

## **Dolphin whistles, are they communicating information?**

C. Bazua-Duran

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Most dolphin species emit two types of phonations: whistles and clicks. Clicks are used for echolocation and during agonistic interactions. Whistles are believed to be used for communication between individuals within a herd. However, it is still unknown how dolphins may be transmitting information through their whistles. To investigate the variability in dolphin whistles, bottlenose dolphins (*Tursiops truncatus*) from the Gulf of Mexico and spinner dolphins (*Stenella longirostris*) from the Pacific Ocean were recorded from motorboats using a single hydrophone. Whistle emission rate and several acoustic measurements taken from the whistle spectrogram were analyzed. Both dolphin species studied produced whistles mainly when dolphins were constantly interacting between them. Little whistle production was recorded when dolphins were traveling and while in rest. Results for the acoustic whistle characteristics show that the duration and frequency range of the fundamental frequency of whistles were conserved, and that there are geographic variations within a species, and variations between both species studied. Therefore, if dolphins are transmitting information between them through their whistles, this information should be contained in the fundamental frequency of each whistle and should be for short ranges. Because there is a lot of acoustic variability in their whistles, dolphins may be able to transmit different levels of information with their whistles. There are still many things to learn about the use that dolphins make of their whistles and the type of information they may transmit with them. Studying the acoustic characteristics of whistles from wild dolphins can help in resolving many questions without having to perform controlled experiments (usually performed in captivity or semicaptivity).

## **Mechanisms of song adaptation to urban noise in the house finch: syllable pitch plasticity or differential syllable use?**

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The influence of ambient noise in shaping bird song attributes has received much attention recently. Recent work shows that some birds sing higher-pitched songs in noisy areas to avoid acoustic interference, yet it is not clear how this is achieved. Higher pitched songs may be produced either by shifting in noisy areas the frequency of the same syllable types that are used in quiet areas (syllable pitch plasticity), or by using different syllable types in silent and in noisy circumstances (differential syllable use). Here we explored both mechanisms in the Mexico City population of house finch (*Carpodacus mexicanus*), a species known to possess a repertoire of several hundreds of syllable types. Birds produced songs with higher minimum frequencies in noisy than in quiet areas. This was mostly due to the fact that the minimum frequency of some syllable types was higher when sung in noisy areas than in quiet locations. Also, males modulated the minimum frequency of the same syllable type during momentary increases of noise. Our results can help explain the enormous success that house finches have had when colonizing cities and provide evidence of syllable pitch plasticity in a passerine bird.

## **Call repertoire of an endemic avian species, the Indian chat *Cercomela fusca***

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Almost all birds produce acoustic signals either in the form of calls or songs or both while communicating. These signals play an important role in their social life. Songs play somewhat restricted role in many species in territorial establishment and mate attraction while calls are generally used for immediate requirements throughout the year and seem to be more important than the songs. The present study deals with the study of physical characteristics and significance of different types of calls used by the Indian Chat *Cercomela fusca*. Study was carried out from January 2006 to December 2007 in the urban area of district Haridwar (29° 55' N and 78° 08' E; Himalayan foothills), Uttarakhand state, India. Acoustic signals were recorded with Marantz PMD670 sound recorder & Sennheiser ME 67 unidirectional microphone and spectrograms were prepared with AviSoft SAS LabPro software. A total of eight types of calls, namely territorial call, begging call, feeding call, alarm call, threat call, contact call, distress call and roosting & emergence calls were observed in the call repertoire of this species. Out of eight, three types of calls were used by the young while adults produce the remaining five types. The possible functions of these call-types have been deduced from the contexts under which they were produced.

## **Individual and sex differences in common raven calls**

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Individual discrimination by vocalizations has been of much interest in ornithology. Especially in complex fission-fusion social systems with a high degree of cooperation, individual recognition might be of high value. Ravens emit many different calls, within which some are highly variable and vocal learning seems to play a role. We here examined morphological structures of different calls and hypothesized that individual variation should be relatively high in long distant calls (e.g. territorial calls) compared to short distant calls that are accompanied by visual displays (i.e. calls used during social interactions). We concentrated on two types of long distance calls, territorial calls and food calls, and two types of short distant calls, calls emitted during self-assertive displays and calls preceding socio-positive interactions. We recorded vocalizations of 10 adults, captive ravens on a monthly basis over a period of 5 months. We analyzed time and frequency parameters of the calls. Individual differences were found in territorial and food calls, as well as in calls emitted during visual displays and calls used during socio-positive interactions. Sexes differed in the usage of calls and structural characteristics of shared call types. Our data thus show that call use and call characteristics are individual- and sex-specific in ravens. Individuality within call characteristics as well as the usage of individual calls supports the possibility of individual recognition across several call types. Testing the ravens' ability to perceive the individual information encoded in the different calls via playback experiments will be the next step.

## **Vocal repertoire of an infant giant panda (*Ailuropoda melanoleuca*) in the first postnatal week**

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At birth, giant panda cubs are very small, blind and almost naked. Besides smell and touch, acoustic signals may be the predominant channel of communication. The level of knowledge about the acoustic communication in the giant panda is sketchy, especially considering vocal ontogeny. This research project is the first to investigate the vocal behaviour and the mother-cub communication from birth on. The male cub Fu Long was born on 23th of August 2007 at the Vienna Zoo. Recordings were made from birth on at 48 kHz sampling rate on a HDD Sound Devices 722 recorder with an AKG condenser microphone. The equipment was placed next to the breeding box. The calls were analysed via the computer program S\_TOOLS-STx from the Acoustic Research Institute, Austrian Academy of Science, Vienna. Each identified call from the cub and the mother was segmented and put into a data base. The corresponding behaviour was extracted from continuous video recordings made within the breeding box. In our poster we will present the vocal repertoire and functions of the calls for the first postnatal week, in which we documented more than 5000 calls produced by the cub. This preliminary data indicate that vocal signals in fact are important means of communication between a mother and her cub. Future analyses will track the call repertoire of Fu Long, the functional context and the development of the calls and their structure over the next two years. We will also record other Panda cubs at different zoos to increase sample size and compare results.

## **On the function of song type repertoires: testing the 'anti-exhaustion hypothesis' in chaffinches**

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Why some bird species have evolved elaborate song repertoires has puzzled biologists for a long time. According to the anti-exhaustion hypothesis, avian song type repertoires have evolved because switching between different songs, involving different patterns of muscle contractions, causes less exhaustion in the singer and thus allows a higher singing rate to be maintained. Although it is a classic explanation referred to in many textbooks, this hypothesis has not yet been tested. We investigated the anti-exhaustion idea in the chaffinch (*Fringilla coelebs*), a species in which males may have only one song type or a repertoire of up to six types. We analyzed the song delivery rates of 101 male chaffinches at several sites in Scotland, taking into account various seasonal, ecological and social variables. We found that males with a repertoire of several song types did not sing at a higher rate than males with only one song type, even though single song type males produced more complex songs on average. These findings indicate that song type switching is not necessary for the maintenance of high song rates in this species. We conclude that preventing motor fatigue did not play an important role in the evolution of chaffinch song type repertoires. Thus other factors, such as direct sexual selection of repertoire size or the use of song type repertoires for vocal interactions, are much more likely to explain why many bird species have evolved such complex vocal repertoires.

## **Bird song and sexual selection**

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One of the main differences between the study of vocal communication in birds and mammals is that, in birds, the emphasis has been very much on the study of song. There are several reasons for this, bird song is one of the most complex and beautiful sounds in nature and its functions are much debated. In recent times renewed interest in sexual selection has also had an impact, and modern sexual selection theory has given the study of song a strong theoretical basis from which to study both function and evolution. In this lecture, I will discuss how interpreting song within the theory of sexual selection has led to the dual function hypothesis; whereby song repels members of the same sex and attract those of the opposite sex. This interpretation of song is one of the major themes of the recent book 'Bird Song, ' a collaboration by myself and Peter Slater. In one chapter of the book we review the evidence for male song complexity as a target for selection by female choice. Although the evidence is persuasive there remain two main issues which need to be clarified and I will attempt to deal with these in the lecture. First, how can song become an honest indicator of male quality? Modern sexual selection theory assumes that reliability is maintained by costs paid by the signaler, but adding a few notes to a song hardly seems costly. I will suggest one possible answer, the developmental stress hypothesis, and then outline some experiments to test it. The second problem concerns the apparent lack of a genetic basis for song, as current models assume it relies crucially upon learning to develop. How can sexual selection work if song structure and complexity has no heritable basis? I will finish by outlining some recent experiments which suggest that song has more of a genetic basis than previously assumed.

## **Individual vocal signature in Australian sea lion, *Neophoca cinerea***

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It is well known that pinnipeds are highly vocal, and several species especially otariids have developed mother-pup vocal recognition. The Australian sea lion *Neophoca cinerea* is an Australian endemic species with a unique breeding cycle since they breed asynchronously between neighbouring colonies and non-seasonally. During the 17-month lactation period, females alternate foraging trips with periods ashore to nurse their pups. At each return, mothers and pups have to find each other amongst all the individuals in the colony. The need for a finely tuned mechanism of recognition is exacerbated by their habit of changing the location where they suckle over the course of lactation. Female sea lions are particularly aggressive to non-kin and so selection pressures for a reliable mechanism of recognition are likely to be high. We have focussed our study on vocal recognition of the mother by the pup. We have performed playback experiments on pups (older than 2-months, see B. Pitcher's presentation) with modified females' calls to demonstrate which acoustic parameters are involved in this identification process. Pups use both frequency and amplitude modulations, but also the exact frequency values of the calls. Since Australian sea lions change suckling locations over the lactation period, we have carried out propagation tests in different environments inhabited by sea lions and over a range of distances to assess the efficiency range of the individual vocal signature. Frequency modulations are highly reliable over distance and across the different studied environments, but this is not the case for amplitude modulations and frequency spectrum that become degraded with increasing propagation distance. Severe degradation occurs in complex environments due to obstructions. In conclusion, Australian sea lions pups can rely on different acoustic parameters to identify their mother but only one (FM) is highly reliable at long range and in obstructed environment.

## **Male domestic canaries, *Serinus canaria*, use song to discriminate kin**

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In vertebrates, different sensory modalities (olfaction, audition, vision), could be used to recognize kin. In birds, acoustic cues seem to provide valuable information on kinship. Most studies have focused on recognition of calls emitted by individuals, but few have tested the role of song experimentally. Thus, the present study proposed to analyze the role of song in kin recognition in an oscine species, the domestic canary, *Serinus canaria*. Since adult males seem to use song as their major means of communication, we tested their ability to discriminate kin via their song. A first experiment was realised to determine if song is a modality used for kin recognition by playing-back songs of males of three different kinship degrees: brother, cousin and stranger. A second experiment tested if relatedness has an influence on male-male interactions by confronting brothers, cousins and strangers and observing their behaviour. Results show that male canaries respond differently to songs according to relatedness, suggesting that male song provides information on kinship. However, we were not able to demonstrate that live males interact differently with males of different kinship degree. This study demonstrates that song seems to be a good indicator of kinship degree in oscine birds. Kin recognition may have an effect on male-male interactions but further experiments testing males in different contexts of competition are necessary to confirm this.

## **Vocal communication in bonobos, *Pan paniscus*: are food calls functionally referential signals?**

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Upon encountering and eating food, bonobos selectively produce an elaborate array of vocalisations such as high-pitched peeps and yelps, and low-pitched grunts. Feeding calls are most often given in social settings, and vocalisations commonly attract others to come to eat at the same food source. Currently, very little has been explored concerning food calling in bonobos, as research generally into bonobo vocal communication is limited. It is known that the presence of listeners in both bonobos (Van Krunkelsven et al 1996) and chimpanzees (Slocombe & Zuberbühler, 2005) has a powerful effect on calling behaviour on feeders. Both species call more in captivity for large, divisible food sources when there are listeners present than if alone. Observational studies on captive and free-ranging chimpanzees, and a captive playback experiment indicate that chimpanzee food grunts serve as functionally referential labels for the preference of the food being eaten by the signaller (Slocombe & Zuberbühler, 2005). To explore the sophistication of vocal communication in bonobos and whether their feeding vocalisations are a possible example of functionally referential communication, we studied the food-calling behaviour of 2 captive bonobo groups in San Diego. We recorded calls of individuals feeding on 9 different foods, which were determined as being high, medium or low preference, following systematic food preference tests. Data will be first presented on the acoustic structure of calls given for the different preference-ranked food items, and secondly regarding the combinations of different calls produced for these foods. Results will be discussed in the context of whether bonobo feeding vocalisations function as referential labels for the food being eaten and/or the signallers' preference to it.

## **Microdialects in the European wren *Troglodytes troglodytes***

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In Oscines, males sing for reproduction and defense of their territory, giving information about their species, group and individual identity and about their physiological state. It has also been shown that these territorial songs can show microgeographic variations leading to microdialects. We will present preliminary results of a new project on the European wren *Troglodytes troglodytes*, focusing on the acoustic parameters underlying microdialects and their ontogeny. The European wren is a common small passerine, singing loud 30-40 syllable songs. So far, we have studied the songs of 14 individuals belonging to three localities separated by about 2 km. We confirm that each male can sing several different songs and that the songs of two neighbours are closer to each other compared to the song of a male from another locality. We can already show that similarities rely on temporal acoustic parameters, such as song length, rhythm and tempo, and on syntactic organisation of syllables shared by neighbours of each locality. This study will help to better understand the acoustic communication system of small and well-separated communities of forest birds.

## **Song consistency reflects age in banded wrens**

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Older males tend to have a competitive advantage over younger males in sexual selection. Therefore it is expected that males communicate their age to potential mates and opponents for rapid assessment. Although song repertoire size in songbirds is often mentioned as an age-related trait, many species do not change their repertoire after the first year and therefore it cannot serve as an age indicator in these species. Here we show that the trill notes in the songs of older banded wrens are reproduced with less variability between them, i.e. more consistently. In a playback experiment we also showed that banded wrens discriminated between younger and older birds based on structural aspects of their song. In a second experiment banded wrens also responded differentially to natural songs versus songs with artificially enhanced consistency. We argue that consistency in trill note reproduction may be achieved through practice with the coordination of two independent sound sources, the left and right syringes. Sexual selection may therefore operate on a phenotypic trait, the expression of which is enhanced by practice.

## **Song influence on the vocalizations of male canaries**

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Bird vocalizations have been extensively studied and their role is beginning to be well understood. Thus, we know that songs, mostly emitted by males, are involved in intra and inter-sexual communication. In the domestic common canary (*Serinus canaria*), it has been shown that males emit songs composed of phrases of different status. The most well-known of them is the phrase A, which provokes copulation solicitation displays and an increase in the number of calls emitted by females and on the contrary, a decrease in the number of calls emitted by males. The aim of this study is to analyze male response (calls and trills) to songs. Trills have rarely been studied. That is why this research attempts to highlight the evolution of calls and trills in males. To do so, males will hear songs constructed from the individual signature of individuals of the same species and end with either a phrase A, or a non-reactive phrase. We believe that male response will differ according to the type of song they were exposed to. We expect that male will emit more trills when exposed to A phrases (expression of stress) and more calls when exposed to non-reactive phrases.

## **Food-associated vocal behaviour in mammal-eating killer whales – is it referential?**

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Mammal-eating killer whales in the coastal Northeast Pacific typically hunt in silence, but consistently emit pulsed calls after a successful predation event. Food-associated vocal behaviour is comparatively simple, consisting of only 3 discrete call types in addition to aberrant and variable calls. Its function remains poorly understood. Vocal behaviour may represent contact calling in order to attract other groups to the site of the kill, or it may serve to delineate social relationships between group members during prey sharing, or to coordinate behaviours during prey handling. Finally, food associated vocalizations may represent emotional signals due to raised excitement levels after a predation event. In order to test these hypotheses, I analyzed the vocal behaviour recorded after 13 predation events (4 harbour porpoise, *Phocoena phocoena*, 2 Steller sea lions, *Eumetopias jubatus*, 2 Dall's porpoise, *Phocoenoides dalli*, and 5 harbour seals, *Phoca vitulina*) in British Columbia and Southeast Alaska during which the prey species could be clearly established. I found that neither the amount of vocal activity nor the repertoire of call types used showed significant variation with the prey species, or with the estimated amount of food available. This suggests that post-kill vocalizations of mammal-eating killer whales are not referential signals, but may reflect the motivational state or hunger level of the hunting group.

## Vocal communication in a hybrid zone between two African dove species

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Avian species-specific vocalizations often function as a pre-mating barrier between species. Hybrid zones illustrate such behavioural barriers are not always impermeable and provide a natural laboratory to examine the causes and consequences of the breakdown of species barriers. Two sister species of African doves, the vinaceous and ring-necked dove (*Streptopelia vinacea* and *S. capicola*), hybridize in Uganda. We recorded vocalisations, carried out playback experiments and used molecular markers to identify hybrids in the field. We compared the vocal variation found in the hybrid zone to that found in the F1 hybrid generation reared in the lab. We found F1 vocalisations are intermediate and range from one parental species to the other and are similar in range and variation to that found in the natural hybrid zone. Playback experiments showed that individuals in the hybrid zone respond equally to natural hybrid and parental vocalizations, whereas the parental species respond most to conspecific vocalizations and least to heterospecific vocalizations. Furthermore, we did not find a hybrid individual's vocal response to be coupled to the characteristics of its own vocalisations, indicating they may learn whom to respond to. The differential response in the parental species suggests the vocalizations may play an important role in reproductive isolation. In the hybrid zone, hybrid male vocalizations are just as effective in territorial interactions as the parental vocalizations. Our results also suggest that hybrids sounding like one of the parental species may be able to settle and reproduce in the allopatric populations, and if they learn whom to respond to this may facilitate this process, allowing for further introgression between species. This suggests the hybrid zone will remain stable between the two species and possibly expand. These results give insight into behavioural characters important for the maintenance or breakdown of species barriers and into avian hybrid zone dynamics.

## Seismic noise induces increase in blue whale call production

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Marine seismic surveys are essential for exploration of natural resources such as gas and oil, whose demand is constantly increasing. The sounds from seismic surveys have the potential to impact marine mammals. The sounds produced during seismic explorations are typically short, broadband, and pulsed, with pulse energies below 300Hz, thus overlapping the acoustic signals and estimated hearing ranges of baleen whales. Consequently, seismic noise could interfere with the detection of essential acoustic signals by baleen whales. We investigated whether blue whales (*Balaenoptera musculus*) changed their vocal behaviour during seismic surveys that deployed low-medium power seismic technology (sparker). We monitored mid-frequency calls (20-200Hz) that are emitted during social interactions and feeding, since their acoustic characteristics (short duration, low-frequency range, transient nature), may make blue whales especially susceptible to masking by seismic pulse noise. Visual surveys and concomitant continuous acoustic recordings using multiple bottom-mounted recorders allowed monitoring the research area during the entire seismic survey period. A ten fold cross-validated logistic regression analysis was applied to compare call detections in 10min-windows on periods with and without seismic noise as well as between days with and without seismic activity. We found that whales called more during the periods and the days in which seismic noise was present. This increase in call production might represent a compensatory response to the increase in ambient noise from the seismic activity. Our study provides the first evidence of an upward adjustment of call production resulting from seismic noise in whales. The finding is consistent with the hypothesis that seismic noise causes auditory masking, and may also impair acoustic communication. This is already the case at considerably lower noise levels than those considered in previous studies. Hence, it has important implications for regulatory and management procedures for mitigating potential impacts of seismic operations on whales.

## **What's love got to do with it? - Conflict and cooperation in duets of the gray-breasted wood-wren (*Henicorhina leucophrys*)**

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Acoustic duets are often considered a cooperative behaviour, used for joint territory defence. Alternatively, duets may reflect conflict within a pair and may be used to preserve an individual's own position in a partnership. We used playback experiments to test for evidence of cooperation or conflict in the use of duets in a neotropical passerine, the gray-breasted wood-wren (*Henicorhina leucophrys*). Male and female wood-wrens initiate duets with equal frequency, so duets are a product of both female and male behaviour. This provides a unique scenario for testing both male and female motivation to duet. We presented 20 wood-wren pairs with three stimuli: duet song, male solo, and female solo. If duets serve a cooperative function, pairs should coordinate their response to simulated intrusions and respond most strongly to duet playback. If duets reflect conflict, individuals should respond most strongly to same-sex solos, initiating more songs and answering a higher proportion of their partner's songs to form duets. In response to duet playback, pairs approached the speaker together and sang duets at a high rate, suggesting that males and females work cooperatively to defend their territory from an intruding pair. Females initiated more songs and answered more of their partner's songs in response to female playbacks, supporting the conflict hypothesis. Males also initiated more songs in response to male solo playback, but answer rate was consistently high across all treatments. In natural situations, males almost always answer their partner's songs, suggesting a cost to the male of allowing his partner to sing solos, again providing support for the hypothesis that duets result from conflict between the pair. Our results therefore provide evidence that both cooperation and conflict play a role in the function of duets in the wood-wrens.

## **Sex differences in responsiveness to begging in a cooperative mammal**

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In species where young are provisioned by both parents, males commonly contribute less to parental care than females and are less responsive to variation in begging rates. Similar differences in the care of young occur among adults in cooperative breeders but fewer studies have investigated whether these are associated with differences in responsiveness. Here, we present results from a playback experiment investigating responsiveness to begging in the meerkat (*Suricata suricatta*), a cooperatively breeding mammal. Although increased begging rate raised the feeding rate of adults of both sexes, there was no consistent tendency for females to be more responsive than males. However, when we examined changes in the proportion of food items found that were fed to pups (generosity), we found that females were more responsive than males to increased begging rate. These results can be explained in terms of sex differences in dispersal: in meerkats, females are philopatric and receive considerable benefits from investing in young, both directly, by increasing group size, and indirectly, by recruiting helpers if they inherit the breeding position. In addition, they emphasize that generosity provides a more sensitive measure of responsiveness to begging than feeding rate, as it accounts for variation in foraging success.

## **Comparisons of behavioural patterns and vocalisations in pair housed and family housed captive howler monkeys (*Alouatta caraya*)**

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The howler monkey, *Alouatta spp*, is characterised by the production of howl vocalisations which potentially impact on social interactions within the family group. The zoo-based captive breeding programme provides an opportunity to compare behavioural patterns and vocalisations of pair housed and family housed howler monkeys. Analysis of activity budgets and vocal behaviours may provide a clearer understanding of the variability in behaviours performed in response to social group structure or surrounding environmental influences. Preliminary results have suggested that howl rate is affected by an interaction of these factors, however further analysis with a larger data set was necessary. Multi-institutional research has been carried out on both breeding groups and pairs of howler monkeys. Observational data on behaviour and vocal performance has been collected to investigate variation between different social groupings. This talk will discuss the effect of social group housing on behaviour and vocal performance in captive howler monkeys.

## **Female voices as cues to fertility?**

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On May 19th, 1962, Marilyn Monroe sang “Happy Birthday” to the then-US president John F. Kennedy, and her deep and husky singing was generally thought to be highly attractive. Interestingly though, a number of scientific studies have suggested that men prefer higher pitched female voices that signal youth and contrast with lower pitched male voices. To shed light on this apparent paradox, we assessed the link between female cycle stage and speech patterns, using hormone measurements to determine the timing of ovulation and speech analysis to characterize speech patterns. Our analysis revealed that during the course of their menstrual cycle, women lower the pitch of their voice, reaching a minimum around the timing of ovulation. The fundamental frequency during the time of ovulation was significantly lower than at the beginning of the cycle, but did not differ from the period directly preceding or following ovulation. Our results corroborate the view that women have evolved to conceal their ovulation, while some subtle cues may still provide information about their fertility status. Perceptual experiments to assess male perception of cycle-related variation in female voices are currently under way.

## **Social correlates of biphonic call type production by killer whales**

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Fish-eating killer whales in the northeastern Pacific live in highly stable matrifocal social groups called pods. Each pod produces a repertoire of 7 or more stereotyped call types. We compared the relative production of call types of free-ranging killer whale pods over time and between social contexts. The relative production of call types by each pod during directional travel was distinct over a 27-year period, however both temporal stability and pod distinctiveness were strongly influenced by a subset of dominant call types within the repertoire of each pod. Some call types within the repertoires contain biphonation (two overlapping independently modulated tones) and have a higher estimated active space than call types containing just one tone. In multi-pod aggregations the relative production of the dominant call types of each pod decreased and the relative production of a subset of biphonic call types that are rarely recorded from single-pod groupings increased. The physical characteristics of these biphonic call types, such as a high active space, mixed-directionality and mixed-on-axis intensity of components may explain why they are used more in inter-pod than intra-pod vocal exchanges.

## **Structural variation in banded mongoose calls in the context of recruitment**

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Studies on birds and mammals have identified specific vocalizations in the context of recruiting conspecifics. These calls attract other individuals to food sources, recruit juveniles to feeding sites, cause other group members to inspect secondary predator cues or to mob predators. However, little is known about the meaning of the variation in the acoustic structure of such calls. Here, we focus on calls emitted in the context of group recruitment in the cooperatively breeding banded mongoose (*Mungos mungo*). Calls were produced while encountering feces of different types of terrestrial predators, alive snakes and foreign groups of banded mongooses. Acoustic analysis of recorded calls revealed that calls in response to predator secondary cues were more tonal compared to the harsher variants elicited by snakes and foreign conspecifics. Playback experiments of these calls caused banded mongooses to approach the speaker, whereby receivers responded faster to the harsher calls elicited by snakes and foreign mongooses than to more tonal calls given to feces. We conclude that the acoustic structure contains information about the risk of the encountered stimuli, which allows receivers to adjust the level of urgency to respond. Calls of intermediate acoustic structure elicited by the different categories of stimuli and the similar response with main differences in the response urgency suggest a graded rather than a discrete call system in the context of recruitment.

## Two sides of the call: vocal tract modelling and vocalizations in lemurs

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For many years now, a model of vocal production based on the relationship between the tract area function and the formant output has been a common design for understanding speech production in humans. However this kind of approach was rarely used for the interpretation of non-human primates vocal production. Morphological measurements of the supralaryngeal cavities were collected to investigate the acoustic properties of the prosimian vocal tract. A liquid silicon compound was injected into the upper airways of 5 naturally dead lemurs (*Eulemur rubriventer*, *E. macaco*, *E. coronatus*, *E. rufus* and *E. fulvus*) to create a cast and derive measurements of the geometry of the vocal tract. The vocal tract was modelled as a number of fixed-length concatenated tubes, variable in cross-sectional area, where the number of tubes changed according to vocal tract length. Cross-sectional areas and length were used to build the oral and nasal tract area functions, which represent the input of MatLab-based vocal tract modelling software using a frequency-domain model. The output of each model was a simulated vocal tract transfer function whose peaks correspond to predicted formants. For the interpretation of these computational acoustic responses, we considered how the results of the models map onto the acoustic repertoire of the species under study. Predicted formant patterns were compared to LPC spectra of natural vocalizations. The results indicate that, alternatively, oral and nasal cavities play an important role in shaping spectral characteristics of prosimian sounds and that these characteristics can actually provide a species-specific cue in lemur communication.

## Does song development in female songbirds follow the same route as in males?

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Song development has been studied in detail in male songbirds. In contrast, female song development has been widely ignored, despite the fact that - at least in the tropics - females of many species regularly sing. In male songbirds the song development involves a 'sensory phase' in which model songs of conspecifics are memorised and a 'sensorimotor phase' in which highly variable 'plastic song' gradually improves to finally 'crystallise' into stereotyped adult full song. These processes can take up to several months as in many temperate zone species or can be completed as quickly as within 90 days as in the zebra finch (*Taeniopygia guttata*). Thus, the temporal course can vary a lot between different species. We were interested in whether it differs in the sexes of the same species. To answer this question, we studied the song development in male and female Red cheeked cordon bleus (*Uraeginthus bengalus*) and Blue capped cordon bleus (*Uraeginthus cyanocephalus*), two closely related African estrildid finches. Birds of both species were reared by their parents in the lab. They were either housed together with their parents and siblings and thus were exposed to live tutors or were housed individually in sound proof boxes where they could induce song playbacks by pecking a key in an operant tutoring apparatus. The young birds were recorded automatically throughout their song development. We will present data on the developmental trajectories of male and female song in our study species.

## **Group signalling: cooperative or selfish behaviour?**

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In many group-living species, individuals coordinate their signalling when interacting with rival groups. Group members may be acting cooperatively to defend a territory and several studies have shown that information about the opposing group, such as its size or identity, can be obtained from such signalling. Although all individuals benefit from maintaining a territory, the motivation to participate in group signalling may differ between group members, particularly when within-group breeding opportunities are skewed. Intergroup interactions may, for instance, provide opportunities for individuals to advertise themselves and/or assess members of the opposing group. Consequently, individuals may differ in their benefits from contributing to any combined signals, but this possibility has been rarely explored. We are investigating the combined vocal-signalling behaviour in a cooperatively breeding bird, the pied babbler (*Turdoides bicolor*), where individual contributions to choruses vary considerably. During intergroup interactions, the breeding pair call for significantly longer, and are more likely to call at the end of the chorus, than non-breeding individuals. Additionally, the breeding pair give sex-specific calls within the chorus. Playbacks of solo sex-specific calls demonstrate a skewed response by the dominant pair; in particular, dominant females respond significantly more strongly to female calls than do their dominant male partner. In general, our findings suggest that, rather than a cooperative group-territorial function alone, intergroup chorusing behaviour could act as a platform for selfish signalling by individuals.

## **Social mechanisms of vocal learning in songbirds and human infants**

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The immature vocalizations of songbirds and human infants are similar in function. Producing early sounds is crucial for the development of mature song and speech. We have found that social learning plays a strong role in vocal development. Responses of conspecifics create social feedback for early sounds that guide the young towards mature vocalizations. In cowbirds, *Molothrus ater*, immature vocalizations of young males elicit reactions from adult females (who do not sing), and this feedback facilitates the development of more advanced forms of song. Mechanisms of vocal learning in human infants, however, have received far less attention. We tested 9-month-olds' ability to learn new vocal forms from social feedback. During a play session, mothers received instructions from an experimenter via wireless headphones. We manipulated the form and timing of mothers' reactions to their infants' prelinguistic vocalizations. Half the mothers (contingent condition) were instructed to respond immediately to their infants' sounds by smiling, approaching, and touching them. The remaining mothers were yoked controls, with the form and timing of their responses determined by the Contingent mothers. Infants who received contingent feedback produced more speech-like vocalizations; yoked control infants did not. In subsequent experiments, we instructed mothers to respond to infant vocalizations with specific speech patterns. Contingent infants produced vocalizations with phonological patterns that significantly resembled those of their mothers' vocal responses. Infant phonemes were not the same as those of their mothers' utterances, suggesting that phonological learning was not imitative but rather a form of pattern recognition. Yoked controls did not learn the new phonological patterns. These data represent the first evidence of statistical learning in vocal production. Infants learn regularities in speech only when vocal responses are contingent on their babbling. Thus, in both songbirds and humans, social feedback to immature sounds affords infants opportunities to refine their vocal repertoires.

## **Why do grey seals vocalise underwater? An investigation into the function of grey seal underwater calls using playback experiments**

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Scottish grey seals (*Halichoerus grypus*) produce at least 10 distinct low-frequency (50 Hz to 1 kHz) underwater call types in and outside the breeding season. We tested behavioural responses of seals to 6 call types (moans, rups, rup, growls, knocks, type10) and compared them to several control sounds (harbour seal call, sine wave, white noise) outside the breeding season. In experiment 1 movement responses of 10 captive female seals and one juvenile male were tested individually in a large experimental pool. Playbacks started when the seal positioned itself in front of a feeding station. The experiment was set up so that seals could either approach the loudspeaker (attraction) or swim away from the sound source (avoidance). Sound projector (J11 transducer) and feeding station were 7.5m apart. All seals showed strong attraction responses (e.g. touching the loudspeaker) when moans, rups and rups were played compared to the harbour seal or artificial control sounds. Only one animal responded vocally. Growls, type 10 calls and knocks did not cause strong attraction responses. None of the sounds caused an aversive response. Consecutively, we tested the three calls that initiated strong attraction responses in the first experiment with wild seals around a haulout site. A significant increase in both female and male seals around the loudspeaker was found in response to these calls while the harbour seal calls did not elicit any response. We conclude that since these three calls caused attraction responses in both sexes outside the breeding season they may serve a more general function than male-male interaction or mate attraction. Given that Scottish grey seals belong to a formerly ice-breeding population we suggest a function as recruitment calls to attract conspecifics to a potential haulout site in a highly variable environment e.g. around drifting ice. Low-frequency underwater calls would be ideally suited for long-distance communication in such an environment.

## **Geographic variation of signature whistle types from Indian Ocean bottlenose dolphins (*Tursiops aduncus*) in coastal Zanzibar**

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Previous studies have identified geographical variation in the whistles of bottlenose dolphins (Wang et al., 1995; Morisaka et al., 2005). However, these have concentrated on acoustic parameters of all sounds with no attempt to classify them into biologically relevant categories. Bottlenose dolphins use highly distinctive signature whistles to maintain contact at sea. These whistles appear to be more stable than others and may show systematic differences between populations in different habitats. This study compares differences in signature whistle types between two genetically differentiated Indian Ocean bottlenose dolphin populations (Berggren et al., 2006) located in close geographic proximity to one another in northern and southern coastal Zanzibar (East Africa). Recordings were made of free-ranging animals during January-March 2008 and photographs of dolphin dorsal fins were taken to determine which animals were present during encounters using standard photo-identification techniques. Signature whistle recognition was performed using a novel technique involving sequence analysis and ARTwarp (Deecke & Janik, 2006). Once identified the whistle frequency parameters, duration and degree of complexity of signature whistle types were compared between and within populations to determine the level of variability. The results of this study fit into a larger scale project investigating geographic and species variation in bottlenose dolphin signature whistles.

## Acoustic character displacement in an avian contact zone

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Acoustic sexual signals could play an important evolutionary role when related taxa come into secondary contact. Acoustic differences may converge, remain distinct, or even show a pattern of more divergence where both taxa meet. Furthermore, patterns in acoustic traits can be similar or contrast with morphological and genetic traits. Two subspecies of the Gray-breasted Wood-wren *Henicorhina leucophrys* replace each other altitudinally across the western slope of the Ecuadorian Andes. The subspecies are morphologically very similar but differ strikingly in temporal as well as spectral song characteristics. We examined variation in morphological, acoustic, and genetic traits across the altitudinal range covered by both subspecies and between two allopatric populations. We found a pattern of convergence in morphological traits, while temporal differences in song remained distinct across the zone. Interestingly, spectral differences between the subspecies revealed a pattern of divergence across the narrow contact zone when compared to both allopatric populations. Additionally we performed playback experiments to test whether the subspecies were able to discriminate between the songs of the sampled populations. We found that the pattern of spectral character displacement was matched by the response patterns in at least one of the subspecies. Our results provide the first example of character displacement in a plastic, vocal trait and suggest that signal divergence under secondary contact can play an important role in the process of speciation.

## Selfish or cooperative? Sentinel calling in a social bird

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Many foraging animals face a fundamental trade-off between predation and starvation. In a range of social species, this trade-off has probably driven the evolution of sentinel behaviour, where individuals adopt prominent positions to watch for predators while group-mates forage. Although there has been much debate about whether acting as a sentinel is a selfish or cooperative behaviour, far less attention has focused on why sentinels often announce their presence with quiet vocalisations (known as “sentinel calls” or “the watchman’s song”). We use observational and experimental data from a wild, but habituated, population of group-living birds to provide the first evidence that group members gain an increase in foraging success by responding to these vocal cues given by sentinels. Foraging pied babblers (*Turdoides bicolor*) spread out more, use more exposed patches, look up less often and spend less time vigilant in response to sentinel calling. Crucially, we demonstrate that these behavioural alterations lead to an increase in biomass intake by foragers, which is likely to enhance survival. We argue that selection pressure to maintain the watchman’s song arises because sentinels benefit (through group augmentation and/or kin selection) from the increased foraging success of others, making it a truly cooperative behaviour.

## Development of referential and motivational information in meerkat alarm calls

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Animal vocalisations were historically thought simply to express the motivation of the caller. It is now clear, however, that many vertebrates also produce specific alarm calls in response to different predators; these referential calls provide listeners with information that goes beyond the caller's motivational state. Although alarm calls are known to develop gradually in many species, little is known about the relative developmental rates of calls signalling different types of information. The acoustic structure of meerkat (*Suricata suricatta*) alarm calls simultaneously encodes information that is both motivational (level of urgency) and referential (type of predator), providing an ideal opportunity to compare relative developmental rates in the same species. We recorded alarm calls from meerkats of different ages, and used acoustical analyses to examine age-related changes in a variety of call features. We found that the alarm calls of young could be correctly assigned to low and high-urgency contexts with a high degree of certainty, and to a similar degree to adult alarm calls. However, in contrast to adult calls, juvenile alarm calls were assigned to the correct predator type with a much lower level of certainty. Furthermore, the discrimination between different predator-specific calls was better in high-urgency compared to low-urgency contexts. Our results suggest that acoustic features related to the level of urgency are expressed earlier in the repertoire than those related to the type of predator, and therefore lend support to the idea that referential calls evolved from motivational signals.

## Teen stress: song learning in zebra finch juveniles

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The period from conception to maturity is crucial for an individual's later performance and it has been shown that stress during early development can have profound fitness consequences. Despite the wealth of studies on the effects of early developmental stress, much less is known to which extent environmental conditions during later developmental periods affect the expression of fitness relevant traits. The developmental period in which secondary sexual characters develop is of particular interest, as these traits can reflect an individual's ability to acquire resources and to cope with environmental constraints by itself. By that time parental care has ceased. In zebra finches, *Taeniopygia guttata*, this is the second month in life: the period of song learning which coincides with moult into adult plumage and gonadal development. As the period for song motor production begins after nutritional independence, impacts on song learning may not only act in the nestling. Thus, we expected the month following nutritional independence, when songs are acquired and when the underlying neural pathways controlling song learning and song production learning continue to develop, to be of fundamental importance. To test this hypothesis, subjects were exposed to qualitatively different nutritional treatments from day 35 until day 65 during song tutoring. After reaching sexual maturity female song preferences were tested in an operant conditioning set up at the Behavioural Group of the University of Leiden, The Netherlands. Males' song was analyzed via two different approaches. First, visual comparison of sonagrams by different observers was performed followed by a complex sound similarity analysis with Sound Analysis Pro software. The results we present show whether male song, a sexually selected trait, and female song preference reflect an individuals' nutritional background. This study contributes to the understanding of epigenetic influences on phenotypic plasticity.

## **Sex role convergence, territoriality and vocal behaviour in Australian magpies**

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In avian species of the northern hemisphere species, small syllable repertoires are associated with sedentary species and large repertoires with non-territorial, often migratory species (Catchpole 1982). This interrelationship makes sense in the context of strong seasonal variations at high latitudes, and among sexually dimorphic species. As Slater and Martin pointed out (2004), however, the model may not hold for tropical and southern hemisphere species. Indeed it does not and this insight is of surprisingly recent date. The Australian magpie (*Gymnorhina tibicen*), perhaps the foremost songbird of Australia and of an ancient lineage, is a good case in point. In this species, sex role convergence arising from partner fidelity and extended breeding seasons fosters collaboration, duetting and communication patterns differing from those of northern hemisphere songbirds. The magpie's main form of vocalisation, the warble, has long been regarded as a song without function ('subsong') precisely because theories of song are built on northern hemisphere songbirds. As will be shown, the magpie's vocally monomorphic song is learned in the absence of tutors, is improvised, and retains high, possibly life-long, vocal plasticity resulting in vocal complexity. Data will be presented to demonstrate that, in magpies, song does not have the function of attracting a female but is of value in territorial contexts, and that in males and females, song frequency may vary seasonally but is not related to breeding. Further, experiments have yielded results on territorial defence, referential signalling and social facilitation. It is argued that the model of song presented here may be an ancient form of song that was preserved due to long isolation and allowed to proliferate in function unlike song adapted for high latitude habitats, which has time constraints and is of more recent origin.

## **What to sing next? - Rules of song type delivery in nightingales (*Luscinia megarhynchos*)**

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In most songbirds investigated so far, males sing more than one song type. These species do not only remarkably differ in repertoire size but in repertoire delivery, too. Our study species, the common nightingale (*Luscinia megarhynchos*), is a territorial songbird known for its apparently endless variety in song. In nightingales, this variety is not achieved by new and spontaneous combination of song material, but by acquisition of song templates mostly in early ontogeny. Song templates are copied precisely and imitations may persist as stereotypic song compounds over several years. During singing males deliver their repertoire in a versatile but not circular style with specific performance rules. These patterns of song acquisition and singing style invite inquiries into the mechanisms and factors affecting the rules of song type delivery. We investigated the repertoire size and song performance in long, undisturbed nocturnal song bouts of free ranging territorial nightingales of Berlin and Haute Provence populations. The analyses (530 successive songs per male) revealed large variation in repertoire size (Median=189, Range 64-298, n=74). Nevertheless there was a clear tendency for a regular recurrence of song-types after 50 to 80 intervening song renditions. Such intervals were found in birds with both small and large repertoires, suggesting that this performance rule is an inherent property of nightingales' singing. In addition, we examined whether performance rules were stable on the individual level by investigating intra-individual variability of repertoire delivery both in the shortterm and longterm. Our results suggest that the development of a large repertoire is not only a matter of producing high versatility, but has to cope with demands on song retrieval as well.

## **Vocal individual recognition in Japanese jungle crows (*Corvus macrorhynchos*)**

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Recent studies on corvid behaviour suggest their highly socio-cognitive skills which are assumed to be based on individual recognition. However, mechanism of individual cognition has been little understood even though corvids are assumed to be good vocal communicators as oscine species. Japanese jungle crows, one of Corvidae family, live in fission-fusion society which requires ability of individual recognition. It is possible that their individual recognition could depend on the vocals because they are originated in tropical forest where visual contact often does not work. To test this possibility, we investigated their ability of vocal individual discrimination. First, through field observation, we determined the call type that served as contact call by observing vocal exchange. We were able to determine that single-note calls were used in vocal exchange within pairs and groups in wild jungle crows. Then we analyzed the acoustic structure of single-note call given by five captive crows to investigate if there is any individuality by discriminant analysis. The analysis revealed that the acoustic structure of single-note call was clearly different between individuals. Finally, we investigated if jungle crows were able to discriminate calls of different individuals by training five captive crows with operant go/no-go procedure. Four crows were able to learn the discrimination task, and they were also able to generalize the response to novel, not used in training stimuli. These results suggest that Japanese jungle crows are able to recognize others by vocalization.

## **How early testosterone treatment affects production of song learning in male zebra finches**

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Songbirds as humans are part of these few groups that exhibit vocal learning. In male zebra finches the sensory and motor phases overlap. Juveniles start to sing and memorize the father's song from 25 post-hatching days (PHD) and they have to be exposed at least ten days with the tutor's song to be able to give, when adult (ca. 90PHD), an accurate copy of the tutor. Song learning and production are controlled by a discrete neural circuit, which undergoes profound developmental changes during the time when song is learned. First singing starts when synaptic connections between two song control areas, HVC and RA, are established, sometime after PHD25. To understand how testosterone influences different stages of behavioural and neural development, we implanted juvenile males (PHD16) with testosterone (T group) or placebo (P group) pellets. We removed the tutor at PHD25 and monitored continuously their vocalizations until adulthood. We compared song development in T and P groups with birds implanted with placebo but that were kept exposed to the tutor's song until PHD35 (C, control) and with juveniles implanted with testosterone that were raised in acoustic isolation (no tutor). We found that administration of T induces a shift in the onset of song production: birds implanted with T started to sing at 19PHD, instead of 25 for C and P groups. Moreover, while not exposed to the tutor's song at the 'critical' period T birds were nonetheless able to learn the tutor's song as C birds did. P birds, as expected, produced a song similar to isolate birds. We discussed these behavioural changes with our findings in the organisation of the neural vocal system.

## **Seasonality in song behaviour revisited: Seasonal and annual variants and invariants in the song of the canary (*Serinus canaria*)**

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The song of the domesticated canary (*Serinus canaria*) is one of the most widely used models to study the neural correlates of behavioural plasticity and the mechanisms of female mate choice. However, only few studies have described the song behaviour in detail and monitored their changes throughout the year and these data are restricted to the “Waterslager” strain. Here, we studied the song characteristics of the male common domesticated canary at different times of the year, the spring breeding and autumnal non-breeding season, and monitored the birds’ songs up to the following breeding season. We found that song length and the proportion of non-repeated syllable types changed seasonally but not annually. Repertoire size remained constant throughout the seasons, although repertoire carry-over was significantly lower on a seasonal compared to an annual basis. Further, the breeding season repertoire contained significantly more potentially sexually attractive syllable types than that of the non-breeding season. These data are consistent with seasonal changes in the songs of wild canaries, the ancestors of the domesticated canary. During breeding, male domesticated canaries had increased plasma levels of testosterone, and therefore the observed song changes are likely to concern hormone dependent features. This appears adaptive as in wild canaries the onset of the breeding season can vary up to 6-8 weeks and is dependent on the presence of green plants. The data further show that overall song structure is retained throughout the year while seasonality occurs in the temporal pattern and in repertoire composition.

## **Individual signatures in communication calls of a nocturnal lemur (*Microcebus murinus*)**

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Individual recognition plays an important role in the social behaviour of many non-human primates. In mammals efficient acoustic recognition systems have been found in situations where high densities or darkness reduce the roles of olfactory or visual cues. Mouse lemurs are nocturnal primates that live in a dispersed multi-male multi-female system in dense forest vegetation. In this species females form temporary stable sleeping groups. Due to their social system and nocturnal lifestyle, acoustic signals which convey individuality may be beneficial for governing social interactions.

To explore whether individual signatures are conveyed acoustically across different call types of the vocal repertoire of the grey mouse lemur, we examined trill calls (used in social cohesion contexts), tsaks (used in agonistic contexts), whistles (used in attention and alarm contexts) and grunts (used in threatening contexts) of males and females. All recordings were taken from captive subjects in a sound attenuated room. A multiparametric sound analysis revealed that some call types, but not all, convey individuality. Thus first analyses showed that individual differences in call structure do occur in the trill call, in the tsak call and in whistles. A discriminant function analysis indicated that frequency parameters best explain the individual differences. Ongoing studies will show to which extent mouse lemurs will use this information to discriminate particular categories (e.g. known/unknown individuals) of their social world acoustically.

## **Vocal performance, song syntax and social context in the domestic canary (*Serinus canaria*)**

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Vocal performance in a wide range of songbirds is defined as the deviation from an upper limit in a trade-off between syllable rate and frequency bandwidth. Several playback studies showed that high-performance level can play a role in both intersexual and intrasexual selection. But, what about song syntax according to vocal performance level and to social context? We tried to answer this question using the domestic canary (*Serinus canaria*) as a model of study. In this songbird species, syllables are repeated in phrases (or trills), and two or more successive phrases form a song. First, we recorded males when in the presence of a female or a male, or when alone. Then, we analyzed males' song syntax in these three social situations according to performance level of each phrase. Our main results showed that males sang a series of two strongly contrasted phrases in the presence of females. This series was composed of a first phrase with a low syllable rate and a narrow frequency bandwidth, followed by a phrase with both a high syllable rate and a large frequency bandwidth. Previous experiments in the domestic canary pointed out that females did not show sexual preferences for the first phrase, whereas they showed a large sexual preference for the second phrase, which was called 'sexy phrase'. We suggest that this effect of contrast in song syntax in the presence of a female could act as an anti-habituation process to attract and maintain the attention of a potential mate.

## **Willow warbler males (*Phylloscopus trochilus*) assess a rival's fighting ability by the frequency of his song**

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Different song features (e. g. length, rate, repertoire size) are proven to influence a female's mate choice in birds. So far, not much attention has been paid to the question of whether males assess the quality of rivals by their song and what clues they use to help them in this. Knowledge of the competitor's fighting ability is necessary for choosing the right strategy during aggressive interactions, the results of which might determine the male's nesting success in that season. We investigated whether the frequency of the male's song in songbirds is negatively correlated with his body size as in other taxa, and whether this feature is used during aggressive encounters to assess the opponent's size and thus his potential fighting ability. In the spring of 2007 we caught 15 willow warbler males, we colour ringed, measured and weighed them. Later, we recorded at least 20 songs from each individual male and we analysed the mean frequency of the songs. The frequency of the songs was negatively correlated with the beak length and with the body weight. To experimentally simulate territorial intrusion, we transposed 10 songs from previous years making them both 250 Hz higher (to simulate a small intruder) and 250 Hz lower (large intruder) and we played them back to territory owners in a completely random order. During a 5 minute trial we noted the distance of the tested bird from the speaker. Responses to playback of the high and deep songs did not differ, but the mean distance from the speaker correlated with the difference in the mean song frequency of the owner and the intruder. These results suggest that willow warblers use the frequency of the rival's song to assess his fighting ability. Moreover they do not judge only from the intruder's song frequency, but they take into account their own size too.

## **Pups of the degu (*Octodon degus*), a communally nesting caviomorph rodent, include ultrasonic frequencies in care-eliciting calls**

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Previous investigation into the vocalisations of the degu, a social Chilean rodent, raised interesting questions regarding the highest frequencies used by pups (Long, 2007). Since the previous study had a recorded frequency restriction of 22 kHz, further work was required to investigate the possibility that pups use ultrasound. Here, I focussed on 'loud whistle' vocalisations unique to pups of age 0 days-6 weeks, used to elicit care from an adult, in order to examine inclusion of high frequency harmonics. A sample of captive degu pups were recorded using equipment of range 20-50000 Hz. 1000 'loud whistle' samples were statistically analysed by one-way ANOVA. Features investigated included maximum frequency, minimum frequency, duration, harmonic quality, frequency modulation, litter origin, pup age and behavioural context. Behaviours observed for analysis included 'pup care/grooming', 'entry of lactating female', 'separation/isolation', 'in nest (other)' and 'out of nest (other)'. Degu pups were found to frequently include ultrasonic harmonics in their 'loud whistle' vocalisations. The average recorded frequency range was 2250 - 41000 Hz with 9 harmonics, much higher than was previously recorded. Maximum frequency varied significantly with behavioural context ( $p < 0.005$ ) and pup age ( $p < 0.005$ ). Call duration and harmonic quality also varied significantly with behavioural context ( $p < 0.005$ ) and pup age ( $p < 0.005$ ). Degu pups include ultrasonics in their vocalisations despite the prevalence of non-ultrasonic vocalisations in adulthood. Since it is not yet clear whether adults are capable of hearing ultrasound, it is possible these harmonics are produced as a consequence of the underdevelopment of the vocal tract. It is further hypothesised that since ultrasound is readily attenuated in the environment, wild degu pups (born in burrows) that become separated from the nest produce this relatively loud vocalisation to elicit care from adults without the risk of being easily detected by predators above ground.

## **Interspecific communication about danger: does alarm-call similarity promote understanding?**

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Many birds and mammals give alarm calls to alert conspecifics of danger, and in some cases individuals respond to alarm calls of other species. Heterospecific calls potentially provide a rich network of information about danger, but little is known about the importance of acoustic similarity compared to learning in the response to other species' alarm calls among birds. In particular, the aerial 'seet' alarm calls of passerines provide a textbook example of signal design because many species appear to have converged on an acoustic design that thwarts eavesdropping by hawks (Marler 1955 *Nature* 176, 6-7). The resulting similarity in call structure might then facilitate communication among these prey species (Marler 1957 *Behaviour* 11, 13-39). We tested the importance of aerial alarm call similarity in the flee response of superb fairy-wrens *Malurus cyaneus* to the calls of white-browed scrubwrens *Sericornis frontalis*. First, if call similarity itself prompts escape independent of learning, we predicted that fairy-wrens living together as well as in isolation from scrubwrens should flee from scrubwren calls. However, fairy-wrens fled only in sympatry. Second, if call similarity is necessary for learning the calls of other species, then fairy-wrens should not respond to sympatric heterospecifics with different calls. We found, on the contrary, that fairy-wrens fled after playback of the very different aerial alarm calls of New Holland honeyeaters *Phylidonyris novaehollandiae*. Furthermore, response depended on the specific structure of the honeyeater's call, rather than general properties like frequency, implying learning. Overall, call similarity was neither sufficient nor necessary for interspecific recognition of aerial alarm calls, whereas learning appears essential in the complex task of sifting the acoustic world for cues about danger.

## **A comparative study of song in the *Thryothorus* wrens**

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*Thryothorus* is a New World genus comprising nearly 30 species of wrens, of which we have been able to study 24 in various Latin American countries. The species vary greatly in their song: in some only the male sings, in others the pair sings more or less well-coordinated duets and in others there are group choruses. Our aim has been to identify places where divergence in singing behaviour has taken place so that selective forces leading to change may be identified. As a basis for this we took blood samples from each species, which enabled us to prepare a molecular phylogeny as well as sexing the individuals involved. The first surprise came from the molecular phylogeny which made it clear that this group of species should be classified as four genera not one. In most cases the style of singing fits in well with this new classification, species within each of the new groups tending to sing in a similar style to each other. However, there are exceptions and the study has enabled us to pinpoint a number of cases where close relatives sing very differently and which therefore deserve further study.

## **Fifty Years on!**

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Now European ethology looks back across 50 years since Lorenz and Tinbergen started their groups. Many have been arguing that ethology is now extinct but this is to confuse its initially very narrow conceptual framework which is, with its approach to the study of behaviour which is now almost totally universal! Actually the ethological approach to communication retains some elements of its early core which are still valuable, although it is impressive how far the boundaries have now been extended. Vocal communication, above all, illustrates the wonderful interplay of inherited biases and individual experience being revealed during development. There is no better exemplification of Tinbergen's 'Four Question' and there are even hints of a related, more awkward question, concerning animal minds. I shall attempt to explore some of these issues and speculate on where we may be going.

## **What do functionally referential alarm calls refer to? Insights from the meerkat 'animal moving' call**

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Functionally referential calls have been defined to refer to specific stimuli in the external environment of the caller, and promote adaptive responses in receivers. Common examples are the predator-specific alarm calls of certain species, which may refer either to specific predator types or species, or the location and behaviour of approaching predators. Here, we present data on the 'animal moving' call in meerkats (*Suricata suricatta*), which appears to refer specifically to the movement of a variety of animal species in the environment of the caller. This call type is elicited by animals moving both on the ground and in the air, regardless of whether the animal is dangerous (predators) or non-dangerous (herbivores, birds) to the meerkats. We suggest that this call type can be considered to be functionally referential and discuss how these findings extend our understanding of functionally referential calls. Furthermore, we consider whether different categories of functionally referential calls are governed by the same underlying cognitive mechanisms.

## **Inter- and uni-modal discrimination by chimpanzees based on auditory and visual information**

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This study aims to understand the audio-visual intermodal abilities of chimpanzees (*Pan troglodytes*). Individual recognition of familiar individuals was studied in one of the 14 chimpanzees housed at the Primate Research Institute, Kyoto University, an adult female named Pan. This subject learned an intermodal Audio-Visual Matching-To-Sample (AVMTS) task consisting in matching playbacks of chimpanzee pant-hoot and human speech to the facial pictures of corresponding vocalizers. Our results showed that 1) Pan was able to correctly perform intermodal individual recognition of familiar adult chimpanzees and humans, 2) individual recognition of infant chimpanzees was poorer relative to recognition of adult chimpanzees, 3) facial cues seemed to be critical for the intermodal matching, and 4) 200 ms vocal segments were sufficient auditory cues for correct recognition. As a way to better understand the acquisition process of the intermodal association between auditory and visual stimuli, we trained five new subjects to perform a unimodal Conditional Position Discrimination (CPD) task in auditory or visual modalities. Unlike the intermodal AVMTS task, which requires a symbolic treatment of information from distinct modalities, the CPD task is expected to rely on the simple association between one type of stimuli and one spatial position. The training process showed that visual CPD was easier to acquire than the auditory CPD although both of these tasks were equivalent in terms of cognitive treatment. Chimpanzees seem to experience greater difficulty taking into account auditory information as a critical cue to produce a correct behavioral response. Together, these data demonstrate generalization and its limits for auditory-visual intermodal matching based on individual recognition in chimpanzees.

## **Changes in groans and calling rate of fallow bucks represent declining body condition and variation in the intensity of sexual selection**

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Most studies of sexually selected vocal communication assume stability of calls over short periods of time. However, social and physiological factors can change during a breeding season, and these can have strong effects on the structure of calls. During the rut, fallow bucks reduce their food consumption, increase the time and energy in vocalising and fighting in order to gain matings, and consequently their body condition declines greatly. The availability of mating opportunities and intensity of competition between males also change. Therefore, we investigated if the acoustic structure of fallow buck groans and the groaning rate changed during the breeding season. We found that fundamental frequency-related parameters were lowest during the middle of the rut, and highest at the beginning and at the end. The measure fundamental frequency-perturbation along the groan (jitter) remained stable throughout the rut, whereas the number of pulses and duration of the groans decreased linearly. The minimum formant dispersion did not vary significantly with time. Groaning rate increased towards the peak of the rut when most mating occurred and then rapidly decreased over the last days of the rut. We suggest that changes in the acoustic structure of groans and groaning rate represent the declining body condition of males, as well as changes in the intensity of intrasexual competition and mating opportunities occurring over the course of the rut. Conspecifics could gain important information on competitors or potential mates by listening to these changes.

## **Duetting in a nocturnal mammal (*Lepilemur edwardsii*) a mechanism for joint territorial defence and prevention of infanticide?**

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Duetting is defined as an interactively organized pair display in which one pair partner coordinates its vocalisations in time with those of the other pair partner. It is present in some tropical birds and pair-living anthropoid primates in which it is suggested to strengthen pair bonds. To date, nothing is known on the presence and function of duetting in dispersed pair-living primates. We studied sleeping associations, home ranges use and the vocal and behavioural activity of 12 radio-collared sportive lemurs (6 males and 6 females) in the Ankarafantsika National Park in north-western Madagascar. Three different periods (mating, pregnancy and offspring care) were covered. Males and females form long term bonds, indicated by an almost exclusive pair-specific usage of sleeping sites and home ranges across periods. Pairs regularly engaged in duetting. Calling was significantly enhanced during the offspring care period. Duetting was associated with locomotion, scanning and feeding and occurred significantly more often at feeding than at sleeping sites. When pair partners showed different behavioural activities before calling, they displayed significantly more often synchronized than different activities after calling. Altogether our results render support for the hypothesis that in dispersed pair-living mammals, duetting acts as a mechanism to coordinate pair activities, to display pair ownership to neighbours and strangers and to limit aggressive encounters and infanticide during the offspring care period. Thus duetting may help to strengthen pair bonds.

## **Vocal duetting in neotropical wrens: acoustic communication in the animal kingdom's most coordinated singers**

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In many tropical animals, male and female breeding partners combine their songs to produce vocal duets. The temporal precision of these displays is often so astonishing that human listeners mistake duets for the songs of a single animal. Our understanding of vocal duetting behaviour is still rudimentary, in part because many duetting animals live in tropical habitats where dense vegetation makes direct behavioural observation difficult or impossible. Here I focus on the vocal duets of neotropical wrens using both descriptive and experimental approaches. In the first section of my talk I focus on the duetting behaviour of Rufous-and-white Wrens from the humid forests of Costa Rica. I use two innovative technical approaches to study vocal duets: an eight-microphone Acoustic Location System (ALS) capable of passively triangulating the position of duetting animals based on recordings of their vocalizations, and dual-speaker playback capable of simulating duets in a spatially realistic manner. Results from ALS recordings provide the first detailed spatial information on duetting animals, demonstrating that breeding partners perform duets across distances more variable than previously imagined and that duets play an important role in maintaining acoustic contact in visually occluded habitats. Results of dual-speaker playback demonstrate that duets play an important role in territory defense during aggressive confrontations with rivals, and that duetting birds use aggressive, sex-specific strategies for interacting with territorial intruders. In the second section of my talk I briefly describe the vocal duets of three related species of wren whose voices were unknown until recently: the Pacific Coast Plain Wren of Costa Rica, the critically endangered Niceforo's Wren of Colombia, and the recently described Inca Wren of Peru. My results support the argument that Neotropical wrens sing the most complex, coordinated songs ever described.

## **The acoustic repertoire of wild dusky dolphin (*Lagenorhynchus obscurus*) groups in Golfo Nuevo, Patagonia**

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During April 2003 and March 2005 sounds and behavioral data of dusky dolphins in Golfo Nuevo, Argentina, were collected. Sound production and acoustic behavior of this species are little known; very basic parameters need to be investigated. Recordings were made with sampling rates of 96 kHz and 48 kHz and a preamplified HTI94SSQ hydrophone. 194 minutes of recordings were obtained in the space of several days at variable times of the day and different locations during a total of 18 encounters with groups with fluid numerical composition (min= 3, max > 60).

Digitalized sounds are described with objective parameters such as type of sound (click, whistle or pulse train), repetition rate, duration, frequency range and signal to noise ratio. Only poor quality sounds were not analysed. A subset of 223 samples of sounds were analysed. Preliminary data suggest that clicks (n= 1249), whistles and pulse trains are all part of dusky dolphin repertoire. 4 whistles were found, the frequency of these whistles ranges from 279,9 Hz up to 1934 Hz. All show inflections, duration is included between 0,06s and 0,116s. So far at least two types of pulse trains are common: type A (n= 21) are long series ( $\Delta t > 1s$ ; mean= 1,5s, repetition rate mean= 450 clicks  $s^{-1}$ ) with increasing repetition rate throughout the pulse train; type B (n= 87%) pulse trains are short ( $\Delta t < 1s$ ; mean= 0,2s) and are subdivided respectively in Type B1 (n=37, without gaps, mean repetition rate= 425 clicks  $s^{-1}$ ), Type B2 (n=26, which show further structure with 3 subcomponents: an initial high repetition rate sequence, a section with lower repetition rate and a final sequence (pt3) with high repetition rate; mean=493) and Type B3 (n=6, with gaps and up to 5 subcomponents; pt3 mean repetition rate=493)

## **Dynamics of vocal tract articulators in the zebra finch (*Taeniopygia guttata*)**

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Both humans and many birds produce exceptionally complex vocalizations that exhibit rapid variations in multiple acoustic parameters. Some of these acoustic parameters serve to encode linguistic meaning in human speech. Speech sounds are modulated using vocal tract resonators and articulators such as tongue, lips and soft palate. Studies on birdsong are beginning to reveal that natural bird vocalizations are also affected by the activities of resonators and articulators in the avian vocal tract. The current study uses high speed X-ray cinematographic imaging to investigate overall dynamic patterns during zebra finch song and to reveal the function of possible articulators such as tongue and beak. The experimental setup allows us to record with a high resolution of 500 frames per second. Preliminary results show that zebra finches expand their oro-pharyngeal cavity during some notes of the song and by that increase the volume of this cavity. This expansion is followed by an opening of the beak. Furthermore a front to back and upwards-downwards movement of the tongue is visible. These results support the assumption that birds like humans change their vocal tract resonances by altering the position of the tongue and the dimensions of the oro-pharyngeal cavity, which in turn could allow zebra finches to use these mechanisms for coding information within their vocalizations.

## **Spontaneous categorization in African grey parrots (*Psittacus erithacus*) during referential communication learning**

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Wild animals often adopt appropriate behaviour in response to a novel stimulus because the latter is similar to a stimulus and appropriate response already familiar to the animal. Such behaviour expresses an ability to categorize. Several laboratory experiments have shown for instance that pigeons and monkeys are able to form perceptual and sometimes functional categories like food/non-food. There is little data on spontaneous functional categorization, indeed in previous studies animals are trained to respond. During a study conducted to compare three methods used to teach parrots to use human words as labels, we also investigated their spontaneous categorical use of these words.

Two African grey parrots (*Psittacus erithacus*), a two-year-old male and a four-year-old female were tested with three different methods:

- Model/Rival method: interactions between two trainers who demonstrate questions and answers in reference to an object, the parrot observes and can take part. He receives the object he labels as a reward for each correct answer.
- Intuitive method: consists of naming an object while the experimenter or the parrot manipulates it.
- Repetition/Association method: the speaker repeats a word several times. Once the bird learns to imitate the word, we begin the second phase of association in which the object is given to the bird each time he says it.

For the subject who is the best learner, the repetition/Association method seems to be the most efficient. When using the Model/Rival and Intuitive methods, we observe spontaneous categorization on the part of both subjects for some food *versus* non-food items. They used differently words they learned in order to ask for different items. Similar observations have been made in children and trained-language primates. We find a pattern of over-extension as Piaget described in humans.

## **Pipit, sing me a song, and I will know who you are, and where you are from**

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Correct species discrimination by acoustic cues is crucial for mate selection and territorial defense in cryptically-coloured birds with conspicuous singing behaviour. Species-specific cues should therefore be relatively conservative. However, repertoires of species with complex songs, which acquire this skill by learning, tend to diverge into local dialects. We analysed the syllable repertoire and structure of songs of a small passerine, the tree pipit (*Anthus trivialis*, Motacillidae), to compare regional and individual variability, identify conservative elements, and to evaluate which components may contribute to individual, local, and species recognition. Spectrograms of 2166 songs of 90 territorial males from five Central European populations were inspected in the software Avisoft, and the order of minimal structural song units (syllables) was described by notation allowing subsequent automatic evaluation of structural parameters (syllable richness, versatility...). We also measured frequency and temporal characteristics of songs. The studied populations partly differed in these quantitative song parameters; however, more substantial differences were observed in compositions of local repertoires. Altogether, we recognised 153 syllable types; of these, only four were found at all studied localities. These widespread syllables usually had very distinct position within songs, and may contribute to species discrimination. Despite the overall high variability of syllable use among individuals, we detected a tendency within populations to unify the beginnings of songs: typically, males started the substantial part of their songs with only a few locally common syllables; these patterns may be associated with dialect recognition. A characteristic feature of tree pipit songs is the regular occurrence of multiple repetitions of two different syllable types. Almost all males used one or a few such bi-syllable repeats in their songs but there was high individual variability, and bi-syllable repertoires among local males often differed strongly. The use of different bi-syllables may contribute to individual and neighbour-stranger recognition within populations.

## **Applied acoustics: real-time localization for studying wild primates in remote areas**

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Remote acoustic monitoring through triangulation of animal loud calls has long been used for studies of unhabituated, wide-ranging, and/or elusive (cetacean or avian) species, however this method has yet to be adopted by primatologists in census or behavioural studies. Recently, a pilot test of Cornell University's Autonomous Recording Units (ARUs) in Ugalla, Western Tanzania demonstrated the efficacy of applying this technique to chimpanzees and other primates in an open habitat. However, ARUs are designed for use in areas where batteries and data storage media can be serviced frequently, rendering the system suboptimal for primatological studies in remote regions. We report here on the design of a recording system built specifically for use in such areas. The system uses real-time localization to offer researchers the opportunity to collect observational data based on caller locations. Each recording unit consists of a miniature omnidirectional microphone attached to a radio transmitter and rechargeable battery powered by ICP Sunsei 2W solar panels. Sound signals from transmitters distributed across a study site are relayed continuously and simultaneously to a Motu-Ultralite audio-digital interface and laptop where streaming spectrographic software localizes sound origin and detects species-specific vocalizations. The system will be described and results from two pilot studies discussed. The first study was conducted in open woodland in East San Diego County using >100 playback loud calls of wild chimpanzees and bushbabies from various distances (25m - 4km) and in various vegetation types (open, closed) to test ecological variables that affect the limitations and accuracy of this new system. Results from a second pilot, conducted with habituated wild savanna chimpanzees from the Fongoli community, SE Senegal will also be discussed, with emphasis on logistical improvements to the system when deployed in a remote region. Application of this system to behavioural studies of elusive primates and conservation research are discussed.

## **Delayed onset of vocal recognition in Australian sea lion pups (*Neophoca cinerea*)**

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Parent-offspring recognition is important in species where offspring survival and development is dependant on parental care, and there is potential for confusion between related and unrelated individuals. Australian sea lions are colonial breeders with females giving birth to a single pup and nursing it exclusively for ~18 months. Mothers remain with the pup up to 14 days postpartum and then alternate prolonged periods at sea foraging with periods ashore nursing. Upon return to the colony after each foraging trip they must reunite with their pup. Both mothers and pups have individual vocal signatures. In the present study we presented unmodified vocalisations to pups at the end of the peri-natal attendance period (n=7) and at two months of age (n=10). Playbacks were of a mother's call and the call of an unfamiliar breeding female. At two months pups responded significantly more to the calls of their own mothers than to unfamiliar calls demonstrating a finely tuned recognition system. However, newborn pups could not reliably differentiate the calls of their mother from unfamiliar calls suggesting that vocal recognition had not yet developed. These findings are in stark contrast to those of Charrier et al. who found that the duration of the peri-natal attendance period in the subantarctic fur seal depended upon the time taken for the pup to learn the mother's call. Australian sea lions do not appear to learn their mother's call before being separated from their mothers for the first time, suggesting that onset of call recognition may be facultative rather than obligatory. We hypothesise that variance in colony density and female foraging patterns may have reduced selective pressures on call recognition in young sea lions, or alternatively, that another sensory system may be used for recognition in the early stage of life.

## Performance limits on bird song: timing and consequences

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A growing body of evidence suggests that limits on vocal performance may shape the expression and evolution of acoustic signal features. In the first part of this talk, I briefly summarize this evidence and discuss the temporal contexts in which performance limits may be expressed. For learned bird songs, adult song structure may be shaped in particular by performance limitations experienced during the sensorimotor phase of vocal ontogeny. A study of song learning in swamp sparrows (*Melospiza georgiana*) illustrates that birds can “calibrate” learning targets during vocal ontogeny, in order to match vocal performance capacities. For bird species in which learning is close-ended, performance-contingent features of bird song may thus provide a reliable indicator of both present-day and former quality status. In the second part of this talk, I outline some possible behavioral and evolutionary consequences of performance limits on vocal production, and present data from our studies of Galápagos finches. Variation in beak morphology, bite force, and proficiency in beak gape modulation map onto song structure, in a manner consistent with a hypothesis of vocal tract constraints on song production. Within a population of the medium ground finch, *Geospiza fortis*, birds with large and strong beaks are found to produce songs with comparatively low trill rates and narrow frequency bandwidths. Divergence of song among large- and small-beak morphs has likely facilitated an observed pattern of assortative mating by morph. Vocally mediated intra-population divergence may contribute to avian adaptive radiation.

## Pyow and hack calls of the male putty-nosed monkey (*Cercopithecus nictitans*) convey information about male identity

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Individual differences within the acoustic structure of vocalisations have the potential to inform signal receivers about the identity of the caller. Individual differences may result from the unique morphology of each individual’s sound production components, or may be the result of selection pressures, if a signal receiver perceiving the caller’s identity enhances call function. Individuals may further modify the acoustic structure of their calls as a result of experiencing the calls of other individuals. Pyow and hack vocalisations of the male putty-nosed monkey (*Cercopithecus nictitans*) were recorded from five recognised individuals within Gashaka Gumpti National Park (Northeast Nigeria). Both call types were analysed to investigate whether variance in call structure was related to the identity of the caller, or to the acoustic structure of neighbouring males. Within pyow and hack calls a selection of spectral-related parameters were found to vary significantly between individuals, and discriminant function analyses assigned both call types to the correct caller with a higher degree of accuracy than would be expected by chance. More parameters were found to vary significantly between individuals within pyows than hacks, and a higher percentage of pyows were correctly assigned to caller. No correlations were found between the acoustic similarity of males’ calls and their geographical proximity. In conclusion, this study provides the first evidence that the pyow and hack calls of male putty-nosed monkeys provide sufficient information to enable individual recognition by signal receivers, but suggests that males do not modify their calls in response to experiencing the calls of their neighbours. Findings also suggest that whilst differences in call production cannot be ruled out, the higher level of individual distinctiveness within pyow compared to hack calls is more likely to be the result of functional than anatomical differences between calls.

## **A study of cross-modal individual vocal recognition in the domestic horse (*Equus caballus*)**

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Although individual recognition is believed to be widespread across taxa, true individual vocal recognition, as opposed to discrimination based on differing levels of familiarity, has yet to be systematically demonstrated in mammals. We used a cross-modal, expectancy violation paradigm to assess whether horses were capable of individual vocal recognition. Subjects were shown an associate who was then lead behind a barrier and either a contact call (whinney) from the stimulus horse just seen (congruent trials) or a call from a second herd member was played (incongruent trials). 24 subjects were given four trials, two in which the visual cue and auditory cues were congruent and two in which they were incongruent. Subjects looked significantly longer in the direction of the speaker when the familiar calls did not match the herd member just seen, indicating that the combination violated the subjects' expectations. Thus horses appear to generate a cross-modal representation of known individuals upon seeing them, a representation containing both unique auditory and visual information. As such this study provides the first clear demonstration of individual vocal recognition in a mammal. Acoustic analysis of the source, filter and temporal features of domestic horse whinnies is being performed to determine what aspects of the call may be instrumental in this recognition.

## **Sperm whale codas at the individual level: repertoires, overlapping interactions and spatial scales**

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Sperm whales (*Physeter macrocephalus*) make short stereotyped patterns of clicks, termed codas. Codas are thought to be communicative because they are often produced in social situations. However, the difficulty of assigning vocalisations to individuals at sea has severely limited our understanding of this behaviour. We have been using new technologies, and a fortuitous feature of sperm whale clicks, the inter-pulse interval, to study codas at the individual level, and here present some of the results of these studies. We used IPIs to assign codas to individuals within a well-studied social unit and, for the first time, compare the coda usage repertoires of individual whales. Coda repertoires were indistinguishable for all unit members apart from a mother and her calf, which possessed significantly different repertoires. We suggest that the similarity among the coda repertoires of most unit members serves to signal a shared social bond. In contrast, the distinctive repertoires of the calf, and particularly its mother, may facilitate reunions between them. These results suggest that sperm whales may be able to adapt their repertoires as their reproductive status alters the trade-off between individual and group identification. Further analyses show that sperm whale coda production is influenced by the timing and types of codas produced by other unit members, resulting in the production of duet-like sequences of coda exchanges between pairs of whales. Patterns of overlapping and matching exchanges do not seem to be correlated with relatedness or social affiliation. These exchanges occur over a range of spatial scales, and are thus likely functional between whales that are both near and comparatively far from one another.

## **Beauty is in the ear of the beholder: Culture and condition affect female songbirds' mating preferences**

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Bird song is a sexually selected signal: song plays an important role in mate attraction and stimulation. Research to date has focused on the information contained in variation in males' signals and much progress has been made in this field, but little attention has been paid to possible causes of variation in preference on the receiver's side. In songbirds, male song is culturally transmitted, raising the question to which extent there is also cultural transmission of song preferences. Songbirds show substantial variation in the extent to which song is a sexual dimorphism, in zebra finches (*Taeniopygia guttata*) for example, females do not sing at all, which allows testing how song preferences are learned independently of song production learning. We combined song learning experiments with brood size manipulations that are a well tested method in this species to manipulate juvenile condition. The results show that how females respond to particular mating signals varies consistently between individuals depending on the type of songs they have been exposed to when young, on their rearing conditions and their own quality. Female mating preferences thus show substantial plasticity resulting both from cultural transmission and state-dependency of mate choice, suggesting a different role for female preferences in signal evolution than sketched by traditional models.

## **Causes and consequences of urban song divergence in the European blackbird**

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Bird species occurring in both urban and natural areas provide an excellent opportunity to study the process of speciation. Strikingly different selection pressures between for example cities and forests have arisen suddenly on an evolutionary time scale and could promote habitat-dependent trait divergence potentially influencing population dynamics. We use the European blackbird (*Turdus merula*) as a model species to investigate the process of "urban speciation". Blackbirds are very common in both urban and forest habitat, where they sing to defend territories and to attract mates. Their song consists of a low-frequency motif part followed by a more complex twitter part of a higher frequency. We compared blackbird song of six populations from three city-forest pairs and found consistent habitat-dependent song differences: city blackbirds produce motifs with higher frequencies compared to forest blackbirds. We explored whether this divergence could be explained by habitat-dependent noise conditions and/ or breeding densities. Subsequently, we investigated if the observed divergence in motif frequency has an effect on the response of territorial males in a natural context. Playback experiments were conducted in one city-forest pair using four stimulus groups that varied in motif frequency (low vs. high) as well as origin of the songs (city vs. forest). Results show that a male's response depended on its own origin (city vs. forest) in combination with both motif frequency and origin of the playback. In conclusion, in blackbirds there is habitat-dependent divergence in both sexual and fitness-related traits suggesting that reproductive divergence between urban and forest birds is gaining potential. The impact on behavioural response confirms the biological relevance of the trait divergence, although there is no straightforward indication of the emergence of a behavioural barrier to gene flow.

## **Vocal processing in the left and right hemispheres**

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The left and right hemispheres of animals process information differently and this includes processing of vocal signals. Research on a wide range of vertebrates has shown that the right hemisphere attends to variance (novel stimuli) and pays broad attention to details of stimuli. The left hemisphere attends to invariance and builds up learnt mental templates based on patterns that are repeated and predictable. Hence, the left hemisphere sets up rules based on experience and the right hemisphere avoids these rules in order to respond to novelty. The functional incompatibility of processing on the left and right sides is essential for smooth performance of behaviour since all animals face the problem of assessing whether stimuli are novel or familiar, and how familiar. The animal must attend not only to the details that mark each experience uniquely (variance) but also build up a record of repeated experiences (invariance). Although such lateralization has been studied mainly for visual responses, there is evidence that auditory perception is lateralized and that vocal communication depends on differential processing by the hemispheres. Our recent findings showing that dogs primarily use the left hemisphere to process their species-typical vocalisations, unless playback of these calls elicits fear, in which case the right hemisphere is used. The right hemisphere is also used to process the sounds of a thunderstorm. Marmosets are similar in that they use the left hemisphere for close contact/approach calls and the right for fear/mobbing calls. These results suggest that hemispheric processing of vocalisations is not simply a specialisation of the left hemisphere for conspecific vocalisations and the right hemisphere for heterospecific sounds, as Hauser found in macaques, but depends on whether the sound is processed using templates and rules (left hemisphere) or for novelty (right hemisphere), fear being more likely in the latter case.

## **Vocal relationships in the neighbourhood: neighbour-stranger discrimination and spatial categorisation of neighbours in a song bird species**

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The skylark (*Alauda arvensis*) is a territorial species of open landscape in which pairs settle in stable and adjacent territories during the breeding season. Due to the heterogeneity of the habitat, territories are gathered in patches spaced by few kilometres, in which each male produces very long and complex songs as a part of the territorial behaviour. We investigated the vocal relationships among birds established in the same patches, by making playback experiments of neighbour and stranger songs, at 3 distinct periods of the breeding season. When broadcasted from the correct boundary (i.e. the boundary separating the focus bird and the neighbour whose song was broadcasted), the two categories of songs elicit different responses at the middle of the season, when territories are well established. Behavioural responses to playbacks indicated a neighbour-Stranger discrimination consistent with the dear-enemy phenomenon, i.e. a reduced aggression toward neighbours compared to strangers. This phenomenon was not observed when the neighbour songs were played-back from the incorrect boundary, thus showing a spatial categorisation of the neighbours. Furthermore, our results showed that neighbours were not dear-enemies at the beginning of the season, when boundaries are disputed, and at the end of season when the density of birds increases after the take-off flights of young birds of the first clutch. Dear-enemy relationships are thus established over time and can be broken up due to naturally varying conditions.

## **On the song structure of an Indian endemic song bird, the Indian chat *Cercomela fusca*.**

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India has a large number of songbirds, which are known for their elaborate, complex and varied songs. Unfortunately, studies on acoustic signals of Indian birds are almost negligible. To fill this gap in the present study attempts have made to understand the physical characteristics of songs in an endemic avian species the Indian Chat *Cercomela fusca*. Study was carried out from March to July 2007 in the urban area of district Haridwar (29° 55' N and 78° 08' E; Himalayan foothills), Uttarakhand, India. Songs of 8 colour-banded males were recorded with Marantz PMD670 sound recorder & Sennheiser ME67 unidirectional microphone and spectrograms were prepared with AviSoft SASLabPro software.

Males of Indian Chat started singing in the first week of March and stopped by the end of July and songs were delivered only during the dawn. Songs of this species were highly varied and complex and consisted of a number of distinct sections called 'phrases'. Each phrase lasted for  $1.26 \pm 0.43$  s ( $n=94$ ) and consisted of a series of units called 'elements'. The number and types of elements in a phrase averaged  $6.18 \pm 2.62$  (range= 3-15) and  $3.60 \pm 1.82$  (range= 1-10) respectively. A particular phrase was repeated many times before switching over to the next one.

The minimum and maximum frequencies of phrases were found  $2.29 \pm 0.29$  and  $5.12 \pm 0.62$  kHz respectively. Preliminary observations on the song structure revealed a total of 94 phrase-types used by different individuals of Indian Chats. In song playback experiments performed in the territories of five males, a significant ( $P$  at 0.01 level) increase in song rate (no. of phrases delivered/minute) and perch changes of males relative to pre-playback levels were observed. Singing throughout the breeding period and aggressive response towards playbacks indicate the role of songs in territory establishment and maintenance. However, at the same time the possibility of the role of males' songs in mate attraction can not be overruled.

## **Relationship between movement and vocal behavior of free-ranging Norwegian killer whales**

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Though the rates of killer whale pulsed call fluctuate according to behavior state, the individual call types are generally considered to be functionally equivalent. We test this assertion using individual movement data and group calling sequences recorded with digital archival tags attached to free-ranging Norwegian killer whales. Twelve animals were tagged and seven engaged in carousel feeding, a vocally active time when herring are trapped at the surface, tail slapped and eaten. On 4 occasions, carousel feeding was preceded by a vocally active period of putative corralling involving broad looping to locate herring at depth. In contrast, in 2 of the 3 instances in which carouseling was anticipated by directional travel, the animals were silent, suggesting they may have eavesdropped to locate conspecific groups that were already feeding on herring at the surface. The recordings were then divided into two general behavioral states: tail slapping (TS) periods that coincided with carousel feeding activity and not tail slapping periods (NTS). We predicted that killer whales depended on orientation cues more during carousel feeding than other behaviors. The relative level differences between the low and high frequency components of pulsed calls may provide such an orientation cue of the signaler to the receiver. Our prediction was confirmed using a rotation test that preserved the serial dependence of the original data: more call types characterized by both components than the low component alone were produced during TS than NTS episodes in 5 of the 7 whales. Collectively, these results are consistent with the premise that Norwegian killer whales use their vocalizations to provide information to conspecifics about their 3D position and orientation as they corral and feed in groups. Additional data collected across multiple days and carousels are required to explore the possibility of more detailed relationships between movement and vocal behavior.

## **Acoustic flexibility in singing birds under noisy urban conditions**

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Birds rely on song for defending a territory and attracting a mate. However, more and more breeding areas are affected by human activities and anthropogenic noise has become almost omnipresent. Consequently, song function in and around cities, and alongside highways, train tracks and airports, is increasingly hampered by noise interference. Several counter strategies in producing sounds, related to changes in loudness, pitch, and timing, can help out under these noisy urban conditions. Observational data have yielded several interesting patterns which show remarkable singing flexibility in different species that are typically common in cities. Here I present data for a new species, the chiffchaff (*Phylloscopus collybita*), for which we collected song recordings in territories alongside a noisy highway and alongside a quiet river. We also played back a series of highway-noise recordings in the quiet territories and recorded the immediate impact on acoustic features in songs during and after experimental noise exposure. Our data show spectral and temporal adaptation which reduces masking alongside the noisy highway. The experimental data from the quiet transect reveal for the first time that a bird species is able to adjust very quickly in the spectral and temporal domain. An immediate response to exposure of highway noise via artificial playback led to consistent acoustic differences in songs sung before and after noise onset. Acoustic flexibility, as shown by male chiffchaffs in the current study, may be key to efficient use of the 'left-over acoustic space' in our modern society. It may determine whether individual birds can maintain their territory and breed successfully. Variation in flexibility among species may explain which birds will remain widespread in the noisy world of the future and which will be pushed back into 'silent' habitat pockets.

## **Wild chimpanzees modify the structure of their calls as a function of audience composition**

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We studied the vocal behaviour of wild chimpanzees of the Budongo Forest, Uganda during agonistic interactions. Previous work has shown that chimpanzees produce acoustically distinct scream vocalizations depending on their social role during agonistic interactions with other group members (Slocombe & Zuberbühler, 2005). Here, we show that victims during such agonistic interactions alter the acoustic structure of their screams depending on the severity of aggression experienced, hereby providing nearby listeners with important cues about the nature of the attack. More specifically, victims receiving severe aggression (chasing or beating) gave longer bouts of screams in which each call was longer in duration and higher in frequency than screams produced by victims of mild aggression (charges or postural threats). We also found, however, that victims modified the acoustic structure of their screams as a function of audience composition. If there was an individual present in the party, who could effectively challenge the aggressor (because he was equal or higher in rank than the aggressor) then victims produced screams that were acoustically consistent with extremely severe aggression. This vocal exaggeration of the true level of aggression only occurred when the chimpanzees most needed aid, that is when they were subjected to severe but not mild aggression. In other observations we found that high-ranking individuals most often provided aid if victims were exposed to severe rather than mild aggression, suggesting that victim screams function to recruit aid and that callers modify them in a goal-directed manner. This is the first study to show that non-human primates can flexibly alter the acoustic structure of their vocalizations in response to the composition of the audience.

## **Communication and social learning in cooperatively breeding primates**

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The study of bird song learning clearly combines vocal communication with social learning. However, the explicit use of communication signals to facilitate (or inhibit) other forms of social learning has been less frequently studied. Cooperatively breeding monkeys (marmosets and tamarins) display some examples of social learning not typically seen in other monkey species tested under very similar conditions. One possibility for the observations of successful social learning in cooperatively breeding taxa is communication between demonstrator and observer. I will discuss the role of vocal and visual signals in facilitating learning socially to avoid noxious foods, to assist infants in learning to feed independently, and in acquisition of novel skills for foraging and food extraction in both juveniles and adults. However, signals from observers may also inhibit the actions of demonstrators by actively reducing rates of food donation in prosocial tasks. Historically, before the advent of modern spectrographic techniques bird song was analyzed in musical terms. Even today we use musical terms (“notes”, “themes”, “variations” as well as “song”) to discuss bird song. Vocalizations of tamarins can also be analyzed from a musical perspective. In collaboration with composer/musician David Teie, we have tested tamarins with music composed for humans and music composed for the frequencies and tempos of tamarin vocalizations. Whereas tamarins are generally indifferent to human music, they respond differentially to tamarin “ballads” versus tamarin “rock” music. The results suggest that emotional effects of music preceded human evolution. These studies of communication and social learning in “musical” monkeys complement Peter Slater’s life work of understanding similar phenomena in birds and cetaceans.

## **The elephant roar: all about a call type associated with high emotional arousal**

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African elephants (*Loxodonta africana*) produce a variety of structurally different call types. The dominating call is the low frequency rumble which is a primarily harmonic vocalization produced in a wide range of functional contexts. The rumble seems to transmit context-, individual-, group-, age- and gender-dependent information. The roar, in contrast, is strongly associated with situations of high emotional arousal or distress and is particularly often produced by calves. We have analysed 200 roars of 11 infant elephants aged from neonatal to 18 months, recorded at the Vienna Zoo and at the Daphne Sheldricks orphanage at the Nairobi National Park, Kenya. The infant roar is characterized by a high within call type variation, but we distinguished three broad roar categories; tonal-, mixed-, and noisy roars. We documented a high amount of non-linear phenomena as for instance subharmonics, deterministic chaos and abrupt transitions between periodic and aperiodic vibratory modes within the infant roars. The amount of non-linear effects increases with the level of arousal or distress. Furthermore, we demonstrate that in situations of medium to high level of arousal, elephant calves often utter roars in combination with rumbles and thus produce more complex utterances. In these combined vocalizations, one call grades into another without an audible break, but still each call is distinctive. The elephants uttered two- and three-call combinations composed of rumbles and all three subtypes of roars. We are going to suggest that non-linear phenomena and combinative roar-rumble vocalizations exhibit communicative relevance in elephants, especially in respect of emotional state. However, playback experiments will be necessary to completely clarify the functional significance of the roar and its acoustic characteristics and variations within the elephant vocal communication system.

## **Human listeners attend to size information in domestic dog growls**

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The acoustic features of vocalizations have the potential to transmit information about the size of callers. Most acoustic studies have focused on intra-specific perceptual abilities, but here, the ability of humans to use growls to assess the size of adult domestic dogs was tested. In a first experiment, the formants of growls were shifted to create playback stimuli with different formant dispersions ( $\Delta f$ ), simulating different vocal tract lengths within the natural range of variation. Mean fundamental frequency (F0) was left unchanged and treated as a co-variate. In a second experiment, F0 was re-synthesized and  $\Delta f$  was left unchanged. In both experiments  $\Delta f$  and F0 influenced how participants rated the size of stimuli. Lower formant and fundamental frequencies were rated as belonging to larger dogs and vice-versa. Crucially, when F0 was manipulated and  $\Delta f$  was natural, ratings were strongly correlated with the actual weight of the dogs, while when  $\Delta f$  was varied and F0 was natural, ratings were not related to the actual weight. Taken together, this suggests that participants relied more heavily on  $\Delta f$ , in accordance with the fact that formants are better predictors of body size than F0.

## **Can songbirds detect recursive syntax patterns?**

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It has been hypothesized that the only uniquely human component necessary for processing language is a mechanism for recursion. However, while there has been no evidence so far that primates are able to discriminate recursive acoustic patterns from non-recursive ones, this capacity has been claimed for starlings. We examined whether another songbird species, the zebra finch, is also able to distinguish recursive and non-recursive patterns. We show that zebra finches, like starlings, are able to distinguish between simple patterns. Various tests, however, indicate that this ability is not based on a recursive mechanism, but on using simple regularities that distinguish the different patterns from each other. These might also explain the results obtained in starlings. While these results show that the cognitive abilities of zebra finches (and starlings) are impressive, it still remains to be seen whether they have the computational mechanism necessary for detecting recursion.

## **Spreading loss influences the underwater communication ranges of Weddell seals**

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Source levels of six common Weddell seal (*Leptonychotes weddellii*) underwater call types were obtained using a two-hydrophone array deployed through landfast sea ice throughout the winter and breeding season near Mawson Station, Antarctica. Call amplitudes ranged from 139 to 185 dB re. 1  $\mu$ Pa at 1 m. Many calls were >110 dB above the likely hearing threshold. In a very quiet sea, if the sound spreads in a spherical manner (dB loss =  $20 \cdot \log(\text{range})$ ), the estimated median detection distance was 7.9 km. This increased by 5 times to 45 km if the sound spreads such that dB loss =  $15 \cdot \log(\text{range})$ . If a noisy ship was nearby, the median detection ranges were estimated to be 0.35 and 4.76 km for the two spreading loss types. Passive acoustic monitoring systems will have to account for in situ transmission losses to determine the area that is being surveyed.

## **Wild chimpanzees distinguish between different scream types: evidence from a playback study**

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When experiencing aggression from group members, chimpanzees commonly produce screams. These agonistic screams vary acoustically as a function of the severity of aggression the caller is facing. We devised a methodological protocol allowing us to conduct a series of field playback experiments with a community of wild chimpanzees in Budongo Forest, Uganda, to determine whether individuals could meaningfully distinguish between screams given in different agonistic contexts. We compared subjects' responses to screams given in response to severe and mild aggression. Subjects consistently discriminated between the two scream types in ways that indicated that they assigned meaning to these calls. In order to control for the possibility that the observed response differences were driven directly by the screams' peripheral acoustic features rather than any attached social meaning, we tested the subjects' responses to a control stimulus. We used tantrum screams, given by individuals that experienced extreme social frustration, but no physical threat. Acoustically, tantrum screams matched severe agonistic screams, although they conveyed very different information, and accordingly subjects showed little interest in these calls. Together, these results demonstrate that chimpanzees are able to extract discrete semantic content from screams, despite the fact that this call type is acoustically highly graded. We therefore suggest that by attending to conspecific calls, chimpanzees can understand the nature of social events they cannot see.

## **Use of vocal production learning to compensate for varying noise or competing signals**

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Many animals hear well enough that their ability to detect a call is limited by ambient noise. These species face a problem of signal detection in varying noise, and many have evolved communication mechanisms to compensate for noise and competing signals. Some of these compensation mechanisms may involve the receiving animal, but others may also involve changes in the vocal behavior of the signaling animal. Potential mechanisms for the signaler to increase the detectability of signals include (1) waiting to call until noise decreases, (2) increasing the rate of calling, (3) increasing signal intensity, (4) increasing the signal duration, and (5) shifting signal frequency outside of a noise band. Even though auditory input modifies the timing of vocal behavior in the first two of these mechanisms, they do not involve production learning by the definition of Janik and Slater (2000) because they do not involve modification of the acoustic features of vocalizations. Janik and Slater (2000) suggest several different levels of complexity in production learning. Variation in the amplitude or duration of a signal may stem from relatively simple changes in the respiratory system. By contrast, variation in frequency parameters of a signal may require more complex changes of the sound production apparatus, including acoustic filters. The last three mechanisms to compensate for noise do qualify as vocal production learning by this definition, with the exception that some may not require hearing signals from other individuals. I will review data from birds and mammals on all of these mechanisms. The problem of communicating in noise or competing signals is ubiquitous and similar enough to classic cases of vocal production learning that I suggest that the role of noise compensation mechanisms may have been underestimated in discussions of the evolution of vocal production learning.

## **Syntax detection by a songbird, the zebra finch (*Taeniopygia guttata*)**

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According to a controversial hypothesis by Hauser, Chomsky and Fitch (2002), recursion is the only characteristic that is unique to human language. Contradicting this hypothesis, Gentner et al. (2006) showed that starlings are able to distinguish between starling songs with and without a recursive structure, unlike non-human primates. In this experiment, we tested zebra finches, another songbird species, for this ability. Like Gentner et al., we used a go/no-go procedure and zebra finch song structures, but added an extra phase and additional tests for the possibility that the birds used simpler rules to distinguish between the song structures. The song structures were constructed of four elements each and elements were selected from four element categories of natural zebra finch song. Eight zebra finches were trained in a go/no-go procedure during several phases. After reaching criterion performance for a specific phase, the birds were abruptly transferred to the next phase. All tested zebra finches learned to discriminate between the different song structures and were able to generalize this to new songs consisting of new elements of the same categories. One even showed generalization to new element categories. This zebra finch was therefore able to discriminate on some differences between the songs structures with and without recursion. However, additional testing showed that this bird used a simpler, non-recursive rule instead of the property of recursion. Therefore, it still remains to be seen whether zebra finches have a computational mechanism that is able to detect recursion. Still, the perceptual ability they showed here is surprising, and indicates that a songbird species lacking complex and variable songs can be highly sensitive to song structure.

## **Identification, usage, and ontogeny of contact calls in belugas (*Delphinapterus leucas*)**

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Contact calls are ubiquitous in social birds and mammals. Belugas are among the most vocal of cetaceans, but the function of their different calls remains a mystery. As a species with high mobility and long-term associations between individuals, we would expect belugas to use a system of discrete contact calls clearly identifiable over long distances. We examined context specific variation in vocalizations of six captive belugas at the Vancouver Aquarium, and identified a particular stereotyped call type that seems to fit the above prediction. This call type has several variants within a common template, and comprised 46% to 100% of the vocalizations during events such as re-union of animals that had been separated, and voluntary or forced isolation. In contrast, this call type comprised only 2% of the vocalizations produced during randomly selected regular sessions. Up to 73% of contact calls were produced in exchanges where a call elicited an immediate response of the same type. One variant was used primarily by an adult female in vocal exchanges with her male calf. His juvenile half-sister utilized the same variant. Some of the calf's calls underwent a progressive loss of variability from birth until 20 months, by which time he was producing a fully stereotyped rendition of his mother and sister's contact call. We used our findings to generate testable predictions about the usage of these signals by wild belugas. We verified, in two wild beluga populations, the existence of signals that match, aurally and spectrographically, the contact calls found in captivity. In Hudson Bay, these were emitted by a temporarily restrained animal; in the St. Lawrence, by an adult female keeping her dead calf afloat. We propose that these calls function in nature, as in captivity, to maintain group cohesion, and that females and their calves share variants used for recognition.

## **Song variation of thrush nightingales in allopatry and sympatry with a hybridising congener**

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Bird songs are often crucial for mate selection and maintenance of pre-mating reproductive barriers. When closely related and partially reproductively isolated species come into secondary contact, natural selection may enhance song divergence to avoid maladaptive hybridisation between the species. Alternatively, copying of heterospecific songs may lead to song convergence, increasing the rate of hybridisation and blurring the species boundaries. A model species suitable for studying these phenomena is the Thrush Nightingale (*Luscinia luscinia*). In the secondary contact zone with its congener, the Nightingale (*L. megarhynchos*), an interspecific hybridisation as well as song convergence has been documented. A substantial part of apparent Thrush Nightingale males in the sympatric region were reported to include in their repertoires phrases copied from the other species; this may be caused either by erroneous learning of juvenile individuals or by copying from territorial neighbours in adulthood. However, the genetic background of these “mixed singers” was not examined, and nothing is known about the singing behaviour of hybrid or backcrossed individuals. We study these two nightingale species in the project focusing on the impact of hybridisation and introgression on the phenotype, ecology, and vocalisation of closely related birds in the secondary contact zone. In the first part of the bioacoustic study, we test whether song characteristics of sympatric Thrush Nightingale males (from southwest Poland) are indeed more variable than those from allopatric populations (northern Poland and Finland). Song recordings are analysed in Avisoft SASLab Pro; we compare temporal, frequency and structural characteristics of the songs as well as repertoire composition. These results will be subsequently compared with the patterns revealed by genetic markers. Similar analyses are planned also for sympatric and allopatric nightingales.

## **To what extent do high frequency calls minimize the risk from eavesdroppers for African wild dogs?**

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The risk from eavesdroppers means there is a potential cost to any vocalization, e.g. wild dog calls risk attracting lions and hyenas. Yet wild dogs obligate sociality is maintained in part by greeting ceremonies involving extensive vocalizing behaviour. Wouldn't such rituals be more safely observed in silence? Marten (1980) speculated that wild dogs' extensive use of high frequencies in such ceremonies might represent an adaptation to minimize this risk. We used playback experiments over 100m to investigate whether lions or hyenas can detect and recognize playback of wild dog calls (versus control recordings of bird calls) and whether they were subsequently attracted to these calls. Lions approach playback of wild dogs (vs. control bird calls) (Fisher's exact test: N=29, p=0.0019). Hyenas less inclined to approach wild dog calls (vs. control bird calls) (Fishers exact test: N=20, p=0.22) and so are significantly less likely than lions to approach wild dogs (Fisher's exact test: N=30, p=0.003). At least over relatively short distances, lions recognize and appear highly motivated to approach wild dog calls despite their use of high frequencies (inconsistency in the hyenas' responses may be because, rather than seeking to kill wild dogs, hyenas may only seek out wild dogs when looking for scavenging opportunities). Furthermore, wild dogs' high frequency calls are typically emitted concurrently with a separate lower fundamental frequency, seemingly negating their postulated adaptive function. However our experiments were conducted over the relatively short distance of 100m and other experiments revealed 400m probably represents close to the maximum transmission distance for these calls, lower frequencies included. Since the vital pre-hunt unification of a pack may not be efficaciously achieved without a specifically audio rallying cue, wild dog greeting ceremonies appear to represent a trade-off between the need to communicate and the need to avoid detection.

## **Call sharing across vocal clans of killer whales: evidence for vocal imitation?**

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Killer whales or orcas (*Orcinus orca*) produce group-specific dialects that differ both in repertoire as well as in the structure of shared call types. The production of calls belonging not to the own but to another group's repertoire has been observed in captive as well as free-living orcas. However, reports were largely anecdotal and neither the structure nor the usage of such «copies» has been investigated in detail. We analyzed occurrence and structure of call copies in free-living orcas when groups known to produce the respective call types were absent during recordings and copies could thus clearly be identified as such. In this context, copies were rare and made up only 0.2% of ~ 7400 calls recorded. Time and frequency characteristics of copies differed significantly from the respective "original" calls, but were more similar to the original than to other call types. The accuracy of the copies varied and ranged from rough renditions of a call type to the resemblance of call subtypes. Our results show that sharing of calls across vocal clans occurs in orcas but is rare and that copies are readily distinguishable from original call types in the absence of the copied groups. We suggest that the observed call sharing represents cases of vocal imitation as proposed by previous anecdotal reports.

## **Individual- and family-specific information in greylag gosling (*Anser anser*) vocalizations.**

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In precocial birds, early recognition among family members is of crucial importance and appears to be accomplished via learned recognition of social rather than genetic parents and siblings, probably using visual as well as acoustic information. In the long-term monogamous, biparental greylag geese (*Anser anser*) individual recognition is a prerequisite for complex social relationships, including social support in agonistic interactions, clan structures and an understanding of third party relationships. To study the development of individual- and family-specific information in greylag goose vocalizations we hand-raised three social groups of greylag goslings with six, six and seven individuals, respectively, from five different nests collected in the wild. We recorded three different calls (distress, greeting and sleepy call) from each individual within twelve hours after hatching and every five to seven days thereafter. We measured time and frequency parameters of the three call types and analyzed at what age individually-specific information emerged as well as if and how this information differed between call types. Furthermore, we compared the similarity of calls from genetic as well as social siblings throughout development. We discuss the implications of our data for the development of social relationships in a precocial bird species. Funding was provided by the FWF (P18 601-B17), the Verein der Förderer der KLF, and the Herzog-von-Cumberland Stiftung.

## **Limits on the independent vocal behavior of the right and left syrinx during two-voice phenomena**

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The vocal organ in songbirds is a bipartite tracheobronchial syrinx, with an independently innervated sound source at the cranial end of each primary bronchus. The syrinx has been demonstrated to have the capacity for varying degrees of bilateral independence during song production. However, the extent to which the two sides of the syrinx are truly independent is not well understood. Several constraints could limit a songbird's ability to produce different, unrelated sounds simultaneously from the two sides of the syrinx. In this study we exploit the propensity for heterospecific mimicry in northern mockingbirds to test assumptions about the independent control of the two sides of the syrinx. We tutored juvenile mockingbirds with computer-synthesized "two-voice" sounds designed to test the limits of two-voice vocal abilities. Our data show that although the phonatory behavior of the two sides of the syrinx is theoretically independent, two-voice song production in mockingbirds is limited both in the absolute frequency difference and the degree to which the two voices can be independently modulated, as compared to the capacity of either side when vocalising alone.

