

# Association for the Study of Animal Behaviour

## Winter Meeting 2009



### INDIVIDUAL SPECIALISATION Programme & Abstracts

THURSDAY, 3 DECEMBER

*Coffee and registration from 9:30*

*10.20 Welcome and Introduction*

#### 1. Task Specialisation

10.30 – 11.20 **PLENARY: *Specialization and optimization of reproduction and work in insect societies***

**Francis Ratnieks**, University of Sussex, UK

11.20 – 11.50 ***Individual specialisation and activity levels in social insects***

**Ana B Sendova-Franks**<sup>1</sup>, **Nigel Franks**<sup>2</sup>: <sup>1</sup>University of West of England, UK;  
<sup>2</sup>University of Bristol, UK

Individual specialisation and behavioural types in insect societies are part of the division of labour, one of the defining features of true sociality. A fascinating corollary of studies of the division of labour among workers is elitism, that is, the high frequency of task performance by certain workers across different tasks. More widely, elitism corresponds to a behavioural syndrome because it represents a multiple positive correlation among the performances of different behaviours. Activity distributions are right-skewed so only a few individuals exhibit high performance and the majority perform much less work. Such distributions could occur as the result of a positive-feedback mechanism or even more parsimoniously through mutual exclusion in time or space. For example, threshold models of

division of labour demonstrate that more sensitive individuals with lower thresholds for a particular task would exclude others from performing it simply by doing the task and reducing the stimulus to a level that is below the thresholds of their nestmates. This may have implications for individual specialisation in general because such a mechanism could give rise to the transformation of many normally distributed biological characteristics into skewed activity distributions that are stable over time. Last but not least, insect societies show that behavioural syndromes may exist not only at the individual but also at the social level.

#### 11.50 – 12.20 ***Individual variation in cerebral lateralization and its ecological consequences***

**Marco Dadda, Angelo Bisazza**: University of Padova, Italy

Cerebral lateralization refers to sensory, motor, and cognitive abilities that are specialized to either the left or right cerebral hemisphere. We did laboratory tests to compare cognitive performance of goldbelly topminnows from lines that have been selected for six generations for high and low degree of lateralization. Poorly and strongly lateralized fish showed similar foraging abilities; however higher performance in more lateralized individuals emerged when foraging was concurrent with another task (e.g. monitoring a predator or evading a harassing male) suggesting that hemispheric specialization favours multitasking. Strongly lateralized fish also showed more efficient shoaling and were faster at learning a spatial task. However fish with strong hemispheric specialization were severely handicapped when they had to take a quick decision between two options (e.g. a large vs. a small shoal) each seen by a different eye, since they tended to choose the option processed by the hemisphere dominant for analyzing social stimuli irrespective of its quality.

#### 12:20 – 12.50 ***Sex roles in parental care: specialisation and cooperation***

**Freya Harrison**<sup>1,2</sup>, **Tamás Székely**<sup>1</sup>, **Zoltán Barta**<sup>3</sup>: <sup>1</sup>University of Bath, UK; <sup>2</sup>University of Oxford, UK; <sup>3</sup>University of Debrecen, Hungary

Biparental care is an Evolutionary Stable Strategy (ESS) if one parent cannot raise the young alone, or if parents only partially compensate for decreases in their partner's care effort. Behavioural and evolutionary models of biparental care generally assume that "care" is a unidimensional variable. In reality, care often comprises several qualitatively different behaviours and investment in one care behaviour (e.g. provisioning) may be traded off against investment in another (e.g. defence). In many species with biparental care, males and females specialise in providing different types of care. We hypothesised that sex-specific costs of care behaviours and ensuing role specialisation could stabilise cooperation between parents, as it would result in compensation becoming more costly or even impossible. We use an individual-based simulation to test this hypothesis. Our results may be applicable to behaviours other than parental care, as individuals can exhibit role specialisation in various social contexts.

12:50 – 14:00 Lunch

## 2. Animal Personality I

14:00 – 14:50 **PLENARY: *Causes and consequences of individual differences in behaviour in three-spined sticklebacks***

**Alison Bell**: University of Illinois, Urbana-Champaign, USA

There is growing evidence that individual animals behave in a consistent way through time and across situations. For example, individual sticklebacks that are particularly 'bold' in the presence of a predator are also relatively aggressive toward other sticklebacks. However, the boldness-aggressiveness behavioural syndrome is not universal in sticklebacks, and varies over both developmental and evolutionary timescales. In this talk, I will argue that examining variation in the strength of behavioural correlations can provide insights into the causes and consequences of within-individual consistency in behaviour, between-individual variation in behaviour, and the evolutionary history of personality. After summarizing some of what we've learned about personality in animals, I will highlight a few unexplored but promising areas for future investigation.

14:50 – 15:20 ***Testing for correlations in boldness and aggression within individuals and across populations of fish***

**Gabrielle A. Archard, Victoria A. Braithwaite**: Pennsylvania State University, USA.

Studies of temperament in animals require the demonstration of consistent individual variation in behaviour across situations or contexts. Consistent differences in temperament between populations can provide evidence for the selection factors that have shaped temperament. In a series of experiments using wild-caught individuals, we tested for behavioural variation between individuals and between populations of the tropical poeciliid fish *Brachyrhaphis episcopi*. Like the guppy, different populations of *B. episcopi* are naturally exposed to different levels of predation pressure. We used open field trials to investigate the repeatability of temperament within individuals. We also compared temperament across three types of assay (open field, novel object and emergence). Fish from high predation environments appeared 'bolder' than low predation fish, there was high within individual repeatability, and 'boldness' scores covaried across the different tests. In a further test we quantified aggression in mirror image stimulation trials. The temperament literature suggests boldness is often positively correlated with aggression. However, fish from high predation populations inspected their image less, not more, and females - not males - were more aggressive in low predation populations.

15:20 – 15:50 ***Behavioural reaction norms: Animal personality meets individual plasticity***

**Niels J. Dingemanse<sup>1</sup>, Anahita J.N. Kazem<sup>2</sup>, Denis Reale<sup>3</sup>, Jonathan Wright<sup>2</sup>:**

<sup>1</sup>Max Planck Institute for Ornithology, Germany; <sup>2</sup>NTNU, Norway; <sup>3</sup>Universite du Quebec a Montreal, Canada

Recent studies in the field of behavioural ecology have revealed intriguing variation in behaviour within single populations. Increasing evidence suggests that individual animals differ in their average level of behaviour displayed across a range of contexts (animal ‘personality’), and in their responsiveness to environmental variation (plasticity), and that these phenomena can be considered complementary aspects of the individual phenotype. How should this complex variation be studied? Here, we outline how central ideas in behavioural ecology and quantitative genetics can be combined within a single framework based on the concept of ‘behavioural reaction norms’. We illustrate using empirical datasets from passerine birds (great tits) and fish (stickleback). This integrative approach facilitates analysis of phenomena usually studied separately in terms of personality and plasticity, thereby enhancing understanding of their adaptive nature.

15:50 – 16:10 *Tea*

### 3. Animal Personality II

16:10 – 16:40 ***Measuring individual differences in reaction norms in field and experimental studies: a power analysis of random regression models***

**Julien G.A. Martin<sup>1</sup>, Daniel Nussey<sup>2</sup>, Alastair Wilson<sup>2</sup>, Denis Réale<sup>3</sup>:** <sup>1</sup>Universite de Sherbrooke, Canada; <sup>2</sup>University of Edinburgh, UK; <sup>3</sup>Universite du Quebec a Montreal, Canada

Interest in measuring individual variation in reaction norms using mixed-effects and, more specifically, random regression models has grown apace in the last few years within evolution and ecology. However, these are data hungry methods, and little effort to date has been put into understanding how much and what kind of data we need to collect in order to interpret results of these models reliably. Here we conducted simulations to address three central questions. First, what is the best sampling strategy to collect sufficient data to test for individual variation in reaction norms using random regression model? Second, when can we be confident that a failure to detect variance in plasticity (defined as the reaction norm slope) represents a biological reality rather than a lack a statistical power? Finally, does the common practice of censoring data from individuals with one or few repeated measures improve or reduce power to estimate variation in reaction norm components? We have also developed a series of easy-to-use functions in the “pamm” statistical package for R, which is freely available, that will allow researchers to conduct similar power analyses tailored more specifically to their own data. Our results reveal potentially useful rules of thumb: large dataset (N > 200) are needed to evaluate individual differences in reaction norm slopes; intermediate number of individuals / number of replicates ratios maximize power to detect random effects; individuals with one or few observations should be included in the

analysis to maximize power to detect variance in plasticity. We discuss the wider implications of these simulations and remaining challenges, and suggest a new way to standardise results that would better facilitate comparison of findings across empirical studies.

16:40 – 17:10 ***Ratings of zoo chimpanzees (*Pan troglodytes*) and orangutans (*Pongo pygmaeus* and *Pongo abelii*) are not anthropomorphic projections***

**Alexander Weiss, Miho Inoue-Murayama, James E. King, Mark J. Adams, Tetsuro Matsuzawa**: University of Edinburgh

Despite findings to the contrary, a critique of using subjective ratings of nonhuman animal personality is that these measures may be products of anthropomorphic projection. We will demonstrate two new forms of principal components analysis using existing personality data and test the hypothesis that personality dimensions in nonhuman primates are the products of anthropomorphic projections. Subjects were 202 chimpanzees housed in U.S. and Australian zoos; 151 chimpanzees housed in Japanese zoos, research institutes, and sanctuaries; and 174 orangutans housed in U.S., Canadian, Australian, and Singaporean zoos. We show that a) personality dimensions emerging from the covariance matrix of animal effects do not differ from the dimensions that were described in previous studies and b) the personality dimensions emerging from covariance matrix of rater effects differ somewhat from the animal dimensions. We also show that c) the dimensions emerging from covariance matrix of rater effects differ between the three samples. These findings are contrary to predictions from the hypothesis that ratings are anthropomorphic projections, highlight the ways in which raters perceive personality, and suggest a new method of assessing the reliability of personality ratings.

17:10 - 17:40 ***Effects of personality on sexually selected signals in great tits***

**Marc Naguib**; Mathieu Amy: Netherlands Institute of Ecology, The Netherlands

Differences among individuals in the expression of sexually selected signals and in their response to sexually selected signals often are attributed to differences in individual quality. Yet, such differences in signals and in response to signals may reflect more than merely differences in quality or motivation such as more intrinsic differences among individuals. Individuals often differ consistently across time and contexts in behavioural traits and such systematic differences are commonly described as behavioural syndromes or personality. Personality has been shown to have social and fitness correlates, but it remains unclear how individuals actually determine others' personality and if personality is reflected in sexually selected signaling strategies. Here we show relations between personality and undisturbed signing in great tits, *Parus major*, and how vocal responses to playback and spatial movements, determined by radio tracking, vary with male personality. We discuss the implications of the results for understanding the evolution of sexually selected signals including individually different strategies in territory defense and spatial behaviour.

17:40 – 18:10 ***Personality and life-history strategies in pea aphids, *Acyrtosiphon pisum****

**Wiebke Schuett**<sup>1,2</sup>, **Sasha R.X. Dall**<sup>1</sup>, **Till Eggers**<sup>2</sup>: <sup>1</sup>University of Exeter, UK;  
<sup>2</sup>University of Osnabrueck, Germany

Individuals are often specialised in their behaviour such that they are consistent in their behavioural expressions over time and/or across contexts but vary from other individuals in the average level of behaviour shown. The function of these so-called personality differences is still widely unknown. However, recent theory suggests that life-history trade-offs favour their evolution. Here, we present an experiment in which we test if personality traits are linked to distinct life-history strategies. Theory predicts that high risk-takers should invest mainly in early reproduction, have high growth-rates and short lifespan; whereas low risk-takers should invest more in later reproduction, have low growth-rates and high life expectancy. To test these predictions we used the pea aphid, *Acyrtosiphon pisum*, as a model system. Pea aphids were repeatedly tested for their risk-taking behaviour towards a predatory ladybird, before they were randomly assigned to either a treatment group which experienced regular ladybird encounters or a control group. Influences of behaviour and treatment on life-history traits are presented and discussed.

*Wine reception and poster session from 18.10*  
FRIDAY, 4 DECEMBER

*Coffee from 9:30*

**4. Individual Niche Specialisation**

10:30 – 11.20 **PLENARY: *Ecological and evolutionary forces maintaining niche variation within populations***

**Daniel Bolnick**: University of Texas, Austin, USA

Many species are regarded as ecological generalists because individuals within a given species collectively use a wide variety of resources. This typological approach to ecology may be misleading, however, because such generalist species are often composed of an ecologically heterogeneous collection of specialized individuals. Where does this heterogeneity come from? At a proximate level, among-individual niche variation reflects genetic and/or environmental variation in physiological, biomechanical, and behavioral phenotypes. Genetic variance reflects evolutionary processes such as disruptive selection, immigration, and assortative mating. Environmental trait variance reflects a combination of social, behavioral, and ecological forces. I provide examples of each of these proximate and ultimate forces, drawing from a variety of case studies but with particular emphasis on three-spine stickleback. In conclusion, I argue that it is more appropriate to view the ecological niche as a property of an individual organism. This redefinition of the ecological niche facilitates study of among-individual variation, niche evolution, and perhaps ecological dynamics. To the extent that behavior plays a role in this niche variation, this approach also highlights the role of individuals' behavior in evolution and ecology.

## 11.20 – 11.50 *Measuring foraging specialisations using stable isotopes*

**Stuart Bearhop**: University of Exeter, UK

While foraging specialisations are one of the most long recognised forms of individual specialisation, they can be notoriously difficult to quantify in many species (e.g. because of difficulties in observing foraging behaviour or accessing dietary information). Even in those species where dietary information is easily accessed, it has to be collected over lengthy periods in order to be able to assess the degree of specialisation, and, aside from being extremely laborious, it is often not possible to do this over the entire annual cycle. This has meant we still have little idea on how such individual traits develop, the length of time they might persist over and the extent to which they are determined by the genetic versus environmental components. For some time now ecologists have been using stable isotope ratios measured in consumer tissues to infer diet and more recently have begun to use the approach to investigate individual based variation in foraging preferences. I will discuss how by carefully selecting among tissues and isotope ratios it is possible to build metrics of individual foraging specialisation which can be then used to investigate the causes and consequences of such behaviour. I will also outline how new Bayesian solutions to isotopic mixing models may enable us to link such inferences to individual dietary components.

## 11.50 – 12.20 *Individual meerkat, *Suricata suricatta*, foraging specialisations and habitat productivity*

**Alice Leyland**<sup>1</sup>, **Sarah J. Hodge**<sup>1</sup>, **Wiebke Schuett**<sup>1,2</sup>, **Sasha R.X. Dall**<sup>1</sup>: <sup>1</sup>University of Exeter, UK; <sup>2</sup>University of Osnabrueck, Germany

Individual foraging specializations are widespread and their study is becoming increasingly popular. Despite this, few studies, and none in social species, have focused on the possibility that individual specializations might vary in accordance with habitat productivity despite a relatively rich theoretical literature which could be applied to such a focus. This theory suggests that individual specializations should increase with habitat productivity. To test this I looked at individual foraging specializations in meerkats, their variation over time and their relationships, if any, with rainfall, a proxy for habitat productivity. I also measured the overall degree of individual specialization in the population over a long period of time (8 years) to ascertain whether meerkats were more specialized at the individual level than the population niche would suggest. My findings suggested that meerkats are generalist at the individual level, with low degrees of individual specialization when compared to other species. Some individual specializations were found to increase with productivity, offering support for the theoretical literature. Meerkats also tended to follow social foraging model predictions, demonstrating efficient space use. This is the first study of its kind to look at associations between individual specialization and habitat productivity in a social species. In conjunction with further such studies it will add to the understanding of adaptive individual consistencies and their effects and evolution in a social species.

12:20 – 12.50 ***Genetic variation in social preference depends on population context in Drosophila melanogaster***

**Julia B. Saltz**<sup>1,2</sup>: <sup>1</sup>University of California, Davis, USA; <sup>2</sup>University of Southern California, USA

What makes individuals unique? Differences between individuals within a population may be due to differences in genetic factors, environmental effects, and the complex interplay between these. Untangling the development of individual differences in behavior is difficult in traditional systems (including humans), because a given genotype may be studied only once before experience and the unavoidable effects of ontogeny make consecutive studies incongruent. The vinegar fly *Drosophila melanogaster* provides a solution to this problem: inbred lines may serve as parents of countless “replicate individuals” whose environments may be manipulated independently. Here, I examine individual differences in social decision-making in male flies: do different genotypes prefer different group sizes? Using a two-choice paradigm, I measured the amount of time that a focal male spent in groups differing in size (i.e., number of individuals) but not sex ratio. I found substantial genetic variation in the amount of time that males spent in groups overall, as well as genetic variation in preference. Interestingly, male behavior and the magnitude of genetic variation both depended on the average size of groups in the arena. Average group size is correlated with population density in flies (Saltz and Foley, unpublished ms), so this indicates that population-level dynamics affect individual decision-making and the expression of genetic variation. This is, to my knowledge, the first examination of genetic variation in social preferences. Understanding choice behaviors is critical to identifying the causes of individual variation because genetically-based choice behavior introduces genetic variation in the environmental contribution to behavior. In other words, different genotypes experience different environments, and these environments affect behavior. Measuring the specific behavioral outcomes of the choices I examine here is the next step in my research.

12:50 – 14:00 *Lunch*

14:00 – 15:00 **TINBERGEN LECTURE: *Parental investment and biparental care***

**Kate Lessells**, Netherlands Institute of Ecology

15:00 – 15:30 *Tea*

**5. Impacts of Individuality**

15:30 – 16:00 ***Some are more equal than others: the consequences of individuality in animal behaviour for transmission of diseases***

**Lisa M. Collins**: Royal Veterinary College, UK

Mathematical models predicting where, when and how infectious diseases will spread often assume that all individuals in a population behave identically. However,

previous research has shown that individuals are far from clone-like in their behaviour. Instead they demonstrate high variability in their decision-making processes and behavioural strategies, relative popularity and ranking in a group and display different 'personality' types. Likewise, group dynamics have been shown to be affected both by individual behaviour, and by externally-imposed environmental effects. It is likely that these individual and group differences together have an impact on disease dynamics, determining who is most likely to be infected and how rapidly the disease will spread through a population. Recent research has highlighted the importance of understanding these differences in the spread of diseases as varied as tuberculosis, Tasmanian Devil facial tumour disease, canine distemper virus, toxoplasmosis and schistosomiasis, in a wide range of species across the animal kingdom. Methods of behaviour analysis from empirical and field studies will illustrate the interdependence of disease and behaviour using social network analysis, time series, eigenbehaviour decomposition, economic tests of preference, time allocation budget and coping strategies. The ways in which individual and social behaviour affect disease dynamics and conversely, how disease impacts on behavioural patterns, sociability and group dynamics, will be considered. Suggestions for how individual behavioural differences can be incorporated into future epidemiological models will be discussed, along with some of the possible restrictions and pitfalls to consider.

16:00 – 16:30 ***Comparing individuality to phenotypic plasticity in facilitating evolution***

**Marios N. Richards, Joanna J. Bryson**: University of Bath, UK

Natural selection requires variation to operate – there is no change without options to select between. Variation is therefore itself subject to selection, including its rate and extent. Individual plasticity (including cognition) is known to facilitate evolution in two ways. First, it accelerates evolution when a species is far enough from its local optima that even unreliable processes like individual learning provide evidence that genetic evolution can exploit about which animals are closer to optimal. But second, plasticity also slows genetic convergence once the adaptive phenotype is close enough to genetic specification that individuals can reliably learn to be 'fit'. This reliability reduces selective pressure, and thus retains diversity. Here we present an extension to a classic model of the interaction between plasticity & natural selection (Hinton & Nowlan 1987), to examine whether increased genetic variation in offspring can play a similar role to individual plasticity. We find that a higher recombination rate significantly accelerates the earlier phase of the model, where the organism is ill-suited to its environment and deleterious traits require elimination from the genome. This indicates that genetic variation plays a role similar to plasticity in this stage. We speculate that a behavioural search for identity in social species may play a similar role.

16:30 – 17:00 ***Rainbow trout use mutual assessment to settle contests***

**Sarah Millsopp**: Queen's University Belfast, UK

Aggression is ubiquitous in the animal kingdom, whenever the interests of individuals conflict (Morrell et al., 2005). Competition by overt aggression may be extremely costly, possibly causing fatal injury, enhanced predation risk, greater

energy expenditure or stress leading to increased susceptibility to pathogens (Huntingford and Turner, 1987). Animal contests are usually settled on the basis of asymmetries in fighting ability or resource holding potential (RHP), resource value and resource ownership (Arnott and Elwood, 2008). Selection is expected to favour individuals that gather accurate information about the costs and benefits of conflict (Parker, 1974). Contestants with information about their own RHP are expected to benefit if they can also assess the ability of their opponent (Arnott and Elwood, 2009). Such “mutual assessment” allows rivals to obtain a reliable estimate of differences in ability between themselves and their opponent. They can then use this information in deciding whether to continue fighting (Arnott and Elwood, 2009). Alternatively, contestants may rely solely on an estimate of their own fighting ability or RHP and persist in contests in accordance with their own fighting ability. This is known as self assessment (Taylor and Elwood, 2003). In order to assess if rainbow trout use self or mutual assessment in settling contests, dyads consisting of either two small (mean: 91g) or two large (mean: 158g) fish were set up. If rainbow trout use self-assessment in deciding whether or not to fight, a higher cost will be incurred by the large pairs when compared with small pairs. However, if mutual assessment is used, no difference would be seen. There was no difference found in the costs incurred by the different sized pairs of fish and so, we hypothesise that rainbow trout use mutual assessment when settling contests. Implications for farmed rainbow trout are discussed.

17:00 – 17:30 ***Caring or not caring, the evolution of maternal care in the European earwig***

**Flore Mas**: University of Basel, Switzerland

Within the order Dermaptera, maternal care behaviours are expressed in a wide diversity of species and studying their variation of expression contributes to our understanding of the origins and specialization of different maternal care strategies across various environments. The close contact between mothers and newly hatched offspring inside a nest promoted interactions between mothers and offspring and set the stage for potential conflict of interests over the allocation of maternal investment within and/or between the broods. Theory of parent-offspring conflict predicts the evolution of offspring signalling that influences the level of parental investment. Thus a mother’s caring behaviour is directly affected by her offspring, but eventually the resolution of conflict also depends on the coevolution of maternal and offspring traits that are expressed in the same individual at different time. I studied the European earwig, *Forficula auricularia*, where I explored the chemical communication and found that offspring produced condition-dependent chemical signals that influence maternal care behaviours (foraging and food provisioning). But allocation of maternal food to offspring depends not only on individual solicitation signalling but also on the interactions with other siblings. Thus maternal decision is a day to day assessment of overall clutch conditions and offspring potentially manipulative signalling which contributes to maintain variation in maternal care specialization.

*End*

## **POSTER ABSTRACTS**

### **Adams MJ, King JE, Weiss A (Univ Edinburgh)**

*Subjective well-being is genetically correlated with personality in orang-utans.*

Differences in personality and subjective well-being are described by dimensions that appear to be conserved across primate lineages. In orangutans, the personality dimensions are Extraversion, Dominance, Neuroticism, Agreeableness, and Intellect. We assessed personality and subjective well-being in 174 zoo-housed orang-utans. In order to understand the evolvability of personality and subjective well-being in orangutans, we estimated trait heritability simultaneously with a multivariate animal model using Markov chain Monte Carlo. Heritability point estimates for the five personality traits ranged from .29 for Agreeableness to .43 for Intellect. The heritability of subjective well-being was .36. Consistent with findings on humans and chimpanzees, orangutan happiness was genetically correlated with Extraversion ( $r_A = .49$ ), Agreeableness ( $r_A = .53$ ), and Neuroticism ( $r_A = -.47$ ). Thus, it is possible for genetic differences in well-being to be maintained by correlated responses to selection for personality.

### **Bergvall UA, Schäpers A, Kjellander P, Weiss A (Univ Edinburgh)**

*Evaluation of methods used in personality research in different disciplines: experiments with fallow deer.*

An increasing number of research measuring different aspects of animal personality, but there have been few attempts to compare different methods. There is also a need for non-invasive methods for measuring personality in wild species in order to get the ecological relevance and the opportunity to compare personality with fitness measures. In this study, we measured personality in the fallow deer using methods from differential psychology, experimental psychology and ethology and behavioural ecology. We used in total 183 measures from 18 novel-object experiments, observer ratings, 78 non-novel object measures including dominance tests, learning tests and behavioural observations for each individual over three years. These methods were used on the same set of 15 animals, and the preliminary results reveals four separate domains named; boldness, dominance, exploration and flexibility. Noteworthy, we found correlations between factor scores for boldness, exploration and dominance measured with different methods. This means that different comparable methods can be used in order to measure animal personality. We also found a domain for flexibility, only revealed by behavioural observations of agonistic behaviour (negative reinforcement) and free shaping (positive reinforcement). The preliminary conclusions are that ratings seem to be a good method to describe personality, and also that exploration and boldness very much interfere when measured in tests and that boldness correlates with food intake in experimental situations. The non-invasive method has also been used on wild fallow deer during two years, and measures from the behavioural observations splits into the same three factors, making this method a good tool in the future.

**Budaev S (Univ Sussex)***Definition and measurement of animal personality*

Individual behavioural differences and personality in animals is becoming a hot topic in modern ethology, behavioural ecology and even in human personality psychology. However, there exist many difficult conceptual issues related to the definition and measurement of personality and other related constructs. In this presentation I am going to discuss several of them. What is personality? In what sense and to what extent is it consistent? How can consistency be measured? How can we avoid anthropomorphism in the study of animal personality and is it possible at all? How human cognitive architecture (of the researcher) could potentially influence personality assessment? Finally, I will briefly discuss applicability of various statistical methods (factor analysis, structural equations, mixed effects models) used for the measurement of animal personality.

**Culloch RM, Pomeroy PP, Twiss SD (Univ Durham)***Pinniped personalities? Preliminary evidence of individual behavioural consistency in wild breeding adult female grey seals (*Halichoerus grypus*).*

Recent studies on various taxa suggest behaviour may not be as plastic as initially thought, and that an individual's behaviour may be constrained, with individuals expressing consistent behavioural responses across contexts. Consequently individuals may have limited scope to behaviourally adjust to short term local environmental variation, which may have important implications for how particular individuals respond to rapid environmental change. To date there have been few purely in-field studies addressing consistent individual behavioural differences. This is primarily accredited to the challenging conditions experienced in-field. However, recent meta-analysis has shown that repeatability estimates were higher in the field than in the laboratory, giving support to the plausibility and importance of carrying out in-field personality studies. Ultimately, in order to understand the ecological and evolutionary importance of personality in wild animals we have to apply these techniques to natural populations. Maternal behaviour of known females (n=11) was recorded over two successive seasons (2007-2008). Females showed evidence of inter-annual consistency in; (i) time devoted to particular behaviours (Presenting & Nursing, ICC=0.55, p=0.03; Comfort Move, ICC=0.84, p<0.001), (ii) sequence duration of key behaviours (Presenting & Nursing, ICC=0.56, p=0.03) and (iii) in some behavioural transitions (Alert → Pup Check, ICC=0.76, p<0.001; Resting → Aggression, ICC=0.67, p=0.01). These consistent individual patterns existed despite large inter-annual variations in their local physical and social environments (for example, median distance to pup, ICC=0.07, p=0.42). These preliminary findings suggest that plasticity for particular behaviours is limited, whilst others remain flexible. We discuss these findings and consider the potential fitness consequences that behavioural constraints may impose upon pinnipeds in their natural environment.

**Gyuris E, Tartally A, Barta Z (Univ Debrecen)***Individual behaviour in Firebugs (*Pyrhocoris apterus*)*

Experimental data have recently been accumulating supporting the hypothesis that not only humans but also several animal species have personalities. A simple

definition of personality would be a set of interconnected behavioural traits which manifest itself across situations (Carere 2005). A model by Max Wolf et al. (2007) explains individual differences in a population, in which individuals apply different strategies in a given situation as a trade-off between present and future reproduction. We tested this model on the two wing morphs, i.e. brachypterous and macropterous specimens of the firebug (*Pyrrhocoris apterus*), since several researchers (e.g. Socha 1993) have already demonstrated that the two wing morphs differ in their life history strategies. Thus these bugs are ideal subjects to test the model, i.e. to reveal whether the specimens with different life history strategies have different personalities as well. The experimental animals had been collected from a wild population. The results showed that the observed bugs do have personalities. We managed to demonstrate that the two wing morphs of the firebug (*Pyrrhocoris apterus*) differ in their behaviour, which accords well with the model by Wolf et al. (2007). However, in the course of our observation we could detect difference only between female macropterous and brachypterous bugs. This means that macropterous females reacted more rapidly to flicks than brachypterous ones, i.e. macropterous females proved to be bolder than brachypterous ones; besides, they visited more novel objects, discovering their new environment more thoroughly in this way.

#### **Hellström G, Magnhagen C (Swedish Univ of Agricultural Sciences)**

*Is risk-taking behaviour inherited or learned? Results from a common-garden experiment with two populations of Eurasian perch.*

Individuals from different populations of Eurasian perch are known to differ in risk-taking behaviour. Variation in predation pressure has been suggested as a key factor causing these differences, but little is known about the underlying mechanism by which predation generates risk-taking phenotypes in perch. We compared the degree of boldness between two natural populations of Eurasian perch, living under different predation regimes, and the same populations hatched and reared under identical conditions, free from predation. By this common-garden approach we sought to find out 1) whether variation in boldness reflects genetic differentiation between populations or is an expression of environmentally shaped phenotypes and 2) if there is any variation in the degree of plasticity between the populations. The wild fish differed in boldness, with fish from the low predation-risk population acting bolder than fish from the high risk environment. The reared populations did not differ in behaviour and both populations behaved boldly. Only the fish originated from the high predation population changed its behaviour between wild and reared ecotypes, hence displaying phenotypic plasticity.

#### **Hirvonen H, Koskinen J (Univ Helsinki)**

*Individual variation in innate and learned antipredator behaviour*

Individual variation in predator recognition and avoidance in fishes has long been thought to be due to differences in learning. However, recent studies on predator-naïve salmonid fry have shown ample individual variation in innate antipredator behaviour. Arctic charr fry, for example, show heritable variation in specialised innate responses to a native predator. Still, it is unclear, if low innate responsiveness can be compensated for by learning, or if individuals with strong innate responses are able to boost their responsiveness by superior learning ability, or neither. Using Arctic charr

fry and a full-sib-half-sib mating design, we examined (i) the relative significance of innate and learned components contributing to variation in behavioural responses to olfactory cues of a sympatric predator, and (ii) how much of the phenotypic variation in innate and learned responsiveness is heritable. In general, charr fry showed strong innate responsiveness to pikeperch odours. Significant variation was found in phenotypic plasticity, i.e. reaction norms between non-predator and predator environments, in some behavioral traits but not in all. Family-based differences in reaction norms may indicate that plasticity has a genetic basis. Repeated conditioning enhanced the intensity of most antipredator responses. However, the relative strength of innate and learned components varied depending on the trait. Either (i) learning was similar and not dependent on innate response level, or (ii) learning overcompensated for low innate responsiveness. The latter was found in a trait showing considerable additive genetic variation in learning, and thus may indicate evolutionary potential.

### **Kluen E (Univ Helsinki)**

*Behavioural syndromes in blue tits (Cyanistes caeruleus).*

Behavioral syndromes are co-varying behavioural responses of an individual that occur across contexts. We studied blue tits in a nest-box breeding population in the Southwest of Finland. We recorded behavioural responses of the birds by means of 'simple' behavioural test (aggression score, breathing rate) when taking measurements of the individuals of both adults and nestlings. We recorded nest-defences of the females just before egg hatching (breeding season). Additionally we carried out a cage experiment in which response to a plastic toy, activity and time to escape from the cage was measured for adult birds in both the breeding season and in winter. All data is collected in the years 2007-2009. We analyzed the data for repeatability of the different behavioural responses for the individuals and test whether the behavioural responses are co-varying.

### **Lantová P, Zub K, Šíchová K, Borowski Z (Univ South Bohemia)**

*Linkages between personality and metabolism in the root vole (Microtus oeconomus)*

The rate of energy metabolism is one of the basic vertebrate characteristics, nevertheless – despite many studies concerning variability on species or population level – high variability among individuals remains largely ignored. Recently, this problem was highlighted and proposed to be studied from the view of inter-individual differences in behaviour. Behaviour and metabolism are both controlled by the same hormonal and neurological axis and should be correlated. Relationship between activity and the rate of metabolism is expected, moreover, reaction to an unknown environment (e.g. respirometry chamber) mirrors individual's ability to cope with stress and may greatly influence measured values. We compared behaviour of root voles in novel environment (open field test) with several metabolic characteristics – RMR, time to get on the level of RMR and min, max, mean of first 10 minutes of measuring. The effect of sex and season were controlled. We identified four behavioural traits and found negative relationship between immobility and RMR. It took careful and tentative voles more time to calm down to the level of RMR. However, some questions remain unanswered and direct observation of animal behaviour in metabolic chambers might shed more light on the topic.

**Muller H, Chittka L (Queen Mary College)**

*Novelty response and bumblebee "personality": Do individuals vary consistently in their response to novel colours?*

The past ten years saw the number of publications reporting the existence of animal personality increase drastically. It is now recognised that many vertebrates and a few invertebrates do show individual-specific consistency in their behaviour across time and context, sometimes in ways that can be paralleled with human personality. To investigate animal personality in a social insect, our work aimed at assessing behavioural consistency in the bumblebee, *Bombus terrestris*. We focused on a behavioural dimension commonly used in personality studies: the response of an individual to novelty (neophilia/neophobia spectrum). A bee's response to novelty potentially has an important impact on her (colony) fitness. Indeed, during her life (up to five weeks) a bee forager will be exposed to numerous flower species, all varying in their profitability. The variability in flower profitability is further enhanced by competition with other pollinators and seasonal effects (every flower type having a limited flowering time). Therefore a forager is likely to have to change her main food source, resulting in her having to investigate novel food sources. There are three potential responses to novelty: neophobia (repulsion), neophilia (attraction) and indifference. Here we used a foraging paradigm to quantify individual bees' responses to novelty and to assess the repeatability of this response over time. We found that 36 out of 81 individuals showed consistency in their response to novelty over a few hours but that only 3 out of the 25 bees tested showed consistency in their behaviour over three days. We conclude that bumblebee foragers, as a group, fail a basic criterion of personality in terms of responses to novelty, i.e. long term consistency. There is a short term consistency that indicates day-to-day variation in behavioural states, and such short term consistency might be deceptive in other studies on animal personality as well.

**Péron F, Bovet D, Nagle L (LECC)**

*Different role taking in a cooperative task in African Grey parrots.*

Three African grey parrots were tested on their social cognitive skills during cooperative tasks. We decided to test the four levels of cooperation defined by Boesch & Boesch (1989). Our birds went easily through the first level of similarity and then show difference in their behaviour in order to solve the synchrony and cooperating levels. At the end we conduct an experiment on collaboration when birds had to play different complementary roles. One bird has to perch in order to release enough space for allowing a second bird to pull a string. Pulling the string moved a tray on which food was placed and then the perched bird can get off and the join the partner to eat. They were trained in a non social situation to realize each task independently. Then they were tested in pair. They improve rapidly in solving the task. We note only three spontaneous role exchange so we decided to place the birds into their non preferred side (task) in order to see what would be their reactions. Most of the time they just wait, looking at the partner and maybe wondering what they have to do. Thus, it seemed that birds show a preference in the task that have to solve and even though they were all trained in the different jobs they continue to solve the task only when they were playing a specific role. This specialization could be explained

with bird personality and abilities. Indeed, the perching bird is calm, and patient and not so good in pulling the string. Zoé has difficulties step in onto the perch. This situation unexpected made us questioning about a new protocol in order to test their specialization in different cooperative task.

**Potter SJ (Univ Exeter, Cornwall)**

*The specialism of generalism: early stages of adaptive radiation by adaptive niche expansion in European lacertid lizards.*

The level of individual diet specialisation is believed to increase with the total niche width of a species, and morphology has previously been examined as a proxy for dietary specialisation with mixed success. Specimens of 6 species of lacertid lizards (*Acanthodactylus erythrurus*, *Lacerta lepida*, *Lacerta monticola*, *Psammodromus algirus*, *Podarcis hispanica* and *Podarcis muralis*) were taken from the collections of the Museo Nacional de Ciencias Naturales in Madrid. Morphological traits were measured and the stomachs removed. Stomach contents were identified to order level and their volume was calculated. From this, individual specialisation and total niche width were calculated following previously demonstrated standard procedures. It was found that increasing total niche width does coincide with increased individual specialisation, meaning that generalist species consist of more specialised individuals. Head volume shows a relationship with dietary specialisation, but the relationship varies between species.

**Robertson AR, Cant MA, McDonald RA, Bearhop S (Univ Exeter, Cornwall)**

*Sett Menus: The Ecological and Evolutionary origins and consequences of individual foraging behaviour in group-living badgers.*

Individual variation in the exploitation of food resources is an important aspect of foraging ecology, with a number of important ecological, evolutionary and conservation implications. 'Individual foraging specialisations' where individuals exploit only a narrow range of the total population niche has been recorded in many species, but to date the drivers and impacts of this behaviour are poorly understood. Variation in diet occurs at many levels within and among individuals (sex, age, rank, location, season etc). In group living species many foraging options are further constrained by territoriality and potentially via the induction of social and/or genetically heritable foraging traits. I aim to investigate the origins and consequences of individual variation in diet in a group living mammal: the Eurasian Badger (*Meles meles*). Levels of foraging specialization among badgers will be quantified using stable isotope analyses (SIA) of several tissue types. These data will then be combined with field data on individual movements, long term pedigree data and optimisation models to answer several questions: 1) How is variation in diet related to variation in foraging ranges and fitness, at both the individual and group level? 2) What is the effect of heritable traits, the natal environment and social learning on the development of individual foraging strategies? 3) How are these foraging strategies constrained by physiological changes and seasonal availability of resources? This study will give insight into the cause and effect of variations in foraging preference and also shed light on the spatial and temporal stability of this behaviour.

**Twiss SD, Franklin J, Culloch RM, Pomeroy PP (Univ Durham)**

*Pinniped personalities? Preliminary evidence of consistent individual behavioural types in wild, breeding male grey seals (Halichoerus grypus).*

Traditionally, individual variation within populations is often considered as 'unfortunate' deviations from an adaptive optimum. However, recent research demonstrates consistent individual variation in behaviour patterns (known as 'behavioural types' or 'personalities') suggesting that such variation may constitute differing adaptive 'solutions' to complex physical and social environments. 'Personalities' (defined as individual behavioural differences that are consistent over time or across contexts) have been quantified in taxa ranging from molluscs to mammals. However, very few studies have examined wild populations, and there are no such studies of pinnipeds. Here, we present two lines of evidence for the existence of 'personalities' in wild male grey seals at the North Rona breeding colony (Scotland). First, we examined detailed activity budgets available for males adopting the dominant, resident strategy over two consecutive breeding seasons (1988-1989). Individual males showed strong inter-annual consistency in their time devoted to alert behaviour with a high repeatability measure significantly greater than zero (ICC = 0.833, 95%CI = 0.415-0.963,  $F_{7,8} = 10.95$ ,  $p = 0.002$ ). Crucially, males' alertness tendencies show no relationship within seasons with any of our potential explanatory factors; (i) state dependent factors (male body size, mass or mass loss rate), (ii) age, (iii) colony attendance parameters (length of stay, arrival or departure dates), (iv) home range size, (v) rates of sexual or aggressive interactions, or (vi) dominance rank. Moreover, alertness was unrelated to measures of within-season mating success or reproductive longevity (number of years males were present at the colony) and therefore independent of short or long-term fitness consequences. We also examined male movement patterns (median hourly distances moved) derived from a sub-metre accurate GIS containing locations of individually identified males during the 2001-2003 breeding seasons. Again, we used only dominant, resident males that were present in all 3 seasons ( $n=13$ ). Individual movement patterns remained consistent across all 3 breeding seasons (ICC = 0.545, 95%CI = 0.212-0.811,  $F_{12,24} = 4.59$ ,  $p = 0.001$ ) despite inter-annual changes in colony attendance patterns, territory size, access to females, number of neighbouring males or degree of inter-annual site-fidelity. Whilst in-field tests of personality are challenging, especially if based purely on observations (as opposed to experimental behavioural assays typical of laboratory based studies), it is important to develop ways to identify and quantify the existence of personalities in natural populations. Only by doing this, can we hope to ascertain the ecological and evolutionary relevance of personalities.

**van der Post DJ (Georg-August-Univ Göttingen)**

*Self-organized learning processes can drive diet "specialisation" in individuals and groups*

Learning is a powerful mechanism through which animals can change their behaviour and specialise, e.g. eating certain food types. Using an individual-based model with a rich environment we show that simple reinforcement learning of food preferences based on food quality, automatically generates divergence in learning. These effects are enhanced according to the diversity and distribution of resources. We observe that individuals diverge in diet by chance due to initial biases in learning, but that this is increased when individuals compete for food in groups. On the other hand group

living can spontaneously generate social influences on learning and cultural inheritance. This generates a new level of individuality. In that case we find that competition increases cultural divergence between groups. In both cases the competition mediated divergence occurs through a structuring of learning opportunities in the environment and only works in a sympatric setting. Our results emphasize the feedback of behaviour on the environment through depletion of resources, which in turn shapes learning opportunities. Such self-organizing processes set the stage for interactions between behavioural and genetic evolution.

**Wells DL, Millsopp S (Queen's University Belfast)**

*Paw preferences in the domestic cat, *Felis silvestris catus**

This study examined the paw use of 42 cats, *Felis silvestris catus*, on 3 tasks designed to explore asymmetrical motor behaviour. Task 1, an exercise involving food retrieval, encouraged lateralised behaviour, while Task 2 (an exercise involving reaching for a toy suspended overhead) and 3 (a challenge involving reaching for a toy moving along the ground) encouraged ambilateral motor performance. Females had a greater preference for using their right paw; males were more inclined to adopt their left paw. Findings suggest there are two distinct populations of paw preference in the cat that cluster very strongly around the animals' sex.