

Invited general lectures NVG meeting Soesterberg 2012

Thinking about language evolution at the zoo: insights from birds, bats and bees

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Spoken language and birdsong share a number of striking parallels. I will summarize the biologically tractable cognitive abilities necessary for spoken language and for birdsong and argue that the similarities are not limited to sensorimotor processes – but may extend to the conceptual and computational systems. I will review evidence for the relevance of the FoxP2 gene and its associated molecular network for language and its role in the acquisition and production of birdsong. Many questions regarding the similarities between spoken language and birdsong remain unanswered, but increasing evidence suggests that human and non-human communication systems may rely on conserved molecular toolkits that act as genetic modules. These may specify the neural circuits subserving these particular behaviors, and organize their function. Elucidating these genetic modules in different animal models, including invertebrates ones, promises insights into the evolution of language and other complex traits.

The Umwelt-concept meets conservation biology: what we see, is not necessarily what other animals get

Hans van Dyck; Behavioural Ecology & Conservation Group, Earth & Life Institute, Université Catholique de Louvain (UCL), Belgium

Since the very start of conservation biology as a field, ecology has been very influential for the strategies to conserve species and ecosystems. More recently, there is a growing recognition for the significance of evolutionary thinking in conservation biology. Conservation studies often assume species-specific, fixed traits ignoring the evolutionary key issue of intraspecific variation. The way the habitat of a species is considered is an example of typological, static thinking biased by human perception. Structural habitat units (e.g., land cover or vegetation types) as perceived by humans may not represent functional habitat units for other organisms. Human activity also interferes with the environmental information used by animals. Therefore, the long-standing Umwelt-concept

from ethology and psychology needs to be integrated in the way we think about habitat and habitat selection. It states that different organisms live in different perceptual worlds and they deal with specific subsamples of the environment as a result of their evolutionary and developmental history. In this context, I will discuss an organism-centered, resource-based concept of habitat, the link with ecological traps, and how perceptual ability of organisms may be subject to adaptive change. However, perceptual ability may also constrain organisms from showing adaptive behaviours in rapidly changing, anthropogenic environments. The field of Umwelt and perception offers exciting challenges for conceptual and applied interactions between behavioural biology and conservation biology.

Cause and effect in Biology revisited

Kevin Laland; Centre for Social Learning and Cognitive Evolution, University of St Andrews, Scotland

In 1961, Ernst Mayr published a highly influential article on the nature of causation in biology, in which he distinguished between proximate and ultimate causes. Mayr argued that proximate causes (e.g. physiological factors) and ultimate causes (e.g. natural selection) addressed distinct 'how' and 'why' questions and were not competing alternatives. That distinction retains explanatory value today. However, the adoption of Mayr's heuristic led to the widespread belief that ontogenetic processes are irrelevant to evolutionary questions, a belief that I will argue has (i) hindered progress within evolutionary biology, (ii) forged divisions between evolutionary biology and adjacent disciplines, and (iii) adversely affected several contemporary debates in biology (e.g. over evolution and development, niche construction, cooperation, the evolution of language). In this talk I will expand on my earlier (Laland et al., 2011, *Science*, 334: 1512-16) argument that Mayr's dichotomous formulation has now run its useful course, and that evolutionary biology would be better served by a concept of reciprocal causation, which is better placed to recognize the roles that behavior, development and plasticity play in evolution. I will further suggest that a new evolutionary paradigm is unlikely to emerge without this change in thinking about causation.

Session talks NVG meeting Soesterberg 2012

The ecology of personalities: how gizzard size reflects the syndrome in foraging red knots

Allert Bijleveld (NIOZ), Georgina Massourakis (NIOZ, UnA), Annemarie Marel (NIOZ, UU), Anne Dekinga (NIOZ), Jan van Gils (NIOZ) and Theunis Piersma (NIOZ, RUG); Marine Ecology, Royal Netherlands Institute of Sea Research (NIOZ), The Netherlands

Individual animals show consistent behavioral responses to others and the environment. There has been a focus on how physiological differences between individuals (through genes interacting with ontogeny) might determine differences in personality. Here we present a case of the reverse process in which personality variations cause physiological changes in digestive organ sizes. Red knots (*Calidris canutus*) are shorebirds specialized in eating hard-shelled bivalves.



These bivalves are swallowed whole and crushed in muscular gizzards. The size of the gizzard sets an upper limit to the amount of shell mass that can be processed and thus limits daily intake rates. Previously we have shown that gizzard size is flexible within individuals and responds to the ratio between flesh and shell mass of their prey (i.e. prey quality). For a group of wild caught red knots we found that exploration behavior in a novel environment was repeatable ($R^2 = 0.56$, $P < 0.01$). At the time of the exploration experiment the captive knots had small gizzards as a result of a diet on artificial soft foods, but to our surprise exploration behavior was negatively correlated with gizzard size at capture several months before ($R^2 = 0.23$, $P = 0.02$), rather than at the moment of the exploration experiment ($R^2 = 0.05$, $P = 0.31$). By selectively offering hard-shelled or soft foods we were able to reversibly manipulate gizzard size and found that individual exploration scores did not change with gizzard size. These results suggest that exploration behavior is part of a behavioral syndrome that controls gizzard size in the wild.

Divergence in sexual communication, part 1: causes, consequences and case studies on moth pheromones

Astrid T. Groot; Evolutionary Biology, University of Amsterdam, the Netherlands

Even though sexual selection is generally hypothesized to be an important factor in the speciation process, it is still unclear when and how divergence in sexual communication occurs; does it follow ecological adaptation, could it drive ecological adaptation, and/or does divergence in sexual communication occur pleiotropically with ecological adaptation, when sexual signals or preferences are so-called 'magic traits'? When signals and preferences are governed by the same or closely-linked genes, Fisherian runaway selection can easily occur. Since in moths female signals and male response are governed by independently assorting genes, it is still a mystery of how moth signal and response may co-evolve. Our research focuses on the identification of these genes to gain insight in the underlying mechanism of divergence, and on the identification of ecological factors that may cause divergence in moth sexual communication. Sources of variation in the habitat that likely affect chemical communication systems include the presence and abundance of species with similar chemical cues and different host plants. In one moth species we found intrapopulation variation in the pheromone signal, in every population sampled so far. We are currently investigating the cause and possible consequence of this variation.

Plastic and genetic scaling of lifestyles in changing environments

Marie-Jeanne Holveck, Augustin Joiris, Hans Van Dyck; Biodiversity Research Centre, Université Catholique de Louvain (UCL), Louvain-la-Neuve, Belgium

Organisms vary considerably in their ability to respond to rapidly changing anthropogenic environments (e.g. climate change, habitat fragmentation). Here we address the case of the speckled wood butterfly (*Pararge aegeria*) that shows a remarkable case of niche evolution. This forest species has recently also colonized agricultural land. As a result, and opposite to most other butterfly species in NW-Europe, *P. aegeria* has significantly increased in regional distribution and in abundance. This ecological expansion is accompanied by several phenotypic changes, including behavioural differentiation between populations in different landscape types. We use this study system to test for adaptive changes in the lifestyles adopting a reaction norm approach. A lifestyle is a suite of correlated behavioural and life-history traits. For a flying ectotherm, agricultural land and forest represent very different environmental settings relative to the degree of habitat fragmentation and thermal conditions for flight and reproduction. We will report on the relative effects of genotypes, thermal environment and genotype x environment interactions on *P. aegeria* lifestyles focusing on flight performance and related morphology and physiology. We bred several populations from different landscape types (agriculture, forest) and two latitudes (climatic differences) under laboratory conditions. We applied a thermal reaction norm approach during larval development with three temperatures using a family-based, split-brood design. We tested the flight performance of the adults in a flight mill set-up connected to a respirometry system allowing the simultaneous quantification of flight metabolic rate. We will discuss the new evidence for changing lifestyles in changing anthropogenic landscapes.

Maternal and early environmental effects on sheep and poultry

Andrew Janczak; Department of Pharmacology & Toxicology, Norwegian School of Veterinary Science, Norway
TBA

Animal personality: changing views and developing concepts.

Jaap M. Koolbaas; Dept. of Behavioral Physiology, University Groningen, the Netherlands

The study of animal personality in terms of consistent individual variation in behavior and neuroendocrinology has rapidly expanded during the last decades. A wide variety of animal species were shown to have individual differentiation in trait characteristics that is stable over time and across situations. While many studies considered the functional and evolutionary significance of animal personality, relatively few studies considered variable traits in more detail. This presentation will emphasize the multidimensional nature of animal personality and the underlying mechanisms that might explain consistency across contexts. The consistency of a given trait characteristic across contexts is likely to be based on the common activation of an underlying



causal mechanism. Hence, the distinction and terminology of trait characteristics used in personality research should be based on the main function of identifiable causal mechanisms. Our studies in rats and mice suggest at least three independent dimensions of individual variation, i.e. coping style or cue dependency as a qualitative dimension, emotionality as a more quantitative dimension and impulsivity. Coping style is causally related to variation in the mechanisms of homeostatic control of the serotonergic system. Emotionality and impulsivity seems to be related to individual variation in amygdala and prefrontal cortex functioning respectively. It will be argued that a neurobiological and an evolutionary approach of animal personality should have common grounds in a better specification of trait characteristics that may reflect both underlying mechanisms and units in the organization of behavior subjected to selection pressure.

Tracing the sources of young children's deviant word productions

Claartje Levelt; Linguistics, Leiden University, the Netherlands

When young children start to produce words, the segmental form of these produced words often deviates from the form they are targeting; sounds disappear or are substituted for other sounds, like in produced [pu] for target poes, or produced [bop] for target brood. The question I will address is where deviations in child language originate during speech production, and how we can trace the error source. Assuming a modular speech production model, the potential sources for errors that will be considered are: the segmental representation (the stored sounds) of a word, the module where sounds are grouped into larger units (phonological encoding), and the module where motor patterns are formed (phonetic encoding). Experimental, empirical and acoustic data help to trace the error sources for specific deviating word productions.

Divergence in sexual communication, part 2: sensory drive in cichlid fish

Martine Maan; Behavioural Biology, University of Groningen, the Netherlands

Divergent ecological selection on sexual communication traits may promote reproductive isolation, but may also lead to geographic variation without speciation. In particular, when sexual signals diverge between populations but sexual preferences do not, speciation may be slow or not happen at all. In contrast, divergent ecological selection on preferences can lead to divergence in signals as well, potentially providing a more powerful mechanism for speciation. Sensory drive, i.e. the adaptation of communication traits to their sensory environment, can affect both senders and receivers of sexual signals. We investigate how these effects may contribute to speciation in the cichlid fishes of Lake Victoria. These fish inhabit diverse underwater light environments, and closely related species often differ in sexually selected coloration. We ask how divergent adaptation to different light environments affects male colours as well as female

colour preferences, to establish whether cichlid colour vision could act as a 'magic trait' in speciation: subject to divergent ecological selection and at the same time pleiotropically determining female mating preferences.

Post-copulatory manipulation of male and female functions via seminal fluid in a hermaphroditic freshwater snail

Yumi Nakadera, Jeroen N. A. Hoffer, Eljerra Swart, Onno den Boon, Joris M. Koene; Animal Ecology, VU University Amsterdam, the Netherlands

Just like separate-sexed animals, hermaphrodites are under sexual selection, so they compete with each other for reproductive success. In contrast to separate sexes, a hermaphrodite theoretically has the unique possibility to manipulate its mating partner's male as well as female functions to its own benefit. Here, we present the first study of such mate manipulation in the great pond snail *Lymnaea stagnalis*. Previous work has shown that proteins in the seminal fluid delay egg mass production in sperm recipients, something that also becomes apparent from multiple mating experiments. We now report that this seems to be beneficial for sperm donors, as delayed egg mass production leads to more investment per egg. In addition, we found that recently-inseminated sperm donors transfer half the amount of sperm to mating partners, which is also due to male accessory gland products. Crucially, we reveal that, as a consequence, these donors obtain less paternity success. This manipulation, which reduces the male function of recipients, would be beneficial for donors if recipients invest more to female reproductive output in response. In other words, they invest less in their ejaculate and more in their eggs. These two manipulative functions of seminal fluid suggest strong sexual selection on division of male and female resources in simultaneous hermaphrodites.

How vervets trade and solve coordination problems

Ronald Noë; Psychology & Evolutionary Ethology, (DEPE / IPHC, CNRS), University of Strasbourg, France

I will discuss two forms of cooperation among multiple agents: "biological markets" and "coordination problems". After introducing the concept of Biological Markets, I will describe an experimental test of BM-theory with free-ranging vervet monkeys. I will then introduce "coordination problems", which can be classified as mild forms of Social Dilemmas (SDs). In SDs multiple agents have common goals or interests, but some or all individuals involved can gain immediate profit by cooperating less, resulting in conflicts between private and public interests. SDs are notoriously unstable, but the fact that humans can solve them, at least partially and at least sometimes, is perhaps one of most typical manifestations of 'humanity', closely linked to other typical human traits, such as language, 'theory-of-mind' and empathy. That does not mean, however, that humans are the only ones capable of solving SDs. I



will show how our vervet monkeys solved a complicated coordination problem during the same experiment described before.

Sperm competition and evolution

Geoff Parker; University of Liverpool, UK
TBA

The easy life of lab birds: comparison of stress indicators in captive and wild greenfinches

Tuul Sepp; Institute of Ecology and Life Sciences, University of Tartu, Estonia

The majority of ecophysiological research, especially development and adjustment of novel methods, is carried out under laboratory conditions. If we want to generalize the information obtained from studying captive animals to natural situations, it is crucial to know how captivity itself affects the model organisms. Captivity may cause stress, which may seriously affect the health and wellbeing of the animals. I studied stress levels in greenfinches, medium-sized passerine birds that have become an increasingly popular model organism in ecophysiological research, using two different stress markers. In one year, I measured leukocyte concentrations in wild and captive birds. The ratio of heterophils to lymphocytes is considered one of the most reliable stress indicators in birds. In the two consecutive years, I compared stress hormone corticosterone concentrations from wild-grown feathers removed at capture and feathers grown during captivity in the same birds. Both markers indicated that captive birds do not suffer stress levels higher than wild birds. Captive birds even tended to have lower corticosterone level in their feathers than wild birds.

Primate social cognition: capacities and their social function

EHM (Liesbeth) Sterck & AM Overduin – de Vries; Behavioural Biology, Utrecht University; Ethology Research, BPRC, Rijswijk, the Netherlands

Primates are large-brained group-living animals that show complex and individual specific social behaviour. These features have engendered the 'Social Brain' hypothesis, explaining their relatively large brain size in relation with their cognitive capacities used to manage social complexity. One advanced social cognitive capacity possibly only present in humans is Theory of Mind (ToM) and visual precursors of ToM have been identified. Establishing these precursors of ToM has received considerable attention, yet their function has not been ignored. Macaques lack ToM, but evidence is found for several visual precursors of ToM. Thus far, macaques use relatively advanced cognitive capacities to obtain food, but only less advanced ones in sexual strategies. Competing for food involves two individuals, and is socially less complex than sexual strategies that typically involve at least three individuals, countering the 'Social Brain' hypothesis. However, it is too early to generalize these findings

and link the social use of cognitive capacities to particular social settings or social complexity.

Linguistic abilities in zebra finches?

Carel ten Cate; Behavioural Biology, Leiden University, the Netherlands

Darwin already mentioned birdsong as the closest animal analogue to language. Over the years this has given rise to research examining whether the way in which songs are learned, produced and processed shares similarities with comparable processes in language, and how this may shed light on the development and evolution of the language faculty. Another approach is to examine whether certain cognitive features considered crucial for language, and often thought to have co-evolved with language, can be found in birds. In my presentation I will address two examples of such research. The first one concerns the abilities of zebra finches to distinguish speech sounds. The second one concerns the abilities for linguistic rule learning in zebra finches. For both I will discuss to what extent their abilities are comparable to those of humans.

Flexibility in chimpanzees: not conformity, but resource-optimisation trumps chimpanzees' conservative nature

Edwin J.C. van Leeuwen, Katherine A. Cronin, Josep Call & Daniel B.M. Haun; Psycholinguistics, Max Planck Institute, the Netherlands

Chimpanzees have been shown to be adept learners, both individually and socially. Yet, their conservative nature seems to hamper the flexible adoption of superior alternatives, even to the extent that they persist in using entirely ineffective strategies. In this study, we investigated chimpanzees' behavioural flexibility in two different conditions under which social animals have been predicted to abandon personal preferences and adopt alternative strategies: i) under influence of majority demonstrations (i.e. conformity), and ii) in the presence of superior reward contingencies (i.e. maximizing payoffs). Unlike previous nonhuman primate studies, this study disentangled the concept of conformity from the tendency to maintain one's first-learned strategy. We found that chimpanzees did not abandon their behaviour in order to match the majority, but instead remained faithful to their first-learned strategy, which is indicative of conservatism, not conformity (experiment 1a and 1b). However, the chimpanzees' fidelity for using their first-learned strategy was overridden by an experimental upgrade of the profitability of the alternative strategy (experiment 2). Contrary to previous findings, these results show that chimpanzees may abandon their familiar behaviour to maximize payoffs, but not to conform to a majority. We discuss our observations in light of adaptive learning strategies.



The genomics of great tit personality: towards a model organism for behavioural eco-genomics

Kees van Oers; Department of Animal Ecology, NIOO-KNAW, the Netherlands

Individuals within populations consistently differ in the way they cope with environmental challenges. This phenomenon is often referred to as animal personality. Personality differences have been shown to be widespread and to influence fitness in natural populations. Quantitative genetic variation underlying personality differences has been demonstrated in studies both on wild as well as captive populations giving scope for evolution to act on these differences. Until recently it was impossible to connect this variation to large scale molecular genetic variation. Such a connection between phenotypes and genotypes is essential to identify regions responsible for phenotypic variation and to study the way these regions interact with the environment in which they are expressed, in order to describe or predict micro-evolutionary processes. Here we show the first results of the genomic characterisation of the Great Tit and its associations with personality in an F2 cross population from lines selected for exploratory behaviour.

To sing or not to sing: how neighbours affect singing activity in the Great Tit (*Parus major*).

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Communication networks are likely to exist whenever groups of animals are within signaling and receiving range of multiple conspecific individuals. Within avian communication networks individuals can use song to communicate: attract mates (social and/or extra-pair), protect paternity and repel rivals from their territory. Singing can therefore be affected by several factors and has previously been linked with fertility stage of the mate and consistent behavioral differences (personality). Besides these factors originating from the male itself and its mate, individuals will also likely be affected by the behavior and personality of their neighbors. Here, in a wild population of Great Tits, we examined if singing activity could be explained by: (1) fertility of the neighboring female, (2) personality of the neighboring males, (3) singing activity of the neighboring males and (4) personality of singing neighbors. Neighborhood effects on singing activity suggest that singing is used in female fertility guarding as well as attracting extra-pair mates. These findings emphasize that understanding animal communication requires taking the social communication network into account.

The evolutionary ecology of individual variation

F.J. Weissing; Theoretical Biology, University of Groningen, the Netherlands

In the past decade, individual differences in behaviour that traditionally were considered as noise have

become a key target of research in the behavioural sciences. From an adaptive perspective, the persistence of consistent and patterned (i.e. non-random) individual variation in behaviour is often not well understood. Here I will review several mechanisms that may contribute to the evolution of such variation. First, frequency-dependent selection can lead to adaptive variation if rare phenotypes have a fitness advantage. I will discuss frequency-dependent selection on behaviour and on individual states, and their interactions. Second, behavioural variation may reflect spatiotemporal variation in the environment, for example if individuals facing an unpredictable environment play a bet-hedging strategy. Diversifying selection does not always result in equilibrium; different behavioural types can persist at the population level even though there is a constant turnover at the local level. Third, large-scale behavioural variation may result from seemingly irrelevant small-scale fluctuations if at least some individuals are responsive to their environment and use a condition-dependent strategy. This explains much variation in the context of social behaviour. Fourth, behavioural variation may reflect constraints imposed by the “architecture” of behaviour, that is, the mechanisms underlying condition-dependent behaviour. I will argue that any real-world mechanism has limitations and I will show by means of examples that such limitations will often result in systematic individual differences in behavioural tendencies.

Applying behavioural biology towards refinement of animal experiments

H. Würbel; Animal Welfare, University of Bern, Switzerland

For most laboratory animals, welfare largely depends on the conditions under which they are being housed. In view of welfare friendly housing conditions for laboratory animals, the EU directive on the protection of animals used for scientific purposes therefore requires that appropriate enrichment techniques be in place. Environmental enrichment is aimed to provide animals with resources and stimuli that satisfy the animals' behavioural needs; facilitate the expression of a wide range of normal behaviour; and offer the animals a degree of choice and control over their environment, which is fundamental to their ability to cope with their housing conditions. Thus, laboratory rodents housed in barren standard laboratory cages develop a range of abnormal repetitive behaviour and other signs of poor welfare that are attenuated by adequate environmental enrichment. Nevertheless, laboratory animal scientists have raised concerns that enrichment might disrupt environmental standardization, thereby compromising the precision and reproducibility of animal experiments. These concerns were based on the assumption that a more complex environment would increase both within-experiment and between-experiment variation in the data. However, we recently showed that the welfare of laboratory mice can be improved by environmental enrichment without compromising the precision and reproducibility of experimental results. In fact, these



concerns were based on a flawed concept of standardization. This concept is based on the true finding that experimental results can differ depending on environmental conditions, and on the false belief that standardization will 'spirit away' such differences. This is what I have referred to as the 'standardization fallacy', the attempt to increase precision and reproducibility at the expense of external validity. Indeed, we recently showed that environmental

standardization increases variation between replicate studies and the rate of false positive results, whereas systematic environmental variation (heterogenization) attenuates these deleterious effects. Based on these findings, simple and effective strategies can be developed to improve both animal welfare and the validity of animal research in the best of meanings of the 3R concept.

Contributed posters NVG meeting Soesterberg 2012

Feed restriction induced change in body mass affects offspring sex ratio in laying hens

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Sex ratio theory predicts that birds will skew the offspring sex ratios in relation to difference in fitness benefits between producing sons or daughters which may vary under certain ecological and social conditions. Previous studies showed indeed that birds have the ability to skew sex ratios. The aim of the current study was to investigate whether laying hens could be induced to produce a female biased sex ratio and understand the underlying mechanisms that may lead to the cessation of killing millions of male chicks each year in the poultry industry. Unlike previous studies, offspring sex ratio in the present study was determined in unincubated eggs to approximate the primary sex ratio. ISA brown layer hens of 35 weeks of age were randomly allocated to a feed restriction group (80% of ad lib for 7 days and 70% of ad lib for an additional 10 days) and a control group (ad lib all the time) containing 30 hens in each group. Hens were inseminated twice a week with pooled extended semen from 15 cocks. Feed restricted hens were after the feed restriction period given ad lib feed again for the following 9 days. Eggs were sexed without incubation by PCR methods targeted to the sex-linked CHD1 genes for determination of the primary sex ratio. Compared to the control group sex ratio (proportion of males) of the feed restriction group decreased gradually with concurrent decrease in hen body mass. Thereafter, sex ratio returned to normal 0.5 when hens were switched back to ad lib feeding conditions. When considering hens of both groups, the sex of the eggs was significantly predicted by the cumulative body mass change and most strongly so when body mass change was calculated over the period of two days before oviposition. This period includes the completion of meiosis-I and thus sex determination. Associations between hen sex ratio with each of fertility rate and laying rate were not significant. These results indicate that meiotic drive could be the most

likely mechanism affecting the sex ratio in birds. In another study under ad lib conditions we did not find an association of testosterone, estradiol, androstendione, progesterone, dihydrotestosterone and glucose in egg yolk with egg sex or offspring sex ratio of hen. To further investigate the mechanism underlying sex ratio manipulation we are experimentally studying the concentrations of hormones in the maternal circulation in relation to sex ratio. Further planned research to study the gene expression changes in ovum during meiosis by microarrays or RNA sequencing can give insights into the mechanisms of sex ratio bias.

Immunity on Colour Morphs of the Lizard *Podarcis sicula*

Simon Baeckens, Jessica Vroonen & Raoul Van Damme; Biology, lab Functional Morphology, University of Antwerp, Belgium

Island populations often differ notably from conspecific populations on the mainland in aspects of their morphology, physiology, behaviour and life history. For instance, in ectothermic vertebrates island populations tend to be more darkly colored. Which of the many hypotheses explaining the evolution of melanism is responsible for this phenomenon remains unclear. A recent idea is that increased pigmentation is a mere byproduct of selection for other traits that enhance fitness on islands. This effect may arise through pleiotropic effects of the proopiomelanocortin [POMC] gene. The POMC gene and its posttranslational products (melanocortins) are part of the melanocortin system, which plays a central role in the melanine-based coloring. Melanocortins may bind to five melanocortin receptors (MC1-5R) and such binding may affect a wide variety of physiological and behavioural characteristics, including immunocompetence. In this study we investigate the relationship between colour variation and immunocompetence in the Italian wall lizard *Podarcis sicula*. This species exhibits great variability in (dorsal) colour patterns, both between and within populations. I compare a melanistic population to a 'normal' coloured mainland population. A high immunocompetence should come with a low parasitic load and a high cell mediated immune response (induced by a phytohaemagglutinin [PHA] injection).



To examine seasonal effects, analyses were performed at an early and late stage in the reproductive season (April and September). The results show that melanistic island individuals differ quantitatively from the mainland population in colour and aspects of the immune function. Melanistic variants have a less pure red skin colour and less bright, but pure blue throat, lower ectoparasitic load and higher immune response. This result confirms the idea that individuals of the melanistic island population, are more immunocompetent and corroborates the hypothesis that a darker colouring may arise as a byproduct of selection for other adaptive traits (here: immunity). In addition, I found that aspects of both colour and immunity may differ considerably between seasons and sexes, and often in a complex way. In general, the mainland population has a higher seasonal colour difference, probably because of the higher predation pressure and inter- & intrasexual competition on the mainland than on the island.

Traveling slow waves in the avian brain

Gabriel Beckers; Behavioural Biology, Utrecht University, the Netherlands

Recent studies have shown that slow waves propagate across the neocortex as a traveling wave during mammalian slow wave sleep. Although waves tend to originate in frontal regions, they can originate in virtually any part of the neocortex. To determine whether the behavior of slow waves described in mammals reflects a fundamental aspect of slow wave sleep, we examined whether slow waves also act as traveling waves in birds, the only other taxonomic group to exhibit unequivocal slow wave sleep. Adult female zebra finches (*Taeniopygia guttata*) were anesthetized with 1-1.25% isoflurane. Local field potentials (LFP) and multiunit activity (MUA) were recorded using a 64-channel NeuroNexus silicon probe inserted into the anterior hyperpallium and underlying mesopallium and nidopallium. LFP and MUA were recorded while the birds remained under anesthesia. The LFP recordings revealed high amplitude slow waves associated with bursts of MUA across most recording sites. This activity swept across the plane of the electrode array as a traveling wave.

Although activity tended to appear first in deeper sites, it could appear first in any part of the array. The wave usually reached all electrode sites, but in some cases only involved specific brain regions. The speed with which the waves crossed the array varied from wave to wave. Several characteristics of avian slow waves are similar to those described in mammals; 1) slow waves are associated with alternating periods of MUA and neuronal quiescence, 2) slow waves are more likely to appear first in certain electrode sites, but can appear first in virtually any part of the brain covered by the electrode array, and 3) slow waves propagate as traveling waves. In addition, the apparent variable propagation speed across the 2-D array suggests that the waves actually propagate in 3 dimensions with some wave fronts occurring orthogonal and others parallel to the surface of the

array. Wave propagation in 3 dimensions is consistent with the nuclear arrangement of stellate-shaped neurons in the avian pallium. The traveling nature of slow waves appears to be a fundamental feature of slow wave sleep.

Fear testing in rabbit does – Inter- and intra test consistency

S. Buijs; Animal Sciences Unit, Institute for Agricultural and Fisheries Research (ILVO), Belgium

We used 23 female rabbits to study the correlations between three tests of fearfulness. More specifically, open field testing was performed on the first four consecutive days, by isolating individual rabbits in a 1.5 x 1.5 m arena and observing their behaviour for 5 minutes. On the fourth day, open field testing was followed directly by a novel object test (a plastic bottle was lowered into the arena and the rabbit's behaviour was observed for another 5 minutes). Heart rate was recorded directly before and after these tests, and the test-induced heart rate increase (post-test minus pre-test rate) was calculated. On day five, an emergence test was performed (i.e., individual rabbits were placed in a plastic box and moved to an unknown, open part of the barn where their latency to leave the box was measured). Locomotion in the open field (lines crossed per 5 minutes) was higher on the first than on the second day (median: 83 (74–95) vs. 56 (35–75), $P < 0.001$). It remained stable during further open field testing ($P > 0.1$), but dropped dramatically after presentation of the novel object (62 (47–83) vs. 7 (2–27), $P < 0.001$). Thus, whereas the novelty of being isolated in unknown surroundings triggered locomotion, the appearance of a novel object suppressed it. Rabbits that showed more locomotion in the open field test had a shorter latency to touch the novel object ($r_s = -0.5$, $P = 0.02$), and crossed more lines after its appearance ($r_s = 0.5$, $P = 0.03$). It seems unlikely that differences in the latency to touch the object were due to differences in exploratory motivation, as almost all animals spent the vast majority of their time oriented towards the object. Instead, the latency to touch the object more likely reflected to what extent the animals fearfulness inhibited them from acting upon their exploratory motivation. Presentation of the novel object greatly decreased rearing (16 (13–21) vs. 1 (0–2), $P < 0.001$), and rabbits that touched the object quicker reared more in its presence ($r_s = -0.8$, $P < 0.001$). However, rearing during the open field testing was not related to novel object latency, and did not differ between test days (both $P > 0.1$). Similar to locomotion, test-induced heart rate increase was greater in the first than in the second open-field test (18 (6–31), vs. 9 (0–18) beats per minute, $P = 0.08$), and was further decreased after the presentation of the novel object (0 (-8–12)). Locomotion and heart rate increase tended to be correlated during the first open-field test ($r_s = 0.4$, $P = 0.06$), but were not significantly related on the other three days. A correlation between rearing and heart rate increase was found on day 4 only ($r_s = 0.4$, $P = 0.05$). Emergence latency was extremely short (<13 seconds for all tested rabbits), possibly due to the fact



that the does were more familiar with open spaces than with small boxes (rabbits were housed in large roofless pens with wire walls). The finding that higher locomotion in the open field reflected decreased fearfulness, whereas rearing was unrelated, contrasts with our previous experiments on juvenile rabbits in which we observed the opposite. Taken together with the surprisingly short emergence latency, this suggests that a correct interpretation of behaviour in fear tests is dependent on age and previous experience.

Asymmetric response patterns to subspecies specific song across a grey-breasted wood-wren contact zone.

Tamsin Burbidge, Thari Parson & Hans Slabbekoorn; Behavioural Biology, University of Leiden, the Netherlands

Barriers to gene flow are key to the understanding of the evolutionary process of speciation. Song is an important factor affecting gene flow in birds as it provides a specific acoustic signal which allows for conspecific recognition and mate choice. Contact zones between closely related species or subspecies are of particular interest, due to the maintenance of separate species given the potential for hybridization. A previous study in the Sierra Nevada Mountain Range, Colombia, has shown discriminatory response patterns between two subspecies of the grey-breasted wood-wren: *Henicorhina leucophrys anachoreta* at high and *H.l. bangsi* at low elevations (Caro et al., 2012). These two series of playbacks were distant from the contact zone, while a third series of playbacks to *H.l. bangsi* close to where both subspecies meet revealed no discrimination of songs from high or low elevation. This lack of discrimination, however, could have been due to the use of non-local *bangsi* stimuli that originated from low elevation. In the current study, we conducted two new series of playbacks in both subspecies, both near to the contact zone and with song stimuli from non-neighbouring but local birds. In concurrence with the previous study, *anachoreta* individuals discriminated between con- and hetero-specific songs, with a significantly stronger response to their own song type. There were no significantly different responses to con- and hetero-specific songs for *bangsi* individuals. The discriminatory responses for one subspecies suggest that song may provide a barrier to gene flow. The asymmetric pattern with one subspecies being non-discriminatory may have implications for the direction of gene flow, and therefore the maintenance of two distinct subspecies and the position of the contact zone.

Social nosing in pigs and its relationship to dominance hierarchy and harmful behaviour

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Social nosing behaviour, i.e. gently touching another individual with the snout, forms a major component of the behavioural repertoire of pigs (*Sus scrofa*), but the

reasons for its performance and its relationship with other behaviours are largely unclear. We examined whether social nosing was related to dominance relationships, likewise social grooming in primates, or to harmful behaviours such as tail biting. Eighty crossbred pigs of eight weeks of age, both males and females, were housed in straw pens (10 pigs / pen). Dominance ranks were determined by a feed competition test. Focal pigs (N = 64) were subjected to continuous behavioural observations for 2 h, divided over five consecutive days. Social nosing occurred on average 36 ± 3 times within 2 h, and mainly consisted of nose-to-nose contact, nosing the head and nosing the body, rather than nosing the ear, groin, tail or ano-genital region. All interactions between pigs, with the exception of aggressive behaviours, were either preceded or followed by significant associations with nosing a certain body region. Dominance rank did not influence the amount of social nosing given or received. Nosing the tail correlated with tail biting ($r_s = 0.37$), but only 1.2 percent of total social nosing was followed by oral manipulation. Pigs which delivered much social nosing did not receive less aggression, and nor did they receive a heightened amount of social nosing in return. Though social nosing did not show clear direct benefits to the actor, it may have an important role in maintaining dominance relationships by social recognition, in affiliative behaviour, or in pigs' intrinsic need to nose. In conclusion, social nosing was associated with most interactions between pigs but was largely unrelated to dominance hierarchy and harmful behaviours.

Can zebra finches learn to discriminate "words" based on affixations?

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Language is considered a key trait that distinguishes humans from other animals. Yet, it is hotly debated to what extent the human language faculty is based on human- and language-specific cognitive abilities and which components of the language faculty are shared with animals. Acrossing the world's languages, the edges of words or sentences play important roles in grammatical functions. Adding verbal material to the word-edges (i.e. prefixion and suffixation) to make morphological transformations occurs quite often. Here, we explore the ability of a songbird species, zebra finch, to learn such affixations in a comparative way. Using Go/No-go experimental setup, we found that the birds were able to learn both prefix and suffix rules, although not always both together. This result suggests some computational and memory mechanisms evolving affixation learning in languages are shared with other animals. Individual birds can differ in the rules they used, which might be related to the nature of the Go or Nogo stimuli.



Equine social cognition: differences in the social exploratory process comparing free-roaming and domestic horses.

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In the wild, horses live in family groups. Social cognition in these groups is an important topic for survival in natural conditions. It also brings social cohesion, and with that it represents a welfare aspect as well. It would be interesting to compare and understand the social exploratory behaviour, as part of social cognition, of free-roaming horse group, with domestic horse groups. In this study, we investigated the exploratory process in a family group of free-roaming horses (A) compared with a family-like group of domestic horses (B) and a non-permanent group of domestic horses (C). The behaviour was recorded during novel object tests in their daily habitat. The tests were focused on the group behaviour dynamics from the moment of notifying the object until their interruption of the exploratory process. Comparative analysis highlight interesting differences between the groups. Group A and B showed calm approaches and investigative processes, without reactive behaviours between members and as individuals. Group C showed faster approaches and several reactive behaviours. These results seem to indicate that group-stability, in which individuals take each other into account to avoid tension, offers a better exploratory process and thus a better cognitive experience.

Monarch butterflies practice herbal medicine: consequences for infectious disease and host-parasite coevolution

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Parasites can dramatically reduce the fitness of their hosts, and natural selection should favour defence mechanisms that can protect hosts against disease. Much work has focused on understanding genetic and physiological immunity against parasites, but hosts can also use behaviours to avoid infection, reduce parasite growth or alleviate disease symptoms. Here, I will describe the phenomenon of trans-generational medication, in which animals actively use medicine to mitigate disease in their offspring. Monarch butterflies are naturally infected with virulent protozoan parasites, and our studies have shown that neither caterpillars nor adult butterflies can cure themselves of disease. Instead, infected adult butterflies preferentially lay their eggs on toxic plants that reduce parasite growth and disease in their offspring caterpillars. These results demonstrate that infected animals may use medicine as a defence against parasites, and that such medication may target an individual's offspring rather than the individual itself. Trans-generational medication directly affects parasite infection and disease, and is likely to act strongly on host-parasite coevolution.

Does larval food affect sex pheromone composition in moths?

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In the noctuid moth *Heliothis virescens* intraspecific variation in female sex pheromone has been found to be not related to genetic differentiation. The present study investigated whether 1) intraspecific variation in sex pheromone could partly be due to drift; 2) larval host plant influences the female sex pheromone composition. This study provides evidence that 1) the intraspecific variation found in *H. virescens* is not due to drift, 2) some precursors for sex pheromone do seem to come from the larval diet and 3) plant defenses could influence the sex pheromone composition in *H. virescens*.

Relative importance of female choice and male competition on mating outcome

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Olfactory signals, such as sex pheromones, increase the reproductive success in insects. In the butterfly *Bicyclus anynana*, the male sex pheromone (MSP) is under directional sexual selection (Nieberding et al. 2008 PlosOne 3(7), 2012 Ecol. Lett.15). Yet, MSP may evolve according to female mating preferences if females actually have the possibility to choose among males. Many lab studies of *B. anynana* mating success were conducted under very high densities (mean=810.9dm³/ind., median=2.319dm³/ind., range=2254dm³/ind., n=28) and male biased sex-ratios (mean=67.8% male, median=66% male, range=9% male, n=29) likely far away from natural, field-like, conditions. Such biased treatments may promote male harassment of females in a species for which female mate choice appears to take the form of escaping unpreferred males. Here using fine-detailed behavioural observations, we thus estimated the relative importance of female choice and male competition in *B. anynana* mating success under varied densities and sex-ratios spanning the ranges used by previous studies. We expect that females exert a choice of mating partners in the more natural, field-like, conditions of male density and sex ratio. We emphasize that a better estimation of the strength and the direction of sexual selection on males and their olfactory trait requires more natural, field-like conditions, although such environmental conditions are rarely met in the laboratory.

Turning shy on winter's day: effects of season on personality and stress response in *Microtus arvalis*

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Many animals of temperate environments have evolved physiological and behavioural adaptations to cope with the cyclic seasonal changes. This may result in changes in personality: suites of behavioural and physiological traits that vary consistently amongst individuals. Winter, typically the adverse season challenging survival, may require individuals to have shy/cautious personality whether during summer, energetically favorable to reproduction and survival, individuals may benefit from a bold/risk taking personality. In order to test the effects of seasonal changes in early life and in adulthood on behaviours (activity, exploration, and anxiety), body mass and stress response, we have manipulated the photoperiod and quality of food in two experiments to simulate the conditions of winter and summer. We used common voles (*Microtus arvalis*) as they have been shown to display personality based on behavioural consistency over time and context. Summer-born voles allocated to winter conditions at weaning had lower body mass, a higher corticosterone elevation after stress and a less active, more cautious behavioural phenotype in adulthood compared to voles born in and allocated to summer conditions. Behavioural consistency over time and context was unaffected. By contrast, adult females only showed plasticity in corticosterone-induced stress levels, which were higher in the animals that were transferred to the winter conditions than to those staying in summer conditions. These results suggest a sensitive period for season related plasticity of personality in which juveniles shift over the bold-shy axis.

Is this my baby crying? Influence of time spent with own baby and of exposure to other babies on offspring recognition

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In humans, crying is the main mean for a newborn to communicate his distress or needs. Therefore, reliable individual vocal recognition between parents and offspring appears as a very adaptive skill. However, very few studies have investigated individual recognition of human infant cries. In addition most of them focused on mothers only although the cooperative breeding hypothesis has claimed, in the recent years, that baby caring skills are not restricted to mothers. The aim of this study was to explore the factors influencing adults' ability to identify a baby among others from listening to its cries. We first recorded and analyzed cries from 29 3-5-month-old babies (17 boys and 12 girls). The acoustic analysis in both temporal and frequency domains was done using PRAAT software. The differences between cries from different babies were assessed running a cross-validated and permuted Discriminant Function

Analysis (R software). The results show that the baby's cry encodes strong information about individual identity. We further tested parents' ability to recognize their own baby from his/her cries alone. We also tested nurses from child care center with babies they were in charge. All results showed no difference between men and women and were significantly affected by the time spent with the baby and the exposure to other babies. Recognition abilities may thus not be a sex-specific adaptation but rather a general ability mainly affected by experience, thus supporting the cooperative breeding hypothesis.

Solving a paradox: context-dependent effects of yolk testosterone in the Rock Pigeon (*Columba livia*)

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Yolks of avian eggs contain considerable and variable amounts of maternally-derived steroid hormones and numerous studies have tried to find their adaptive function. In the majority of bird species testosterone (T) concentrations in the egg increase over the laying sequence: eggs are laid with intervals of at least one day and later laid eggs contain higher concentrations of testosterone than earlier laid eggs. Since later laid eggs hatch later, providing a competitive disadvantage of these chicks relative to their earlier hatched siblings, the Hatching Asynchrony Adjustment Hypothesis proposed that the increase in yolk T would compensate the effects of hatching asynchrony, boosting the last hatched chick. However, this has created a paradox: why would avian mother first produce hatching asynchrony, classically interpreted as a tool to reduce brood size in poor food conditions, and at the same time compensate this by maternal T? This compensation would be only favourable in good food conditions, when the full brood can be raised, but detrimental under poor food conditions when rapid brood size reduction should occur. We hypothesized that maternal hormones have context-dependent effects, being beneficial for the chick under good food conditions, but detrimental under poor food conditions. We studied this in the rock pigeon, a species in which first eggs contain much lower T concentrations than second eggs. We created clutches of two first eggs, one injected with T to the level of the second egg (T chicks), and one injected with vehicle (C chicks). Pairs were then housed under either good or poor food conditions. In the good food condition T chicks grew faster than C chicks, and the reverse was the case in the poor condition. In the latter only, T chicks had a much higher early mortality than C chicks. Both T treatment and poor food negatively affected the humoral immune system. These results not only may solve the paradox mentioned above, but also explain contradictory results of in ovo T injections in the literature.



Quantifying the energetic costs of mating in a simultaneous hermaphrodite

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Although sexual reproduction is a joint effort, reproductive interests of mating partners are often in conflict because traits that are favoured by one sex can be costly to the other sex. Most work on sexual conflict has been conducted in species with separated sexes. However, sexual conflict also acts on simultaneous hermaphrodites and has been shown to lead to evolutionary arms races. An important consequence of sexual conflict is that it can increase the costs of mating interactions. The direct energetic costs of mating in simultaneous hermaphrodites have not been quantified, so far. Therefore, we measured these costs in the simultaneously hermaphroditic freshwater snail *Lymnaea stagnalis*. Via experimental manipulation we allowed animals to perform male courtship only, male courtship plus insemination and no courtship and copulation. We then measured how much resources these hermaphrodites subsequently put into egg laying. The results show that courtship is the most costly part of male mating behaviour. To tease apart which component of the male courtship behaviour is most costly, we measured respiration rate throughout mating sequences. This revealed that the probing stage, when the donor searches for the female gonopore with its muscular penis-carrying organ, is the expensive part of courtship in terms of respiration rate. Hence, the energy required for each behavioural component of mating can be quantified by measuring respiration in *L. stagnalis*. Taken together, these findings reveal why male mating has previously been found to be expensive and add to the general understanding of the relevant costs involved in mating.

Correlations between surface behaviour and underwater acoustics revealed by D-tag data in pilot whales

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Pilot whales (*Globicephala melas*) have rich vocal repertoires, which suit their marine environment well, in which sound is much more useful than vision for orientation and communication. However, the function of these repertoires of highly diverse sound types is still poorly known. Attempts have been made to correlate sounds to surface behaviour, but these suffered from several methodological difficulties. The use of (omnidirectional) hydrophones, for example, often led to interference of target sounds of the focal group by nearby vocal activity of other animals. Furthermore, the behavioural measurements used were typically of a qualitative nature, which makes comparisons among studies difficult. In the current study, we made use of D-tags, on-animal devices that record both soundscape and dive depth of an individual. Moreover, we measured the surface behaviour using a protocol that generates quantifiable

parameters in a standardized way. We categorized the recorded vocalisations into clicks, pulsed sounds and three different types of whistle sounds. Correlations between different vocal categories and behavioural parameters were analyzed using Random Forest analysis. Our results revealed that sound types are correlated to behavioural parameters in such a way that allows future use of observations on surface behaviour to infer underwater activities. In addition, our study provides further insights into the function of vocal variation in pilot whales and delivers a standardized methodology to study other marine mammal species.

Singing behaviour of male great tits reveals personality and phenotypic quality

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Variation in songbirds singing behaviour has been shown to reflect male quality as well as its attractiveness to the opposite sex. On the other hand, linking singing patterns to personality traits is still under debate. In this study, we investigated how male singing traits of the great tit (*Parus major*) relate to its partner's behavioural traits and pair's reproductive performance. Using playback experiments we found that male's song repertoire size and rival song overlapping differed consistently between individuals. One of these traits, the song repertoire size, was positively related to clutch size. We also found that males with higher rates of song overlapping were paired with females exhibiting more aggressive threat display against a nest predator, the great spotted woodpecker (*Picooides major*). Given that high rate of song overlapping can be associated with male aggressiveness, this result supports the prediction that males are paired with females alike. Our findings contribute to previous knowledge that males singing behaviour may indicate individual quality, and some aspects of personality of a wild living bird can be captured by using simple repeatable test that can be conducted in the field.

Genetic integration of dispersal and exploratory behaviour in Great Tits

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Dispersal – the movement of individuals from their place of birth to the place of breeding – is an important ecological parameter influencing population dynamics and gene flow. In wild animal populations, there is often large variation in the distance of dispersal. Part of this variation may have a genetic basis, but this has rarely been tested. Recently, it has been suggested that consistent and heritable individual differences in basal behavioural traits, such as exploration, boldness, sociability, and aggression – often described as variation in ‘animal personality’ –



may be functionally linked to individual life-history and dispersal strategies. While there is good empirical evidence for phenotypic correlations between dispersal and personality traits, it is unclear whether dispersal and personality are also genetically integrated. Here, we show dispersal and exploration behaviour to be both heritable, and genetically coupled, in a common wild songbird, the Great Tit (*Parus major*). Using pedigree and phenotypic data from a wild great tit population, we found quantitative genetic variation both for the distance of dispersal within our study area and the rate at which individuals explore a novel environment measured in a standard behavioural test. Moreover, we found a positive genetic correlation between dispersal distance and exploration rate, thereby providing evidence for the genetic integration of animal personality and dispersal. These findings indicate a potentially important behavioural mechanism underlying between-individual differences in dispersal, show that dispersing individuals may form a genetically non-random subset of the population, and highlight the potential for dispersal to evolve in response to selection.

You mob my owl, I'll mob yours: birds play tit-for-tat game

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Reciprocity is fundamental to cooperative behaviour and has been verified in theoretical models. However, there is still limited experimental evidence for reciprocity in non-primate species. Our results more decisively clarify that reciprocity with a tit-for-tat enforcement strategy can occur among breeding pied flycatchers *Ficedula hypoleuca* separate from considerations of byproduct mutualism. Breeding pairs living in close proximity (20-24 m) did exhibit byproduct mutualism and always assisted in mobbing regardless of their neighbors' prior actions. However, breeding pairs with distant neighbours (69-84 m) either assisted or refused to assist in mobbing a predatory owl based on whether or not the distant pair had previously helped them in their own nest defense against the predator. Clearly, these birds are aware of their specific spatial security context, remember their neighbours' prior behaviour, and choose a situation-specific strategic course of action, which could promote their longer-term security, a capacity previously thought unique to primates.

Immunity, stress and personality in wintering great tits in Northern Europe

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According to the life-history theory, individual variation in the capacity to mount immune responses against novel antigens is caused by the costs of immune responses to the hosts. We studied these costs

by immune challenging wintering great tits (*Parus major*) with a novel antigen, killed *Brucella abortus* suspension. We found that immune challenge depleted somatic resources as indicated by a body mass loss and elevated relative proportion of heterophils to lymphocytes (H/L ratio) in the peripheral blood of birds. Birds with high pre-immunisation H/L ratios mounted weaker antibody response, which is indicative of stress-induced suppression of humoral immune response and is consistent with the concept of an antagonistic cross-regulation between different components of the immune system. The latter finding suggests a novel diagnostic value of H/L ratios, which reinforces the utility of this simple haematological index for prediction of the outcomes of complicated immune processes. We also found some associations between immunity and behaviour: tolerance to captive conditions on the basis of damage inflicted to tail feathers, and propensity to produce alarm calls at release. The birds that had highest H/L ratios at capture inflicted the maximum extent of tail damage during the week spent in captivity, and produced lowest antibody titres against the novel antigen, which indicates a strong covariation between the tolerance of captivity, perceived stress and immune responsiveness. Propensity to produce alarm calls was lower in birds which tolerated captivity better. It was found that bold individuals mounted stronger immunity against *Brucella abortus* and survived better under conditions of severe winters.

IGF-1 and developmental speed in great tit (*Parus major*) nestlings: a brood size manipulation

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In the post-hatch period all nestlings are in the race to achieve the best nutritional status possible, which dictates the developmental speed and overall fledging condition. Insulin-like growth factor 1 (IGF-1) and its downstream signalling are the main mediators that regulate growth-rate of the maturing animals by stimulating cell proliferation, differentiation and survival in most tissues. The following study tested through brood size manipulation, how the fledglings of free-living Great Tits (*Parus major*) vary their IGF-1 levels in the changing environmental conditions and how it affects their condition. We found that fledglings in reduced broods had elevated IGF-1 levels, which mediated increased fledging condition and more profound mass gain during nesting phase. Although the studies with wild birds are almost completely lacking, our results suggest that IGF-1 plays an important role in how nestlings are able to cope with changing environmental conditions, when trying to assimilate the available energy for their growth and development.

Can feather corticosterone level predict behavior under stressful conditions?

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Stress response is a measure to counteract with unfavorable environmental conditions which involves activation of the hypothalamic-pituitary-adrenal axis. As a result glucocorticoid hormones are released and several physiological as well as behavioral changes occur to overcome stressful conditions. Measuring avian stress hormones (corticosterone) from bird feathers enables to attain a long-term and integrated measure of individual's stress response. We were interested in whether wild-grown feather corticosteroid levels relate to birds activity in captivity and predict behavior in stressful conditions (exposure to predator image). We used two different locomotor activity components – hopping and flapping against cage bars, which can respond differently to stressors. Wild-caught greenfinches with higher feather corticosterone content showed decreased activity levels in terms of hopping when compared to birds with lower feather corticosterone levels. The same result held up in under stressful conditions. Current study elucidates how stress can affect behavior with potential effects on life-histories of birds.

Tutor song recognition independent of syllable order in zebra finches

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Young male zebra finches learn their songs from an adult conspecific (a 'tutor') during a sensitive period early in life, comparable to speech acquisition in human infants. Both songbirds and human infants first memorize the vocalizations of their parents, after which they start vocalizing themselves. Although female zebra finches do not sing, they do form a memory of the tutor song, which they prefer to novel conspecific songs. In this study, we investigated whether the temporal order of song elements (syllables) is important for tutor song recognition. We tested this by exposing adult female and male zebra finches that were reared with their parents to tutor song (i.e. the song of their father) in which the sequence of syllables was systematically altered, versus novel song with the same modifications. The normal sequence of syllables tutor and novel songs were used as control for tutor song preference. We compared this with songs in which the middle two syllables or the first and last syllables were switched, or in which we completely reversed the song syllable sequence. Both males and females recognized their father's song in all tests. We found a significant preference for the tutor song in females in all tests. In males, we found a significantly greater level of vocal responsiveness towards novel song compared to tutor song. Thus, although both sexes recognized their father's song in all tests, this was expressed through different behavioural responses. We suggest that the behavioural difference arises from territorial behaviour in males, but not females, where males showed greater levels of vocalization in response to the novel song. Since there were no differences between the tests with different song modifications, the temporal structure of

a song is not important for recognition. Rather, acoustic features of the song seem to be sufficient for recognition. These results do not exclude the capability of detecting differences in song syllable sequence. Further research is needed to investigate whether differences in temporal song structure are detected without influencing recognition, and which acoustic features are used for recognition of the tutor song.

Precopulatory assessment and sex role during mating in the simultaneous hermaphrodite *Eisenia andrei* (Oligochaeta, Lumbricidae)

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In simultaneous hermaphrodites, precopulatory assessment and reciprocal mating (sperm exchange) are expected to reduce the cost of copulation, maximizing the product of male and female fitness. Nevertheless, unidirectional transfer of sperm occurs more frequently than thought in species that are considered to mate reciprocally. In the present study, we show that in the earthworm *Eisenia andrei*, sperm transfer is not reciprocal in at least 20% of the cases. In order to identify the factors that are responsible for the adoption of sex roles in this species, we performed a series of experimental and observational studies under laboratory conditions. We focused on the analysis of within-pair variation in body size, reproductive history and number of copulatory setae - a male-biased trait involved in manipulation of the partner's reproductive behaviour. The results show that body size and reproductive history, although sometimes found to be important, are not reliable predictors for whether sperm transfer is unidirectional or reciprocal. Interestingly, mating pairs collected from a breeding population revealed a positive relationship between the total number of copulatory setae of mating partners, suggesting that assortative mating might occur based on this character. Taken together, these findings hint at the possibility that unidirectional sperm transfer may result from uneven mate manipulation (via setae) and that earthworms choose to avoid partners with a larger number of copulatory setae than themselves to reduce the overall costs of mating.

The effect of the temporal structure of noise on the swimming behaviour of the European seabass

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Sound is extensively used by fish for a variety of functions, including predator-prey interactions, conspecific communication and soundscape orientation. However, the use of sound by fish may be hindered by the noise from human activities in and around waters. In order to make reliable noise impact assessments, it is crucial to understand how various features of man-made noise affect fish behaviour. For example, some noises are intermittent (e.g. seismic surveys, pile-driving) while others are continuous (e.g.



ships, wind turbines). Moreover, their amplitude may be fluctuating or consistent over time. In this study, we investigated if noise intermittency and amplitude fluctuation contribute to changes in fish behaviour. Groups of four European seabass were exposed to a series of four noise treatments (continuous with consistent amplitude, continuous with fluctuating amplitude, intermittent with consistent amplitude and intermittent with fluctuating amplitude) in a large basin. Their behavioural changes were video-recorded and subsequently analysed with computer software. All noise treatments affected sea bass behaviour by causing startle responses, increased group cohesion and increased swimming depth. In addition, noise intermittency significantly prolonged the recovery time of the changed behaviour. This shows that the severity of underwater noise impact on fish is not simply related to the total sound intensity and sound exposure alone, as commonly assumed in noise impact assessments. In fact, the behavioural impact depends on the temporal structure of noise and less noise (intermittent compared to continuous) can even have a stronger effect.

Long-tailed macaques (*Macaca fascicularis*) understand what conspecifics can see in a competitive situation

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The presence of Visual perspective taking (VPT), an understanding of what others can see, is a prerequisite for advanced cognitive capacities like Theory of Mind. The presence of VPT in monkeys is a much-debated topic, and several different paradigms have been developed to test its existence. However, all face interpretational problems since results can be explained by simpler cognitive mechanisms than VPT. Therefore, we adjusted one method where two individuals compete for access to food, visible or invisible for the dominant competitor (Hare *et al.* 2000). The new set-up prevented monkey subjects to use two alternative mechanisms: behavioural reading or approaching the less accessible food. Our results show that long-tailed macaques tended to have a preference for the food item invisible for their dominant competitor. Surprisingly, they occasionally adopted an alternative strategy to obtain both (visible and invisible) food items, by first approaching the most at risk food item visible for their competitor, whereas in cases where only one food item was retrieved by subjects, they significantly preferred the invisible food item. In contrast with previous research, our results cannot be explained by alternative simpler cognitive mechanisms, since behavioural reading was prevented by a one-way mirror between the dominant competitor and the food containing occluders, and accessibility was equal to both food items. Therefore, this is the first unequivocal evidence of VPT in a monkey species.

Differences in novelty behaviour for pigs with different coping styles

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Studies in various species have shown that an animal could react either proactively or reactively to a challenging situation. The backtest has been used in pigs to classify them as either proactive or reactive animals. In this test a piglet of about two weeks of age is put on its back and manually restrained. During one minute, the number of escape attempts is counted along with other measures such as for instance the number of vocalizations. Piglets that struggle much are considered to be high resisters (HR) or the more proactive animals and piglets that hardly struggle are considered to be low resisters (LR) or the more reactive animals. Many studies have been done to investigate whether pigs with different coping styles (i.e. HR or LR pigs) differ in behaviour, physiology and immunology. Until now, the results are inconclusive. We performed a study with 480 pigs that were tested in a backtest at one and a half week of age and subsequently tested at 7 weeks of age in a group-wise 10 min human approach test (HAT) and at 13 weeks in an individual 10 min novel environment test (NET), where after 5 min a bucket was dropped from the ceiling. During the HAT, HR pigs tended to spent more time near the person than LR pigs. During the first 5 min of the NET, we found hardly any differences between HR and LR pigs, but after the drop of the bucket, HR pigs were more vocal, more active, and tended to touch the bucket sooner than LR pigs. In contrast, LR pigs stood more alert than HR pigs. These results show that pigs with different coping styles indeed react differently in response to a challenging situation.

Song divergence in grey-breasted wood-wrens: an experimental test of immediate noise-dependent plasticity

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Song divergence among populations of the same bird species can yield reproductive divergence and promote speciation or restrict hybridization. Environmental factors such as habitat-specific ambient noise have been shown to shape song divergence among bird populations. However, with the exception of urban habitat, it typically remains untested whether such divergence concerns long-term evolutionary adaptations or short-term phenotypic plasticity. Two genetically distinct subspecies of the grey-breasted wood-wren (*Henicorbina leucophrys*) replace each other along an elevational gradient in the tropical mountain region of the Sierra Nevada de Santa Marta in Colombia. One subspecies resides in noisy low-elevations habitat and the other in relatively silent



high-elevation habitat. In the current study, we used multi-day automated recordings, which confirmed habitat-specific ambient noise patterns and distinct subspecies-specific songs. In addition, in concert with these recordings we used experimental exposure to test whether an artificial high-frequency noise band, typical for the low-elevation habitat, affected the singing of the high-elevation subspecies. We did not find any spectral or temporal changes related to the exposure treatment, suggesting that the subspecies song differences are not just based on short-term flexibility. Our findings do not exclude the possibility that song variation in other avian species of tropical forests may exhibit short-term phenotypic plasticity and we highly recommend future studies using our method of experimental exposure.

Tracking the social lives of Great Tits

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In nature an individual's personality could have a significant influence on its interaction with the social environment. Yet very few studies focussed on how personality interacts one on one with a social, non-artificial environment. Until now researchers were unable to simultaneously identify the personalities of individuals and quantify the pair-wise interactions between individuals in the wild. By using a state of the art tracking technology called Encounternet, in a natural population of personality typed great tits, we now can study the social interactions of a large number of individuals in the wild simultaneously. In the beginning of the breeding season 2012, we equipped over 25 Great Tits with radio-transmitters which transmitted a signal every 5 seconds that could be received by wireless receiving stations distributed throughout the forest for a number of consecutive days. Giving us detailed information over more than two hundred close range encounters (within 5 meters) and several hundred longer range encounters.

Stress Effects on Parental Provisioning in Two Forest Passerines

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Recent studies have found that perceived predation risk affects several aspects of reproduction via the trade-off between foraging and antipredator behavior. However, how the presence of predators changes parental provisioning rates and food allocation between different-sized nestmates is poorly understood. In this study, the Pied Flycatcher (*Ficedula hypoleuca*) and the Great Tit (*Parus major*) were used as model species to investigate parental provisioning strategies when exposed to the Sparrowhawk (*Accipiter nisus*) model. Species-specific differences emerged in overall provisioning rates as well as in food allocation decisions within the brood. Pied flycatchers, but not Great Tits, reduced provisioning rates remarkably after the encounter with the predator. Pied flycatchers

preferred senior chicks to juniors under normal conditions, but this preference for bigger chicks disappeared under predation risk. In contrast, great tits increased the preference for bigger chicks under predation risk. Moreover, the duration of nest visits was reduced by predation risk only in the females of great tits. We conclude that small passerines alter several aspects of their behavior in response to fear stress, and these predator-induced changes are species-specific. If danger to parents occurs repeatedly, temporal reductions in provisioning rates or in brooding bouts may have cumulative and potentially harmful consequences on offspring performance.

A "distance-dependent" mechanism for a survival advantage of vigilant individuals in groups

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Many animals use vigilance to escape from predation. In models of vigilance in groups, an intrinsic survival advantage of vigilant individuals over non-vigilant individuals is often assumed. Proposed mechanisms include delayed reactions, and imperfect transmission of information in groups, leading to reduced likelihood of reactions by non-vigilant individuals to the detection of predators by vigilant individuals. Here we demonstrate a previously unreported mechanism through which a survival advantage for vigilant individuals can arise. In our spatial model there are no a priori specified differences between vigilant and non-vigilant individuals except for vigilance. The novelty in our model is a distance-dependent probability to detect a predator, which in addition to the assumption that a predator targets the closest individual, easily gives rise to an advantage for vigilant individuals: non-vigilant individuals have a lower survival probability when they happen to be closer to the predator than vigilant individuals. We expect that this distance-dependent effect is compatible with previously described mechanisms. However, we find that the advantage for vigilant individuals depends on group size, movement and spread. We therefore expect that in models where both group size and vigilance can co-evolve, a "group-movement dependent" and "group-spread dependent" advantage of vigilance will play an important role.

The position of male broiler breeder feeding places in cages in relation to fertility and welfare.

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In order to reduce ammonia emission group cages for broiler breeders were developed. A problem was that the fertility of broiler breeders in these cages was too low. An experiment is performed to generate suggestions for a layout that could improve male welfare and, thus, fertility.



Welfare of exotic pet species in the Netherlands

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Housing conditions, care taking and availability of adequate and correct information at the points of sales and at the pet owner are the most plausible situations and contexts where the welfare of exotic companion animals might be at stake (Vinke, 1998; Anonymous, 2007). In the present research, part of the Research Program Welfare of Companion Animals and in commission of the Dutch Ministry of Economic Affairs, Agriculture and Innovation, many stakeholders and organisations, like shelters, rescue centres and pet shops, but also veterinarians, were approached for in-depth interviews and questionnaires, to get insight into the welfare problems of exotic companion animals (fishes, birds, reptiles, amphibians and mammals). In the results, specifically, regular exotic pet species, like the rabbit, guinea pig, and the goldfish, appear the most affected species addressing the nature, the intensity and the number/frequency of health and welfare problems during trade and in companionship. Specific points of interest towards welfare and health were identified per species. Herewith, it was alarming to identify that most of the mentioned problems could be classified under the verb neglecting and serious symptoms could definitely be prevented if owners would be better informed and more alert on their animals' health and welfare. The results of this research should directly be applicable to be discussed and implemented by the public authorities and government as a basis for future policy on animal trade and the use of exotic animals as companion animals in The Netherlands. As aforementioned vulnerable

species will probably be categorized as positive on the positive list (art 33, GWWD) in the future, this finding(s) will give a complex applicability into the present intended policy. To effectively improve the welfare of pet animals in the Netherlands, more attention should be paid to education and information and several trade channels to the consumer should be confined and focussed on species specific products and quality.

The function of brain lateralization

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The function of cerebral lateralization is yet unknown even though several theories exist. Improved cognitive performance might be a benefit which may have developed by evolutionary selection. The advantages may have been especially relevant in dual-task processing. In humans the left hemisphere is generally more involved in language, while the right hemisphere is more involved in visuospatial tasks. Using functional transcranial Doppler sonography (fTCD) individual strength and direction of lateralization is assessed during a word generation task (language) and a 3D mental rotation task (visuospatial). The relationship between cerebral lateralization (pattern and strength) and both single- and dual-task performance was examined in 43 participants, right-handers and non-right-handers, to have access to different lateralization patterns. We found that having a more strongly lateralized brain does indeed correlate to a better task performance both on single and dual task performance.

