

# Contributed presentations NVG meeting Soesterberg 2010

## Twitter evolution: Brains for birds and brats

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Vocal imitation, an important prerequisite for the evolution of spoken language (speech), is shared with certain marine mammals, parrots, hummingbirds and songbirds, but appears to be absent in non-human primates. There are striking behavioural similarities between auditory-vocal learning in human infants and in songbirds. In both cases, auditory learning takes place during a sensitive period early in development, and there is a transitional period of early vocalisation which is called 'babbling' in humans and 'subsinging' in birds. There are also analogies with regard to the neural organisation of auditory memory and vocal production, genetic mechanisms underlying vocal learning and basic rules of syntax. Different orders of birds evolved a gross-anatomically similar network of brain regions for song learning and production, with analogies to human cortical regions and basal ganglia. Comparisons between different songbird species and humans point towards both general and species-specific principles of vocal learning and have identified common neural and molecular substrates, including the FOXP2 gene. Taken together these findings suggest neural homologies as well as evolutionary convergence of behaviour and cognition between humans and songbirds.

## Structural and functional changes between seasons in the songbird auditory forebrain

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The song control system of seasonal songbirds shows remarkable seasonal plasticity. Male starlings (*Sturnus vulgaris*) sing throughout the year, but in the breeding season, when concentrations of testosterone are elevated, the song is highly sexually motivated. We investigated both structural and functional seasonal changes in regions involved in auditory processing. Using in vivo Diffusion Tensor Imaging (DTI), we measured in breeding and non-breeding seasons volume and tissue characteristics of several brain regions of nine adult male starlings. We demonstrate that the songbird brain exhibits an extreme seasonal plasticity not merely limited to the song control system (SCS). Volumetric analysis showed seasonal telencephalon volume changes and more importantly also a volumetric change in the caudal region of the nidopallium (NCM), a region analogous to the mammalian secondary auditory cortex. Using functional Magnetic Resonance Imaging (fMRI) we measured the seasonal changes in auditory processing of behaviourally relevant social stimuli. We recorded brain responses to songs that correspond to clear and distinct classes of sounds with different functions and social values. This allowed us to test for potential differential responses in the brain of adult male starlings and for a possible correspondence between these responses and the functional aspects of songs. This study extends our view on a seasonally dynamic

avian brain which not only hones its song control system but also auditory in order to be prepared for the breeding season.

## Are natural testosterone levels in female blue tits (*Cyanistes caeruleus*) adaptive?

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Although testosterone (T) has predominantly been perceived as a male hormone, female birds also have detectable testosterone (T) levels. The discrepancy between the sexes in T-levels is fuelling the debate about the function of female T and antagonistic sexual selection. Previous studies, finding detrimental effects of female T, used supra-physiological levels over extended periods in which T-levels normally return to baseline, questioning the biological relevance of such studies. We manipulated T-levels in free-living female blue tits within the physiological range for only a short period, just prior to egg laying, coinciding with the natural elevation of T. In others we blocked the androgen receptors and a third group was sham-treated. We did not find detrimental effects of female T as reported in the above mentioned studies. Instead, T stimulated nest building and territorial behaviour. These preliminary data do not support the antagonistic sexual selection hypothesis but suggest that physiological levels of T in females may be adaptive.

## Insights into worker policing in the honeybee *Apis mellifera*

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The social insects are famous for their intriguing communication systems, sophisticated colony organization, and highly cooperative behaviour to the extent that the most advanced of them are sometimes referred to as superorganisms. Yet, these seemingly perfectly harmonic eusocial societies bear potential for conflict, e.g. over male parentage in that workers usually are capable of producing unfertilized eggs which will develop into males, thereby competing with each other and the mother queen for the production of male offspring. In the honeybee, however, only very few workers try to reproduce in the presence of the queen, due to a very efficient policing mechanism, whereby over 99% of worker laid eggs are removed by other workers. This worker policing behaviour, being first described in the honeybee, *Apis mellifera*, and subsequently found to be effective in ants, wasps and Asian honeybees, has become a textbook example of kin selection. Despite numerous studies on policing in

general, relatively little effort has been put in detailed behavioural observations. Here, we provide insight into the organization of worker policing by following cohorts of individually marked bees inside an observation hive. We show that policing bees vary in age between 10 and 36 days, the average being 21 days. Additionally, there was a large variation in the amount of policing carried out by different individuals, which suggests that some bees are specializing in policing. Genetic analysis revealed that bees from different patriline police to different extents, which again points to specialisation in this behaviour.

### **Better Safe than Sorry – An Agent-based model Concerning Mechanisms of Socio-Spatial Organisation in Primate Groups**

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In primates the spatial organisation of group members often reflects the dominance structure, with central dominants and peripheral subordinates. It has been shown earlier that this socio-spatial pattern can arise by self-organization as a result of subordinates fleeing from dominants after a fight (fleeing model). However, in real primates subordinates often prevent aggression by spatially avoiding potential aggressors (dominants) already at a distance. Using an agent-based model, we investigated how avoidance may affect the central-peripheral pattern within primate groups. Adding avoidance to the basic fleeing model reinforced the central-peripheral group structure and resulted in more spread out groups. Moreover, individual variation in avoidance tendency is already sufficient to generate spatial centrality of dominants, independently of fleeing after a fight. Not only spatial dyadic distances between potential interaction partners do determine the encounter rates in the model; avoidance appears to be crucial for who encounters whom how often. A high degree of avoidance, e.g. in highly aggressive species, may result in subgroup formation and even break down the spatial centrality of dominants.

### **What does it take two tangoing tits to avoid disturbance by urban noise?**

*Halfjiverk W. & Slabbekoorn H.W. (IBL, Leiden University)*

Cooperation between males and females during the breeding season can dramatically increase a pair's reproductive success. However, the costs and benefits of raising young together differ between the sexes and the pair-members therefore have to communicate to reach some sort of agreement on their individual investments. Many socially monogamous species use sounds for within-pair communication, which may have a function in reducing conflict and increasing cooperation between pair members. Unfortunately, the world is getting more and more polluted by human-generated noise, which may interfere with evolved communication mechanisms that underlie reproductive cooperation. We studied within-pair

communication in the great tit (*Parus major*) across the egg-laying period when males and females spent a lot of time interacting. Males sing towards their mate's nestbox at dawn and females respond by calling. This dawn chorus ritual peaks at the start of egg-laying and is related to sexual promiscuity and possibly (future) parental investment. Next, we exposed females to artificial traffic noise inside the nestbox, while leaving the singing male unaffected, to test whether the within-pair communication was disrupted. Our results showed that birds rapidly adjust their behaviour to maintain contact, suggesting that within-pair communication is robust and does not suffer from urban noise disturbance.

### **Maternal care and selection for low mortality influence mineralocorticoid receptor levels and behavior in laying hens**

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Feather pecking is a major welfare problem in laying hen husbandry indicatively caused by underlying genetic components and early-life environment. Selection experiments resulted in a low mortality line (LML) and control line (CTL). Studies have shown behavioral and physiological differences between LML and CT. Sociability, fearfulness and neuroanatomical alterations are potential markers of animal welfare. Interactions between genetic selection, absence or presence of maternal care on Mineralocorticoid Receptor levels, and behavior were studied in the selection lines. Brains from second generation LML and CTL, reared with or without maternal care, were collected at 40 weeks of age and immunocytochemically stained for MR. No differences were seen between selection lines in MR expression. Brooding hen presence lead to MR lateralization in the nidopallium caudolaterale, and a trend to increased MR levels in left hemisphere nidopallium caudolaterale. No differences were seen in the hippocampus. At 1-4 weeks of age, behavior of fourth generation LML and CTL was studied in T-maze tests and human approach tests. At 12-16 days LML spent more time with conspecifics and showed a significant learning curve in the amount of time to find conspecifics in the T-maze, whereas CTL did not show a learning curve. At 26 days LML had shorter latency to approach in human approach tests. Thus, brooding hen presence during rearing period leads to increased MR expression in the left hemisphere and increased MR receptor lateralization in later life. Selection for low cannibalism in laying hens leads to

increased sociability and reduced fearfulness at young age.

### **Aerial displays of thousands of starlings: causation of flock shape and density**

*Hemelrijk, Charlotte K., Hildenbrandt, Hanno.*

Aerial displays of starlings (*Sturnus vulgaris*) at their communal roosts are complex: they consist of multiple flocks of thousands of individuals which are continually changing shape and density, while splitting and merging. Unlike fish schools, their density does not depend on group size and groups are seldom oblong. These traits are still obscure: It is neither known what causes the variability of flock shape nor the low occurrence of an oblong shape nor why groups of different sizes have similar density. In the present talk, we will provide explanations for these phenomena using a model of self-organised flocks of starlings, called StarDisplay. Flocking patterns in StarDisplay greatly resemble those of real starlings. By omitting each factor in turn, we will show that variability of group shape depends on many traits, i.e. on attraction to the roost, aerodynamics and banking while turning, the low number of interaction partners (typical of starlings) and on large flock size. The rare occurrence of an oblong shape and similar density of flocks comprising different numbers of individuals is mainly due to the low variability of speed. We explain the biological advantages of low variability of speed.

### **Bold to be shy: unexpected response to playback in great tits with personality**

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Animal personality refers to consistent individual differences in behaviours across time and in different contexts. Many studies have used an exploration score, from relatively shy to very bold, based on a standardized indoor test to reveal correlated outdoor behavioural variation among individuals. Although performance in interpersonal relationships forms a core topic in personality research in humans, very few studies have addressed personality in animal interactions under natural conditions. We tested great tits (*Parus major*) that were characterized as being more shy or bold on how they responded to a simulated territorial intruder through a playback experiment. Surprisingly, we found shy males to approach the speaker closer and respond longer than bold birds. Furthermore, shy birds also sang differently from bold birds in switching less between different song types, which is a singing style regarded to be more bold. We will also come up with a bold explanation.

### **How hens cope with changes in social density and group size**

*Paul Koene*

High density and large group size have strong impacts on physiology and behaviour and consequently on

health and welfare of farmed animals. Effects of social density and group size on vocalisation and behaviour of laying hens selected for high or low immune response on Sheep Red Blood Cells (SRBC-lines) were measured. Subsamples of 60 laying hens were pretested for differences in tonic immobility and open-field behaviour. They were tested repeatedly in 25 crossed combinations of group size (2, 4, 6, 8, and 10 birds) and density (1, 3.2, 10, 17.8 and 31.6 hens/m<sup>2</sup>) during tests of 15 minutes. Using behavioural sampling, all vocalisations and behaviours were measured. Data reduction was done using factor analysis. With a polynomial GLM the relations between factor scores of vocalizations and overt behaviour, density, group size and SRBC-line were analyzed. Tonic immobility duration of the SRBC-lines (High 310 sec vs. Low 626 sec;  $p < 0.001$ ) may indicate differences in coping style. The four factors extracted from the test variables - with highest loadings of chasing, preen, ground pecking and contact call - were labelled Aggression, Comfort, Pecking and Calls. A significant negative linear relation between Comfort and social density was found ( $B = -1.74$ ,  $P < 0.001$ ). Also a negative relation was found between Calls and group size ( $B = -0.62$ ,  $P < 0.001$ ). No interactions between social density or group size and SRBC-line were found. Although the frequency of behaviours and vocalizations differ between SRBC-lines, the absence of interactions between SRBC-line and density or group size indicates that the SRBC-lines cope in the same way with increases in social density (less Comfort) and group size (less Calls). Keywords: coping style, welfare indicator, density, group size, laying hen

### **The long-term memory in willow warblers (*Phylloscopus trochilus*): Never fly into the same mist-net twice.**

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Capability of animals to remember events over long time periods is widely discussed. However, the experimental evidences of the long-term memory, especially in small passerine birds, are scarce. In this study we bring the evidence that a single event – capturing into mist-net – can be remembered by the willow warbler males within the time span of a year at least. During the breeding season 2010 we tried to lure 25 naive (not captured before) and 27 re-trapped (already banded from previous years) willow warbler males into the mist-net using song playback. We noted the latency to capture. If we did not capture the male within 10 minutes, the trial was classified as unsuccessful. Naive males were easy to lure into the mist-net in comparison with the re-trapped males (96% to 33% of successful trials respectively). However, when we tried to re-trap 18 of the naive males later in the season (within 30 days after the first capture), the rate of successful trials decreased also to 33%. This suggests that the decreased responsiveness

of re-trapped males is not caused by the potential difference in age between the naive and the re-trapped males, but that it rather results from the capture event itself. We further focused on the re-trapped males which were successfully captured. We found that the latency to capture was significantly longer for the re-trapped males than for naive males. This suggests that even the successfully mist-netted re-trapped males anticipated the danger associated with the presence of the mist-net.

### **On the evolutionary potential of (hormone-mediated) maternal effects: Heritable variation in and early environmental effects on yolk hormone deposition**

*Wendt Müller (University of Antwerp), Vivian Görlich (Linköping University), Jonas Vergaunen (University of Antwerp), Ton G.G. Grootbuis (University of Groningen) and Marcel Eens (University of Antwerp)*

Maternal effects – although representing examples of non-genetic inheritance – do require a genetic basis. To be more precise, their inheritance depends on the genetic basis of the maternal trait that generates phenotypic effects in offspring and on the genetic constitution of the responding offspring. One important maternal trait that significantly modulates offspring development is the deposition of maternal hormones in the yolk of bird eggs. However, little is known on the genetic basis of yolk hormone deposition, although such knowledge is crucial for our understanding of the selection on and evolution of hormone-mediated maternal effects. Furthermore, we currently lack knowledge on the mechanisms of yolk hormone deposition. One of the most central questions is whether and how the deposition of yolk hormones is coupled with the levels of these hormones in the maternal circulation, which has again significant implications for the evolution of hormone-mediated maternal effects. The testosterone response to gonadotropin-releasing hormone (GnRH) has recently been suggested to be an important link in this process. We will present estimates of the heritability of yolk testosterone deposition in captive canaries and show the potential of the (early) environmental conditions to inflate the heritability estimation. We also investigated the GnRH-dependent link between yolk and plasma testosterone concentrations in female canaries of which the embryonic exposure to yolk testosterone had been experimentally manipulated. This allowed us to study not only processes involved in yolk testosterone deposition, but also potential mechanisms underlying long-lasting hormone-mediated maternal effects.

### **Comparative vowel perception: Are birds like babies?**

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Different vowels in human speech differ in several acoustic features. A major question in speech perception concerns whether the different acoustic features are weighted differently ('acoustic cue weighting') when distinguishing between vowels. Human infants for instance, are more sensitive to low frequency components when discriminating speech. Unclear is the origin of such biases: are they linked to experience with speech and unique to humans or not? We provided zebra finches and human adults with the same task of distinguishing words incorporating vowels differing in several formant frequencies. We show that they both exhibit a highly similar acoustic cue weighting bias. In contrast to human infants, both zebra finches and human adults pay more attention to high frequency components. Our results demonstrate that cue weighting is not a uniquely human feature and thus need not be closely linked to experience with speech in general or with vowels in particular. We suggest that both humans and zebra finches are born with specific perceptual biases, which at least for humans might shift developmentally, perhaps as a result of their acoustic environment.

### **Learning how to eat like a pig: effectiveness of mechanisms for vertical social learning in piglets**

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This study investigated which mechanisms of learning from the mother about foraging are important in piglets. The first experiment compared observation versus participation with the sow during eating. Piglet pairs could observe or participate with the sow eating a flavoured feed in a test room for 10 minutes/day during five days. Piglets that could eat food without cues from the sow and control piglets that had cues nor food were exposed to the test room with their sow without food. Piglets were then tested during three days for 1 ½ hour/day and could choose between flavoured food eaten by the sow and another flavoured food. Observation and participation piglets showed the shortest latencies to eat and higher consumption and preference for the flavour eaten by the sow than control and eat without cues piglets. The second experiment compared local versus stimulus enhancement. Piglets observed the sow eating a flavoured feed from one of two feeders on different sides of the room for 10 minutes/day during five days. During the test phase there was a match or mismatch between the location and the flavoured food that the sow was eating. Match piglets ate sooner from both feeders than mismatch piglets and ate longer and more from the feeder where the sow had fed. Consumption of and behaviour towards the sow flavour did not differ between treatments, suggesting that piglets

prioritized information of stimulus over location. Observation, interaction and stimulus enhancement are thus important ways for piglets to learn from the sow.

### **Auditory fMRI on songbirds: Establishment, Validation and First applications**

*Colline Poirier and Anemie Van der Linden (Bio-Imaging Lab, University of Antwerp)*

Speech is a unique characteristic of human beings playing a crucial role in our human everyday life. Auditory impairments can limit or even worse, prevent speech comprehension and as such, represent a major deficit for concerned people, affecting their social integration. Understanding how human brain processes auditory information in general and speech in particular is thus of crucial importance. Some aspects of human brain processing cannot be directly investigated on human beings for ethical reasons, and animal research is still necessary. Songbirds are up to now the best-developed animal model of human speech learning. However, like for other animal models, songbird neuroscience research is mainly based on electro-physiological recordings. The lack of direct link between electro-physiology and fMRI, a major tool in human neurosciences, diminishes the translational value of animal research to human beings. The use of fMRI on animals, in addition to traditional electro-physiological techniques, has the power to circumvent this limitation. The goal of this talk is to describe the establishment, the validation and the first applications of auditory fMRI on songbirds.

### **Emergence of coalitions in a model**

*Ivan Puga-Gonzalez & Charlotte K. Hemelrijk. University of Groningen, the Netherlands*

In most primate societies individuals help others in fights by forming coalitions. Since supporting another involves risks, it has been argued, for instance in the theory of reciprocal altruism, that a supporter should receive a benefit in return (e.g. support or grooming). Evidence for reciprocation of support and its exchange for something else has indeed been found in several primate studies. However, the cognitive processes underlying reciprocation and exchange are debated: they may involve record keeping or simpler cognitive processes. What simple processes may suffice is still an open question. In this study, we show that patterns of coalition may emerge by self-organization in an individual-based model. In the model, GrooFiWorld, individuals group and when meeting each other they decide whether to fight, groom or rest, but they do not intentionally form coalitions. Yet, in our model we observe coalitions when two individuals, one after the other, attack the same victim by coincidence. Moreover, reciprocation of support and its exchange for grooming appear to emerge as a side-effect of the combination of attack being risk-sensitive and the spatial configuration of individuals. Our model shows that little cognition is needed to generate these coalition patterns. The model

can be used as a null-model for the generation of hypotheses to be studied in real primates.

### **Interactions Between Behaviour And Genetics In Wild And Domestic Bird Populations**

*T.B. Rodenburg (ABGC, Wageningen University), K. van Oers. (Department of Animal Ecology, NIOO)*

Personality traits can be favoured by both natural and artificial selection, if they result in increased fitness or productivity, and therefore play an important role in both wild and domestic populations. Here, we review how personality traits affect and are affected by natural and artificial selection by focusing on studies from both wild and domestic bird populations. Further, we will also explore how artificial selection affects personality and fitness traits in a domestic population. We will use the great tit (*Parus major*) and the laying hen (*Gallus gallus domesticus*) as our model species. When comparing the studies on behaviour genetics in great tits and laying hens, it is fascinating to see that two fields of study that seem quite far apart have so much in common.

### **Handedness in a pre-industrial society challenges the fighting hypothesis as an evolutionary explanation of left-handedness**

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In past and present human societies right- and left-handers have coexisted with left-handers always being in the minority. Left-handedness is substantially heritable and has been associated with fitness costs (such as reduced lifespan). Its continuous presence in the population therefore indicates benefits associated with left-handedness. It has been proposed that left-handers have an advantage during fights and are subject to negative frequency dependent selection. This fighting hypothesis is supported by studies showing that in interactive sports the percentage left-handers is significantly increased. Furthermore a cross cultural study showed that populations in which homicide rates were high, the frequency of left-handers was also increased. However measurements of handedness in the population with highest recorded left-handedness was either based on film material not intended for laterality research or on indirect measures only. Therefore, we measured handedness in one of these pre-industrial societies in a more direct and detailed way. We measured preference of hand-use in 11 tasks such as knife use in 621 individuals. Furthermore we measured hand skill using a peg-board task and a ball throwing task. All tasks were validated in a study on a student population in The Netherlands. We found extreme low levels of left-handedness in this

society. This can not be explained by a change in selection pressure due to the recent abandonment of war fare in this population as we found no relationship between handedness and age. This undermines the fighting hypothesis.

### **Sexual stimulation accelerates reproductive senescence in three-spined sticklebacks**

*Mirre Simons, Ton Grootbuis, Simon Verhulst (all Behavioural biology, University of Groningen)*

The disposable soma theory predicts that organisms invest in reproduction at the expense of investment in somatic maintenance, which accelerates senescence. We investigate this trade-off in individually housed male three-spined stickleback. Under a constant long photoperiod nest building activity was monitored daily for 24 weeks. Reproductive potential was measured as the period that individual sticklebacks could maintain nest building activity. We show that the length of this reproductive period is sensitive to senescence. A group of stickleback that aged one year under lab conditions seized nest-building activity sooner than a younger control group. To experimentally test the disposable soma theory we increased reproductive effort in two ways. Either via increased sexual stimulation by the daily presentation of a conspecific female or via stimulation of nest building by daily nest destruction. Only sexual stimulation increased senescence resulting in a shortened period of reproductive activity. We expect female stimulation to have increased 11-keto-testosterone increasing sexual colouration and possibly other costly androgen dependent traits. This possibility was confirmed by elevating 11-keto-testosterone experimentally using hormone injections which reduced the duration of nest-building activity compared to controls. Future directions are to map out the possible traits involved in this trade-off. These include hormone levels, nest size, growth, oxidative stress and sexual colouration.

### **Costly begging for extra milk in domestic piglets**

*Špinková, M., Illmann, G., Haman, J., Šimeček, P. and Šilerová, J.*

In domestic pigs about 20 % of nursing episodes end without milk transfer (non-nutritive nursings, NNNs). The function of NNNs has not been satisfactorily explained yet. Here, we suggest that NNNs may be a part of an honest signaling system that enables the sow to provide more frequent nutritive nursings (NNs) to those litters that can prove their need through exceptionally frequent milk ejection solicitations. We further propose that the system is kept stable by the accelerating costs attached to the solicitation in the form of non-nutritive nursings. Based on this hypothesis, we predicted that (P1) with an increasing number of all nursings (ALL= NNNs + NNs) the number of nutritive nursings (NNs) should increase and that (P2) with an increasing number of ALL the proportion of NNNs should increase. We tested P1 and P2 using a meta-analysis applied to data from eight

studies (n=203 sows) that recorded the number of NNs (n=8993) and NNNs (n=2208) in domestic sows for periods of 6 to 24 hours. We confirmed both P1 (NNs increasing with ALL,  $p < 0.0001$ ) and P2 (proportion of NNNs increasing with ALL,  $p < 0.0001$ ). In combination, these results show a steeply accelerating cost of each additional nutritive nursing that piglets instigate and that this sets limits to their ability to solicit higher maternal investment through more frequent nursing solicitations.

### **Effects of predation on social behaviour and neuroanatomy in the guppy**

*William T. Swaney, Maria-José Cabrera-Alvarez, Susie E. Henlett & Simon M. Reader. Behavioural Biology, Utrecht University, Utrecht, The Netherlands*

Shoaling is a basic social behaviour in many fish species which is thought to reduce predation risk by increasing rates of predator detection and increasing confusion in potential predators. We studied shoaling in two populations of guppy (*Poecilia reticulata*) that have undergone divergent predation pressure over recent years in order to investigate the neural mechanisms regulating social behaviours in these fish. Burgers Zoo (Arnhem, NL) houses a large feral guppy population, derived from domesticated guppies, which have been extensively preyed upon by resident birds for 20 years. A comparison of shoaling and predator inspection behaviours in feral and domestic guppies demonstrated that feral guppies spend longer in close proximity to a conspecific shoal than do domestic guppies, both in the presence and absence of a predator threat. These feral fish also have reduced numbers of vasotocin neurons in the preoptic area of the brain. Vasotocin is the teleost homologue of the neuropeptide vasopressin which is involved in the regulation of diverse social behaviours in mammals. These data suggest that this neuropeptide family's role in the regulation of social behaviours may have ancient evolutionary origins.

### **The role of predispositions and experience in song acquisition**

*Sita ter Haar (Behavioural Biology/ LIBC/ LUCL, Leiden University), Wiebke Kaemper (Behavioural Biology, Leiden University), Clara Levelt (LIBC/ LUCL, Leiden University), Carel ten Cate (Behavioural Biology/ LIBC, Leiden University)*

Language and birdsong both show population specific and universal sound patterns. The population specificity can be explained by cultural transmission, whereas the universals suggest a predisposition. During the acquisition process, variation may be realized as a result of experience (i.e. cultural transmission), while due to predispositions some sounds are favored over others, resulting in universals. Here we investigate this issue using zebra finches (*Taeniopygia guttata*) as a model. Juvenile zebra finches were raised without their father's presence. Since female zebra finches do not sing, the birds were

deprived of song input. During their sensitive phase for song learning, the male birds were tested for their preference for songs containing either universal or non-universal note types. The first test was without ever hearing song. Additionally the birds were exposed to (tutored with) either a universal or a non-universal song to see how experience influences their preference. Results of the first test show that birds have a preference for songs with universal note types, prior to song experience. This preference changes when the birds are tutored with a song containing non-universal note types. The bias for universals prior to song acquisition indicates a predisposition, which can explain the universals present in different populations. The change in preference due to song experience indicates that cultural transmission can possibly overrule this initial bias. This explains the variation found between populations. Taken together these results illustrate how cultural transmission and predispositions may shape the patterns found in acoustic signals such as language and birdsong.

### **A Computational Model of Corvid Caching: Applications to Social Cognition**

*Elske van der Vaart (CEES & ALICE), Rineke Verbrugge (ALICE) & Charlotte Hemelrijk (CEES)*

Many corvids – members of the crow family – hide food underground, saving it for later. They recover their caches by memory, but also pilfer those of others, if they know where to find them. Cachers employ many different techniques to prevent their caches being stolen, such as caching far away from conspecifics, and recaching in new locations if they can't help being observed. But which mechanisms underlie these cache protection behaviors? Are they evidence of visual perspective taking, or is a simpler explanation sufficient? In our work, we tackle this question using an approach new to the field: Computational cognitive modeling. We implement a set of assumptions about corvid cognition as a working computer program, and then expose it to a virtual version of a real experiment. In this way, we can very precisely test the behavioral consequences of different cognitive assumptions. Previously, we have used this technique to provide new insights into corvid memory and learning. In this talk, we extend the same model to account for the results of two experiments by Dally, Emery & Clayton (2005), where scrub jays must cache and recover in front of various onlookers, such as dominants and subordinates. In the process, we derive new hypotheses for the birds' recaching behavior which do not depend on visual perspective taking.

### **Physiological determinants of song behaviour in European starlings: physiological condition parameters, carotenoids and testosterone**

*Van Hout AJM, Pinxten R & Eens M*

The male sex hormone testosterone is often involved in the expression of secondary sexual signals.

Furthermore, yellow-to-red (sexual) colour signals are often dependent on carotenoid pigments, which display an antioxidative capacity and can promote immunocompetence, resulting in a potential allocation trade-off. Recently, it has been suggested (but not investigated) that carotenoids may also affect non-visual signals involved in sexual selection. Moreover, it is generally expected that sexual signals convey information regarding individual quality, such as body condition. Using adult male European starlings, we performed a study which examines these aspects of sexual signalling for song behaviour. First, we used correlational analyses to investigate whether song rate in adult male European starlings during fall could potentially function as a signal of body condition and/or plasma carotenoid levels. Our results suggest that overall non-breeding song rate reflects inter-individual differences in plasma carotenoid levels as well as physiological parameters of body condition. Secondly, we experimentally examined a potential effect of dietary carotenoid supplementation on song rate for these males. We observed a significant positive effect of carotenoid availability on overall song rate after only 3-7 days. In addition, subsequent testosterone implantations significantly increased overall song rate and nestbox-oriented song rate in non-supplemented starlings, while carotenoid-supplemented starlings shifted song production towards nestbox-oriented song, without changing overall song rate. Thirdly, we investigated the short term effect of the testosterone implantations on song repertoire size and observed a significant increase in testosterone-implanted but not sham-implanted starlings.

### **Kin selection theory OK!**

*Wenseleers, T. (Dept. of Biology, Leuven)*

Recently, kin selection theory has come under attack by a paper by Nowak, Tarnita and Wilson, published in the journal *Nature*. The paper claims to show that inclusive fitness theory only works under very restrictive conditions, such as weak selection and gradual evolution, strict pairwise interactions, the absence of synergistic effects, and the absence of nonadditive allelic effects. Here I will formally show that inclusive fitness theory has none of these supposed limitations, provided that one works with the average effect of social actions. Previously, the concept of average effect was used by Fisher in the early 1900's to reconcile the gradual notion of evolution favoured by biometricians such as Pearson, and the more mechanistic view of evolution, based on particulate Mendelian inheritance, favoured by scientists such as Bateson. This shows there is little new about the current ongoing debate.

### **Timing in traffic: are singing winter wrens able to avoid temporal overlap with anthropogenic noise?**

*Yang, X.-J. & Slabbekoorn, H. (Institute of Biology Leiden, Leiden University)*

Many bird species have the ability to adjust their song timing by which they can minimize acoustic interference from singing competitors. It remains an open question whether this ability can also help out birds in busy urban areas with typically fluctuating noise levels due to traffic. We first tested the temporal flexibility of singing winter wrens (*Troglodytes troglodytes*) to playback of conspecific songs at three different, manipulated song rates. Although winter wrens did not

adjust their timing dependent on the song rate treatment, and increased their song rate only after playback exposure, they overlapped playback songs at levels much lower than expected by chance in all treatments. Subsequently, we tested whether singing winter wrens could exploit this plasticity during experimental exposure to intermittent white noise in their natural territories.

## Contributed posters NVG meeting Soesterberg 2010

### **Heritability of telomere length in the zebra finch**

*Els Atema, Ellis Mulder & Simon Verhulst*

Telomeres are tandem repeats of (TTAGGG)<sub>n</sub> mostly at the end of linear chromosomes. Telomeres shorten with age, but environmental and behavioural stressors can accelerate telomere shortening. In addition telomere length may be genetically determined. Terminal Restriction Fragment (TRF) analysis is widely used to measure telomere length. This electrophoresis method measures telomeres up to 50 kb long at the end of the chromosome (Class II telomeres). However, within the avian genome also interstitial telomeric repeats (Class I, 0.5 – 10 kb) and ultra-long telomeres (Class III, up to 1.0 Mb) exist, which are not measured using the electrophoresis method. In contrast, qPCR measures all telomeric repeats in the genome. We applied both TRF analysis and qPCR to measure telomere length in 34 sibling pairs of the zebra finch (age 9 – 139 days). By comparing the outcomes of the two methods we aim to estimate the genetic contributions to the length of Class II versus Class I plus III telomeres. We find that the similarity between Class II telomeres of sibling pairs is higher compared to that of the total number of telomeric repeats in the genome, indicating higher heritability of Class II telomeres. We consider it likely that the length of the interstitial repeats is determined genetically, since they are in the middle of the chromosome and hence cannot shorten. This suggests that in particular the ultra-long telomeres (Class III) are influenced by the environment during early development.

### **Male accessory gland proteins influence behaviour in a simultaneous hermaphrodite**

*Koene, J.M. & Hoffer, J.N.A.*

Seminal fluid is an important part of the ejaculate of internally fertilizing animals. This fluid contains substances that nourish and activate sperm for successful fertilization. Additionally, it contains components that influence female physiology to further enhance fertilization success of the sperm donor, possibly beyond the recipient's optimum. Although behavioural evidence for such substances abounds,

relatively few studies have unravelled their identities, and focus has been exclusively on separate-sex species. I will present our work on the seminal fluid composition of a hermaphrodite, the pond snail *Lymnaea stagnalis*. One newly-identified seminal fluid protein, called Ovipostatin, is found to suppress egg mass production. I will show how this is consistent with previous findings looking at mating costs in this species. Hence, seminal fluid proteins can evolve even when the sexes are combined. More importantly, what is unique to hermaphrodite mating systems is that accessory gland proteins can theoretically also influence the male function of the sperm recipient, I will show that there is indeed another seminal fluid protein that suppresses the amount of sperm transferred by the recipient in a subsequent mating. The latter finding clearly highlights how our understanding of sexual selection is enhanced by considering different mating systems.

### **Toward developing a Cognitive Bias task for pigs**

*Murphy, E. Nordquist, R., van der Staay, F.J.; Programme Emotion and Cognition, Department of Farm Animal Health, Utrecht*

Although measuring emotions in animals is of interest to various disciplines, reliable and valid methods for assessing emotional state in farm animals are still scarce. The aim of our project is to develop and validate a cognitive bias task for pigs. The present experiment looked at behavioural responses to tone cues predicting reinforced or unreinforced trials. Eight group housed female piglets were tested in a 10m-long runway with a goal box attached. 25 daily sessions (12 trials/session) were carried out. After a 5s tone cue was played (200Hz or 500Hz, balanced for rewarded and unrewarded across subjects), the piglet was released from a start box and latency to reach the goal box was recorded. Results were analysed at group and individual level. An ANOVA, with the between-subjects factor Pig (1-8) and two within-subjects factors, Session (1-25) and Trial (rewarded, unrewarded), revealed effects of all factors with complex interactions, suggesting a differential response

to the two cues. However, great variability in individual response curves to cues was observed. Only four subjects appeared to show an increased latency for unrewarded runs (i.e. learned the association), as confirmed by appropriate statistical analysis within individuals. We conclude that group averages mask the fact that half of the pigs were non-learners. Consequently, individual learning curves need to be analysed. Furthermore, the task needs to be optimized to increase the number of learners and to reduce variability within and between individuals, before the task can be used to assess cognitive bias.

### **Melody and Rhythm in Nightingale Song**

*Tina Roeske<sup>1</sup>, Philipp Sprau<sup>2</sup>, Iva Ljubicić<sup>1</sup>, Eathan Janney<sup>1</sup>, David Rothenberg, Gary Marcus, Ofer Tchernichovski<sup>1</sup> and Marc Naguib<sup>2</sup>; 1. Biology Department, The City College of New York, New York, NY, USA; 2. Animal Ecology Department, Netherlands Institute of Ecology (NIOO-KNAW), The Netherlands*

Nightingales are skilled singers with large repertoires of about 200 song types. However, most songs share common rhythm elements and each individual bird has a unique rhythm signature which may be used in individual recognition. Similarly to human melodies, small pitch intervals in nightingale melodies are mostly descending. However, in contrast to human melodies, there is no step inertia but a tendency to frequently switch interval direction.

### **The importance of underwater sounds for migration of aquatic mammals and fishes**

*Ilse van Opzeeland (Alfred Wegener Institute) & Hans Slabbekoorn (Institute of Biology Leiden)*

Aquatic mammals and fishes often migrate over large distances through oceans, seas, and river systems. These underwater migratory activities may be affected by coincident noisy human activities in several ways. Deterrence away from noise sources could lead to changes in optimal migration routes, obstruction of passage ways through river systems, or disturbance of group coherence. Deterioration of signal-to-noise ratios can cause masking of critical orientation cues, reflections from echo-location clicks, and social calls. Furthermore, artificial noise conditions may further raise physiological stress levels in periods of already increased pressure due to migratory swimming expenses. The presence of anthropogenic noise may therefore result in considerable detrimental effects on migration efficiency in both aquatic mammals and fishes.

### **Screening the satiating properties of dietary fibre sources in adult pigs**

*C. S. da Silva; W.J.J. Gerrits; J.J.G.C. van den Borne; B. Kemp; J. E. Bolhuis (Department of Animal Sciences)*

Restricted-fed female pigs suffer from hunger, often signalled by increased feeding motivation. We assessed effects of dietary fibre that might enhance satiety in various ways on feeding motivation in adult female pigs. Sixteen pair-housed pigs received four diets: lignocellulose (LC), pectin (PEC), resistant starch (RS),

all exchanged for starch, and control (C), in four periods in a Latin square. For each period, pigs received a low dose (L) followed by a high dose (H) of fibre (7 days each). At 1h, 3h, and 7h postfeeding, feeding motivation was assessed in an operant test (10g feed for wheel turns in a progressive ratio, PR1) and in a runway test (20g feed for walking 22.5 m route). Pigs were observed in their home-pen for 6h, using 90-sec instantaneous scan sampling. Data were analyzed with mixed models including fibre type, dose, and their interaction as fixed, and pen and period as random effects. In the operant test, at 1h postfeeding pigs fed H diets obtained more rewards compared with pigs fed L diets, and at 1h, 3h, and 7h postfeeding pigs fed PEC obtained more rewards compared with pigs fed other diets. At 3h postfeeding pigs fed RS-H obtained less rewards compared with pigs fed most of the other diets, including the RS-L. In the runway, at 1h postfeeding pigs fed PEC walked faster for food compared with pigs fed C and RS. At 3h and 7h postfeeding pigs fed H diets tended to walk slower for food compared with pigs fed L diets. At 7h postfeeding pigs fed RS tended to walk slower for food compared with pigs fed other diets. In their home-pen, pigs fed PEC showed more feeder-directed behaviour compared with pigs fed RS, with pigs fed C and LC in between. In conclusion, PEC was the least satiating fibre. Despite being the lowest in metabolizable energy, RS was the most satiating fibre, possibly due to its fermentation properties.

### **Did he stay or did he go – spatial movement predicts territory defence in Nightingales (*Luscinia megarhynchos*)**

*Sprau, P. (NIOO-KNAW), Naguib, M. (NIOO-KNAW)*

Animals often use signals in competition over resources. In vocal communication, different signaling strategies can be used to successfully expel intruders dependent on the threat the intruder constitutes. Territorial songbirds, for instance, may assess the potential threat of intruders by their song posts and thus by their movements. However, little is known about defense strategies against spatially moving intruders as most studies simulated rivals singing from a single song post. Here we tested whether territorial males integrate information about moving intruders into decision making. Using playback experiments we simulated male nightingales (*Luscinia megarhynchos*) that either stayed within the territory boundaries or that left the territory of a resident after intrusion. One hour later the same intruders were simulated to sing at the territory boundary and resident's defense behavior was measured. Residents approached the loudspeaker closer, changed their song posts more often and sang more songs in close proximity and more trills when the simulated rival had stayed within the territory than when it had been expelled previously. These findings suggest that resident male nightingales distinguish between rivals they had successfully expelled or not and perceive staying rivals as more threatening. Taken together, by using more realistic playback approaches

our experiments give new insights into the ecology of resource maintenance in songbirds.

### **Effects of personality on learning performance in great tits**

*Mieke Titulaer, Kees van Oers, Marc Naguib*

Adaptation to environmental changes is facilitated by good learning abilities. Individuals differ in their learning abilities, but little is known on how such variation is linked to consistent behavioural differences among individuals (personality traits). Great tits differ consistently in their exploratory behaviour in a novel environment, and this correlates with a range of behavioural traits. It thus can be used as proxy for personality. Here we subjected birds to a dimensional shift learning paradigm to study the link between learning and personality. First, they were trained to find food under one of two colours or at one of two locations, after which the previously unrewarded colour or location became rewarded (reversal). Then, two new colours and locations were given (intra-dimensional shift) and finally, the rewarded dimension was changed from colour to location or vice versa (extra-dimensional shift). Previous studies have shown that fast exploring individuals are less flexible than slow explorers. Therefore we expected slow explorers to perform better in the reversal and extra-dimensional shift, which are established measures of flexibility. Our results revealed sex-specific personality differences in performance in the reversal stage. These findings provide insights into behavioural mechanisms that may lead to personality-dependent fitness differences in the wild.

### **Social parasitism in the common wasp *V. vulgaris***

*Van Oystaeyen, A., Benaets, K., Wenseleers, T. and Billen, J.*

### **Do dogs and bees possess a ‘theory of mind’?**

*Jeroen van Rooijen, retired*

Scientists were surprised that dogs performed better in pointing experiments than nonhuman primates. They took the human mind as starting point and assumed that dogs understood the intention of the pointer (they assumed that dogs have a theory of mind). They assumed also that dogs developed this capacity during domestication. In my opinion the main reason for domestication of wolves by our ancestors, the hunter gathers, was its usefulness during hunting. Wolves were useful because (1) wolves, like humans (but unlike nonhuman primates), have a cooperative foraging strategy, (2) the pointing behaviour of wolves resembles human pointing (Van Rooijen, 2010). When we take dancing (pointing) of bees (also with a cooperative foraging strategy) as starting point we can argue that dog pointing is a result of natural selection without insight. Following the principle of parsimony we should favour this last explanation (Van Rooijen,

1987). Of course we have to be open for data that justify more complex interpretations.

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