



ASAB WINTER MEETING 2017

# Sexual selection: do we still need to test the alternatives?

7<sup>th</sup> & 8<sup>th</sup> December 2017

Organisers:  
**Nina Wedell &  
David Shuker**



## ABSTRACTS OF SPOKEN AND POSTER PRESENTATIONS

## **SPOKEN PRESENTATIONS**

**THURSDAY 7<sup>TH</sup> DECEMBER 2017**



### **PLENARY: Hope Klug**

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#### **The operation of mate acquisition revisited**

Sexual selection is one of the most fundamental concepts of evolutionary biology and a major evolutionary driver. However, despite decades of theoretical and empirical development, the founding principles of sexual selection are still debated and in some cases misunderstood and even dismissed. Empirically, unexpected patterns are the norm and post hoc explanations rather than well-supported a priori predictions prevail in sexual selection studies. Recently, there has been debate over the key factors driving sexual selection. This debate has revealed that in many cases we cannot reliably predict when sexual selection will operate or how it will vary across scenarios. Thus, while previous work has provided strong insight into the factors affecting sexual selection, our conceptual understanding of sexual selection is in need of refinement. In this talk, I will discuss the importance of various factors in driving patterns of mate acquisition and sexual selection. In particular, I will focus on well-studied factors, including the operational sex ratio, and factors that have received relatively less attention, such as general resource competition and chance, and explore how such factors influence mating dynamics and sexual selection.

### **Peter D. Sozou**

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#### **Who's the one? Male selection of a courtship target under female choice**

If a male meets several females but can court only one, how does he make his selection? Going for a top female leads to a potentially high payoff if he succeeds in mating, but may also make it more likely that the female rejects him in favour of a superior suitor. I explore this trade-off by means of a two-period model. In period 1, each individual (female and male) encounters a number of members of the opposite sex, drawn at random from a large population. Each male then selects which female to court. In period 2, each female who has received courtship attention mates with the best male from those who have courted her. Optimal strategies are calculated. I show that the male

should not necessarily court the best female he meets. Results will be presented showing how the optimal selection strategy for the male depends on the encounter rate in period 1, on his own quality, and on the statistical distribution of female quality (and how this determines the male's payoff from mating). Possible biological systems where this form of analysis could be applicable will be discussed.

**Gonçalo S. Faria**, Susana A. M. Varela & Andy Gardner

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### **The relation between R. A. Fisher's sexy-son hypothesis and W. D. Hamilton's greenbeard effect**

Recent years have seen a growing interest in the overlap between the theories of kin selection and sexual selection. One potential overlap is in regard to whether R. A. Fisher's "sexy-son" hypothesis, concerning the evolution of extravagant sexual ornamentation, may be framed in terms of W. D. Hamilton's greenbeard effect, concerning scenarios in which individuals carry an allele that allows them to recognize and behave differently toward other carriers of the same allele. Specifically, both scenarios involve individuals behaving differently toward social partners who exhibit a phenotypic marker, with linkage disequilibrium between marker and behaviour loci ensuring genetic relatedness between actor and recipient with respect to the behaviour locus. Here, we explore the mathematical connections between the sexy-son and greenbeard effects, and we use the resulting conceptual bridge to import theoretical results from the field of kin selection to sexual selection, and vice versa, yielding new insights into both topics.

**Szymon M. Drobniak** & Zofia M. Prokop [TALK CANCELLED]

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### **Genetic variation in male attractiveness: seeing the forest for the trees**

Female choice based on multiple male traits, rather than on any single one, has been reported in many species and may well be a rule rather than an exception. However, the implications this has for selection acting on choosiness itself remain underappreciated. We argue that this constitutes one of the important impediments to our understanding of the evolution of mate choice. We discuss this issue primarily in the context of the Fisherian model of sexual selection. We review theory and empirical data, showing how the crucial parameter of the model—genetic variation in male attractiveness—can be estimated when attractiveness is a function of multiple traits. Based on the reviewed

theory, we show how relying on individual male traits, instead of overall attractiveness, can produce biased estimates of Fisherian benefits of female choice. This bias can be substantial, especially when many traits contribute to male attractiveness. We discuss a number of methodological issues that, we hope, will stimulate future studies and help resolving the long-standing mystery of mate choice.

**PLENARY: David Hosken**

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***Drosophila simulans*: a study in sexual selection.**

*Sexual selection: Testing the Alternatives* remains one of the most insightful books on sexual selection, and our work with *Drosophila simulans* addresses many of the issues raised there. This ranges from assessing direct and indirect costs and benefits of female preference through to testing for inter-sexual genetic correlations. I discuss this work and more and highlight the pragmatic approach we have been using in our work.

**Liam R. Dougherty**<sup>1, 2</sup>, Emile van Lieshout<sup>1</sup>, Kathryn B. McNamara<sup>1</sup>, Joe A. Moschilla<sup>1</sup>, Göran Arnqvist<sup>3</sup> & Leigh W. Simmons<sup>1</sup>

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**A sexual arms race drives the correlated evolution of male and female genital morphology in a seed beetle**

The correlated morphology of male and female genital traits seen across animal species is hypothesised to arise via two main co-evolutionary processes: sexual selection (via cryptic female choice) or sexual conflict (via sexually-antagonistic coevolution, or SAC). However, in most species it has proven difficult to distinguish between these two processes. One important feature of SAC is that it is driven by fitness costs imposed on one sex by the other. Such costs are expected to be particularly strong for species in which the male genitalia are able to physically harm females (a phenomena known as traumatic mating). In this study, we examine the evolutionary association between harmful male genital morphology and female immune function and copulatory tract thickness across 13 populations of the seed beetle *Callosobruchus maculatus*. We find clear evidence of SAC in the form of male-imposed costs to females: the degree of female tract scarring (a proxy of the amount of harm received by females) was greater in those populations with both longer male genital spines and a thinner female copulatory tract

lining. Our study thus provides rare evidence for SAC (or a 'sexual arms race') of male and female genital traits at the species level.

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### **Restricted diet affects the relative importance of pre- and postcopulatory selection in the guppy**

Over the last decade there has been growing evidence that environmental variations may cause the intensity of sexual selection to vary in space and time. Among the ecological traits that could affect the reproductive performance of males and females, food availability may alter both mating rate of females and the expression of male sexual traits. Here we used the guppy (*Poecilia reticulata*), a species living in a highly dynamic environment and a model for sexual selection studies, to investigate how food availability affects the intensity of both the episodes of sexual selection. Our variance-partition analysis revealed that the relative importance of sperm competition (the largest source of variation in male reproductive success) was greater when fish were fed *ad libitum* compared to their food-restricted counterparts. On the contrary the relative contribution of mating success on male reproductive success was significantly higher when fish were food-restricted than when fish were fed *ad libitum*, indicating a stronger precopulatory selection under food-restricted conditions. Our results suggest that the relaxation of selection alternatively on pre- and postcopulatory traits through small-temporal scale variation may help maintaining genetic variability in those traits.

**Marc Naguib**<sup>1</sup> & Simon C. Griffith<sup>2</sup>

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### **Sexual selection and beyond: why do birds sing?**

Animal signalling and specifically birdsong has been key in understanding fundamental issues in behavioural ecology and sexual selection. There is striking evidence from many species that male bird song plays a key role in mate attraction and territory defence and thus is under direct inter and intra sexual selection. Yet, males often sing at times and at rates where the function is less clear. In zebra finches, *Taeniopygia guttata*, males sing substantially when being exposed to females and many laboratory studies have shown that females show clear preferences for specific male song traits. Yet, the evidence for high song rates indeed making males more attractive has been mixed, and

a lack of data on male singing phenology in the wild hampers a good understanding on the selection pressures on male singing under natural conditions. Here we will present data from laboratory mate choice experiments and standardized large-scale field recordings and experiments from a well-studied field population in the Australian Outbacks on male singing activity across various breeding stages and on responses to playback, providing new insights into the potential function of bird song beyond male attraction and territory defence.

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### **Paternal care, female reproductive costs and the evolution of female colour in birds**

Female ornamentation has traditionally been considered as a genetic byproduct of male ornamentation tempered in its conspicuousness by natural selection. However recent theoretical work predicts that male mate choice may promote the evolution of female ornamentation depending on the balance between paternal care and female reproductive costs. Here we provide the first comprehensive test for the role of these factors on the evolution of female plumage colouration using spectrometric data from songbird species belonging to closely related passerine families. Our results indicate that the evolution of female colouration is governed by complex interactions between paternal care and female reproductive costs, which may explain why female ornamentation is more labile than male ornamentation. This finding underscores the need for a paradigm shift when it comes to the origin and evolution of female ornaments.

**Eleanor Bath**, Juliano Morimoto & Stuart Wigby

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### **The belligerence of breeding: mating mediates female aggression**

In the traditional sexual selection framework, competition and aggression are thought to be the domain of males, regardless of their species. However, female-female competition is widespread across species, from flies to birds to humans. Winners in female competitions may produce more, or better, offspring; gain more productive territories; or acquire higher quality mates. Despite these dramatic consequences for females and their offspring, we know little about what causes female aggression, its

relationship to sexual selection, and its fitness consequences. In this study, we show that female aggression in the fruit fly *Drosophila melanogaster* is strongly stimulated by the receipt of sperm at mating, and in part by an associated seminal fluid protein, the sex peptide. We further show that the post-mating increase in female aggression may be decoupled from the costs of egg production and from post-mating decreases in sexual receptivity. Our results suggest that a trait influenced by sexual selection – the male ejaculate - can have a surprisingly direct influence on aggression in recipient females. Male ejaculate traits thus influence the female social competitive environment with potentially far-reaching ecological and evolutionary consequences.

### **Ingo Schlupp**

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### **Male mate choice, female ornamentation, and female competition**

Within sexual selection theory, the concept of mate choice plays a critical role. Thirty years ago, in the book edited by Bradbury and Andersson, the idea that - in addition to females -, males might also evolve to choose their mating partners did not capture much attention. Recent advances in theory and a growing number of empirical studies are now pushing male mate choice more into the mainstream of the discussion. I will briefly review some of the general hypotheses for mechanisms and conditions under which male mate choice may evolve. For this I will use examples from livebearing fishes, and other animals. Furthermore, I will make a strong connection with female ornamentation and female competition. Does male mate choice drive the evolution of female ornaments, just like female choice drives the evolution of ornaments in males? And can the existence of male mate choice lead to the evolution of female competition? I think currently there are more good questions on this than answers, and I hope to incite a lively discussion on the topic.

**FRIDAY 8<sup>TH</sup> DECEMBER 2017**

### **PLENARY: Suzanne H. Alonzo**

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### **Sexual selection: Will embracing complexity help us find simplicity?**

Sexual selection has been debated since first proposed by Darwin. We now know that sexual selection is an important evolutionary force, driving the evolution of striking

traits that can appear not only beautiful, but also counter-intuitive and even ridiculous. Researchers in the field have generated extensive theory and gathered large amounts of data across a diversity of organisms, aimed at understanding the prevalence and dynamics of sexual selection. Perhaps surprisingly, this impressive accumulation of theory and data has often fed rather than reduced the intensity of the debate. Fortunately, one of the powerful things about biology is that when lost among alternative theories and embroiled in controversies, we can go out and ask the organisms what they actually do. In this talk, I review what I have learned about sexual selection from over two decades of research on the ocellated wrasse (*Symphodus ocellatus*). I will review the somewhat surprising patterns of sperm competition, mate choice, sexual conflict and parental care we have found in this species and then describe what I think these unexpected but understandable patterns tell us about sexual selection in this species and beyond. I suggest that the debate surrounding the field of sexual selection may have more to say about us humans- how we ask questions and the way do science- than about the idea of sexual selection or its importance and prevalence in the natural world.

**Leonor R. Rodrigues**, Flore Zélé, Inês Santos, João Alpedrinha & Sara Magalhães

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### ***Wolbachia* modifies sperm precedence patterns in spider mites**

In spider mites, only the first mating of a female is effective. Still, males often copulate with mated females. This behaviour may be adaptive if it decreases the costs of incompatible crosses that occur, for example, when uninfected females mate with males infected by *Wolbachia*, an endosymbiotic bacteria. Such crosses result into cytoplasmic incompatibility (CI), entailing the embryonic death of fertilized offspring. *Wolbachia*-uninfected females are thus expected to evolve strategies to avoid the costs of CI. For example, they may mate multiply to recover offspring viability. However, such recovery may not be effective in species with first male precedence and its occurrence may be contingent upon infection history. To test this, we performed experimental evolution of spider-mite populations that were infected or uninfected by *Wolbachia* (controls), or in which *Wolbachia*-uninfected females were placed with *Wolbachia*-infected and *Wolbachia*-uninfected males at each generation (selection treatment). After 20 generations, *Wolbachia*-uninfected females from the selection treatment reduced the degree of CI by mating with an uninfected male after mating with an infected male. This was not the case when *Wolbachia*-uninfected individuals were from control populations. Our results suggest that the evolution of CI-reducing strategies is contingent upon the evolutionary history of infection.

## **Andreas Sutter**

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### **Impacts of meiotic drive on sexual selection in house mice and beyond.**

Meiotic drivers distort Mendelian segregation in their favour, commonly through gamete interference in males. Drivers reduce organismal fitness, leading to intra-genomic conflict. Drive in males can have drastic consequences on sperm competitiveness, which can impact both female and male reproductive strategies. Pre- and/or postcopulatory sexual selection may enable females to avoid the fitness costs associated with fertilisation by driver-bearing males. Here, I summarise experiments on the interplay between sexual selection and the *t* haplotype, a meiotic driver in male house mice that is associated with strong fitness costs due to genetic incompatibility. While I found no evidence for precopulatory discrimination against male carriers of the *t* haplotype, these males are strongly disadvantaged in sperm competition, providing a fitness benefit to polyandrous females. Interestingly, sperm precedence patterns change when *t* males compete against each other compared to competition between wild type males. I discuss the implications of the presence of meiotic drivers in study populations for detecting multiple mating and its fitness consequences, the heritability of sperm competitiveness, and sperm precedence patterns.

**Rebecca A. Boulton**<sup>1</sup> & David M. Shuker<sup>2</sup>

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### **Unravelling the evolutionary causes and consequences of polyandry in a monandrous wasp**

The recent realisation that polyandry, multiple mating by females, is all-but ubiquitous has led to the expansion of sexual selection theory to encompass post-copulatory processes. In addition to understanding the consequences of polyandry, substantial progress has been made in understanding why it is so common. However, most studies seeking to understand the evolution of polyandry focus on highly polyandrous species. This provides information regarding why polyandry is beneficial, but may conflate the factors driving the evolution of polyandry with those maintaining it. The characteristically monandrous parasitoid wasps represent one group of insects that can help to resolve this. The parasitoid *Nasonia vitripennis* represents an interesting case study because polyandry evolves repeatedly under mass-culture conditions. We show that female *N. vitripennis* benefit from multiple matings with virgin males. Polyandry can be costly however, because it delays sperm processing and so reduces fitness under adaptive sex allocation. Under mass-rearing conditions selection on sex allocation is

relaxed, this reduces the costs of polyandry and increases the potential benefits (by increasing the availability of virgin males). Our results demonstrate how the environment, here in terms of the local mating structure, can alter the costs and benefits of mating and drive the evolution of polyandry.

**Natalie Pilakouta**<sup>1,2</sup> & Per T. Smiseth<sup>1</sup>

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### **Female mating preferences for outbred versus inbred males are conditional upon the female's own inbreeding status**

Inbreeding occurs when relatives mate with each other and often has detrimental effects for the fitness of the resulting offspring. Inbreeding may shape mate choice through the avoidance of outbred, related individuals, in order to prevent inbreeding, or through the avoidance of inbred, unrelated individuals that have been produced through inbreeding. Although the former has been studied extensively, little is known about mating preferences based on the inbreeding status of potential partners. It is also unclear whether these mating preferences are influenced by the inbreeding status of the choosing sex. Here, we examine female mating preferences for outbred and inbred males using dichotomous choice tests in the burying beetle *Nicrophorus vespilloides*. We show that these mating preferences are conditional upon the female's own inbreeding status: inbred females preferentially mate with outbred males, whereas outbred females do not show such a preference. Our findings suggest that inbred males suffer reduced mating success only when interacting with inbred females. In species where this is the case, the fitness costs of inbreeding with respect to male mating success will therefore depend on the frequency of inbred females relative to outbred females, which is determined by the rate of inbreeding in the population.

### **2017 TINBERGEN LECTURE: Christine Nicol**

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### **Among the Chickens**

Although perhaps one of the less glamorous areas of animal behaviour science (the title being a direct nod to Iain Duncan-Hamilton's far more exotic life *Among the Elephants*), the study of the behaviour of farmed animals has had a major impact in Europe and is increasingly doing so worldwide. Taking 35 years of work on chickens as the material for this talk I will focus first on studies of chicken cognition and emotion, and then describe some areas of work on avian decision making. Chickens are adept at

social learning and that they also react to the emotional state of others. The combination of these abilities facilitates flexible teaching behaviour directed by mother hens towards their young, and this occurs in than one context. Such studies may appear at first sight to have little practical application but they have contributed to the legal acceptance of chickens as “sentient beings” (1997 Treaty of Amsterdam protocol; 2009 Treaty of Lisbon article), with profound implications for the way in which these birds are viewed by society at large. Such studies have also led directly to improvements in commercial rearing environments, such as the introduction of dark brooders to mimic aspects of maternal care. The second focus of the talk will be on animal decision-making, and how this has become a cornerstone in the assessment of animal welfare. From the earliest preference tests to more recent considerations of intuition and rationality, and value and reward, interpreting the expressed choices of farm animals (particularly the choices of chickens) has proved an intellectual challenge. However, such work has agai fed directly into legal and assurance scheme standards and has had a positive impact on the lives of billions of birds. The talk will finish by considering the process by which small scale laboratory studies can achieve such impact.

**Josie D’Urban Jackson**<sup>1,2</sup> Natalie dos Remedios<sup>3</sup> Kathryn H. Maher<sup>1</sup> Sama Zefania<sup>4</sup> Susan Haig<sup>5</sup>, Sara Oyler-McCance<sup>6</sup> Donald Blomqvist<sup>7</sup> Terry Burke<sup>3</sup> Mike W. Bruford<sup>2</sup> Tamás Székely<sup>1</sup> & Clemens Küpper<sup>8</sup>

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### **Polygamy slows down diversification in shorebirds**

Here we introduce a novel hypothesis concerning the role of sexual selection in speciation. As an alternative to sexual selection leading to reproductive isolation, the “dispersal to mate” hypothesis predicts that sexual selection pressure may act to slow speciation since polygamous individuals can access additional mates by increased breeding dispersal. High breeding dispersal should hence increase gene flow and reduce diversification in polygamous species (i.e. species under elevated sexual selection pressure). Here we test this hypothesis to assess how polygamy affects population divergence in shorebirds using genetic differentiation and subspecies richness as proxies for diversification. Across 79 populations of ten plover species (genus: *Charadrius*), in addition to subspecies data from 136 shorebird species, our results suggest that dispersal associated with polygamy may facilitate gene flow and limit population divergence. Therefore, intense sexual selection, as occurring in polygamous species, may act rather as a brake than an engine of speciation in shorebirds. We

encourage future research to further investigate this hypothesis using theoretical, direct tracking and genetic approaches which will inevitably improve our understanding of the relationships between sexual selection, dispersal and diversification.

### **Dianne H. Brunton**

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### **Female song, but not male song, predicts reproductive success in the NZ bellbird**

Bird song is commonly regarded as a male trait that has evolved through sexual selection. However, recent research has prompted a re-evaluation of this view by demonstrating that female song is an ancestral state for songbirds. The endemic NZ bellbird (*Anthornis melanura*) is a model that can provide insights into selection and song. We have previously demonstrated that female bellbird song is important in intra-sexual interactions and here we demonstrate that female song predicts reproductive success. Female bellbirds contributed significantly more towards parental care than males and female song rate in the vicinity of the nest was higher than that of males during incubation and chick-rearing stages and strongly predicted the number of fledged chicks. Several measures of female song complexity were good predictors of breeding success, whereas male song complexity did not. It is unclear why male song rate was not associated with success and we speculate that unknown levels of extra-pair paternity may shed light on this observation. These results highlight the need for a change in how we view the significance of female song and show that species with female song provide opportunities to study selective pressures specific to females within the wider context of social competition.

**Jen Perry**<sup>1</sup>, Colin Garroway<sup>2</sup> & Locke Rowe<sup>3</sup>

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### **Sexual arms races: testing the alternatives.**

Key examples of sexually antagonistic coevolution include insects where male and female antagonistic traits are correlated among populations, consistent with a sexual arms race occurring over short time scales. However, other non-exclusive processes exclusive might drive sexual covariation among populations. These include ecologically-driven or neutral evolution in one sex with correlated evolution in the other sex, through either sexually antagonistic selection or a positive genetic correlation for antagonistic traits. It is therefore unclear whether current case studies truly represent sexually antagonistic coevolution with each sex evolving in response to the other. To investigate these hypotheses, we evaluated the contributions of intersex genetic

correlations, ecological context, neutral genetic divergence, and sexual coevolution in the correlated evolution of antagonistic traits among populations of *Gerris incognitus* water striders. We detected a shared genetic architecture between the sexes for body size, but a sex-specific genetic architecture for sexually antagonistic traits. Co-ancestry, ecological variation and spatial autocorrelation were all related to population variation in female spines, which help females resist males. Nevertheless, population covariation between sexually antagonistic traits remained strong and positive after accounting for these processes. This suggests ongoing sexually antagonistic coevolution in a contemporary sexual arms race.

Gilbert Roberts & **Marion Petrie**

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### **How females use males: the impact of sexual selection on genetic evolution**

When females choose males they have an impact on genetic evolution. Choice for high quality males reduces mutation load. It is commonly thought that mutation rate should be minimised because there are more ways to damage phenotype than improve it. However, we show how female choice can not just reduce deleterious mutations but can select for rare beneficial mutations to the extent that an increase in mutation rate occurs. This can resolve the lek paradox, namely the problem of how genetic variation is maintained in the face of strong female choice for high quality males. It does this because female choice allows a higher input of variation, whether through mutation or recombination rates, whereas most treatments of female choice focus on reduction in variation. This is because female choice selects strongly for rare beneficial mutations, whereas with natural selection, individuals are better off on average with minimal mutation rates. We show how female choice must be considered in models of genetic evolution and models of the evolution of sex itself, and how we must also consider that female choice can favour the evolution of evolvability.

**Joanne L Godwin** & Matthew J G Gage

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### **Does sexual selection improve population fitness?**

Sexual selection was traditionally considered to work in opposition to natural selection due to the cost of maintaining sexually-selected signals. However, genic capture theory states that mating success, especially in the face of competition, is ultimately determined by condition, and therefore shaped by a large number of naturally selected genes. Sexual selection may therefore augment natural selection by improving the purging of

deleterious mutations and the fixation of beneficial ones, creating population-level fitness benefits. Here, I test this idea using experimentally evolved populations of the promiscuous flour beetle, *Tribolium castaneum*, which differ only in their contrasting opportunities for male-male competition and female choice across more than 50 generations of selection. Following these divergent histories of sexual selection, we tested population resilience to abiotic stresses, ability to biotically invade new populations, and resistance to extinction under genetic and environmental stress. Results show that investment in sexual selection creates improvements in resistance to extinction under genetic and environmental stress, and ability to invade competitor populations across multiple generations. Overall these findings provide convincing empirical support for genic capture models, and for benefits from sexual selection upon overall population-level fitness.

## POSTER PRESENTATIONS

THURSDAY 7<sup>TH</sup> & FRIDAY 8<sup>TH</sup> DECEMBER 2017



**Kris Sales**<sup>1</sup>, Thomas Trent<sup>1</sup>, Jessie Gardner<sup>1</sup>, Alyson J. Lumley<sup>1</sup>, Ramakrishnan Vasudeva<sup>1</sup>, Łukasz Michalczyk<sup>2</sup>, Oliver Y. Martin<sup>3</sup>, and Matthew J.G. Gage<sup>1</sup>

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### **Using experimental evolution to understand why male homosexual behaviour occurs in an insect model.**

Male same sex sexual behaviour (SSB) is widespread in nature. Its prevalence is puzzling: why does evolution allow costly SSB, when reproduction is primarily achieved through heterosexual matings? Two broad hypotheses explain SSB: 1) SSB is adaptive, evolving through sexually selected male-male competition for gaining more fertilisations; 2) SSB is maladaptive, existing due to errors in female mate recognition. We examined SSB using experimentally evolved lineages of *Tribolium castaneum* flour beetles maintained for ~10 years under divergent adult Operational Sex Ratios. Our Male-biased regime (90M:10F) generates strong selection on males from intrasexual competition, while demanding improved ability to locate and identify rarer female mates. By contrast, our Female-biased regime (10M:90F) generates weak sexual selection and most adults are female, relaxing selection to discriminate among mates. If SSB is adaptive in intrasexual competition, it should evolve greater prevalence in Male-biased regimes. However, if SSB is mate recognition error, it should be prevalent in

Female-biased regimes. After 82-106 generations of experimental evolution, we measured SSB in focal males given a simultaneous choice of male and female mating targets. We found a significant reduction in SSB among males evolved through the Male-biased regime, so conclude that SSB evolves due to mate recognition errors.

**Márta E. Rosa**<sup>1</sup>, Zoltán Barta<sup>2</sup>, Attila Fülöp<sup>2</sup>, Tamás Székely<sup>3</sup>, András Kosztolányi<sup>1,2</sup>

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### **The effects of adult sex ratio and density on parental care in *Lethrus apterus* (Coleoptera, Geotrupidae).**

Population density and adult sex ratios (ASRs) often predict mating systems and parental care, however, most studies are correlational. We experimentally manipulated sex ratio and density of *Lethrus apterus*, a burrow-dwelling biparental beetle species to explore the effects on parental behaviour and reproductive success. In a field experiment, under semi-natural conditions, we assigned individuals into nine groups differing in adult sex ratio (three levels; male-biased, even, female-biased) and density (three levels; low, mean, high) using a factorial experimental design. We found that as the sex-ratio became more male-biased and as the density became higher, pairs spent more time inside the burrow and less on parental activities. Offspring number also decreased under male-biased sex ratio but only in low and high densities. Since nest attendance is a possible form of avoiding sperm competition, these results indicate a conflict of interest between the sexes over paternity and brood provisioning or brood size. Taken together, our study gives an experimental evidence that both ASR and individual density may play important role in shaping breeding systems.

**Valentina Z. Caorsi**<sup>1</sup>, Márcio Borges-Martins<sup>1</sup>, Camila Both<sup>2</sup>, Lívia Rose Miron<sup>2</sup>, Sonia T. Zanini Cechin<sup>2</sup>

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## **Challenges for amphibian communication: anthropogenic noise and invasive species**

Biological invasions and anthropogenic noises often occur in synergy; therefore it is important to evaluate their combined effect on animal communication. This study aimed to investigate how road noise and vocalizations of the invasive species bullfrog (*Lithobates catesbeianus*) interfere in the communication of two native anurans from Brazil. The study was conducted at CPCN-Pró Mata, a conservation area in the south of the country. We performed a set of field playback experiments exposing male frogs to 15-minutes playbacks, three minutes per stimulus: i) control (silence); ii) road noise; iii) bullfrog calls; iv) both sounds combined; v) control (silence). The order of the stimuli was randomized to each individual. Focal species were *Boana bischoffi*, which call frequency overlaps with the specific noises and *Boana leptolineatus*, which vocalization has a dominant frequency higher than the noise. Call parameters were compared through a Variance Analysis of repeated measures by randomization. *Boana bischoffi* altered call rate in response to treatments and time. Males decreased call rate when exposed to both noises simultaneously. *Boana leptolineatus* altered call rate, duration of notes, interval between notes, and dominant frequency in response to time.

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### **The validity of the Darwin-Bateman paradigm**

The Darwin-Bateman paradigm predicts that sexual selection is stronger on the sex that produces the smaller gametes size, also sexual selection affects parental care and sexual dimorphism. Despite this hypothesis was first proposed fifty years ago, no study so far has validated the whole theory through reliable evidence. We collected data of sexual selection, gamete size, sexual dimorphism and parental care from species throughout all animal kingdom to check the validity of the hypothesis using phylogenetic comparative methods for example phylogenetic path analyses. Our results did not support the Darwin-Bateman paradigm however we propose alternative cause-effect associations.

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### **Factors affecting sexual dimorphism in Parrots.**

Sexual dimorphism has been primarily attributed to sexual selection, with polygamous species showing striking sexual differences compared with monogamous species. Certain studies suggest that sexual size dimorphism in birds is associated with social mating systems, while others suggest that sexual dichromatism is related with extra-pair mating. However, other ecological factors besides sexual selection could explain sexual dimorphism in birds. A comparative study explaining plumage colouration in passerines showed that larger species are more colourful and less sexually dichromatic. This result supports the hypothesis of less predation risk on larger species and stronger selection for crypticity on smaller species. Although parrots are generally considered socially monogamous, they show sexual dichromatism. A study performed with 27 Australasian parrots showed that only structural-based colours (produced by the interaction of light with the microscopic structure of feathers) were sexually dimorphic, and researchers suggested that this colouration could be under sexual selection. However, a comparative study to understand the actual *factors* affecting sexual colour dimorphism and also sexual size dimorphism in parrots is needed. We performed a comparative analysis to evaluate if direct or indirect sexual selection or life history traits can explain sexual dimorphism in parrots.

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### **Do females prefer males with resistance genes?**

One of the main theories concerning the potential benefits of male choice to females is based on male resistance to pathogens. Male attractiveness is proposed to reflect the individual's condition, and the condition is thought to be negatively affected by pathogens and parasites, making males less attractive. According to the theory, by choosing healthy males, females will gain indirect benefit by transmitting these resistance genes to their offspring. However, there are very few empirical data to support this theory. In our study, we tested if/how presence and absence of pathogens (*Pseudomonas entomophila*) and male resistance would influence female mating choice, and if this choice can impact offspring resistance in *Drosophila melanogaster* flies. When the choice is made in presence of pathogens, we found that female choose more resistant males, and yet have a more resistant offspring. Interestingly, the choice was reversed when made in the absence of pathogens, and offspring of chosen males were less resistant. This study brings highlights on how pathogens might act as an important

factor influencing sexual selection, and on how genetic variation in males is maintained despite a one-sided female choice.

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### **Sexual dimorphism of quantitative traits in *Rumex hastatulus***

The question of what drives the incredible differences between males and females has long puzzled evolutionary biologists. To date the study of sexual dimorphism has been largely focused on animal systems, even though differences between sexes in a wide range of traits are prevalent in many plant species with separate sexes (dioecious). In this project we analyze quantitative trait variation in males and females from 30 populations of the dioecious plant species *Rumex hastatulus*. We examine how sexual dimorphism varies across the life-cycle, its two chromosome races (XY1 and XY1Y2) and its broad geographic range. Given the different reproductive functions of males (pollen dispersal) and females (seed set and dispersal), we predict temporal variation in patterns of sexual dimorphism between the sexes. We also examine the relationship between the degree of sexual dimorphism across time, chromosome race and population taking into account demographic parameters. Finally, we explore trait correlations as a mean of sexual dimorphism evolution via indirect selection. This study fills an important gap in our understanding of how patterns of sexual dimorphism evolve in plant taxa and how this may vary across the life cycle according to differences in the reproductive roles of males and females.

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### **The Relationship between Pre-Copulatory Investment and Male Preference**

Mate preference in males has evolved in a various species of livebearing fishes. However, the factors that select for the evolution of male mate preference, in this system, are not well studied. Theory suggests, that male pre-copulatory investment, like courtship, may be a key factor in the evolution of male preference. Therefore, males that invest more into reproduction benefit more from being choosy. My study aims to compare the preferences of two closely related poeciliid species that vary in male pre-copulatory investment, *Limia perugiae* and *Limia zonata*. *L. perugiae* is a species that displays courtship, while *Limia zonata* is a non-courting species. Additionally, many live bearing fishes have been shown to have a preference for fecundity (i.e. large females). If theory is supported, we expect to see *L. perugiae* with a more exaggerated preference for large females than *L. zonata*. In this study, we use preference function to better

understand the role of male mate-preference in sexual selection. Additionally, this study provides insight into the evolution of male preference in livebearing fishes. Finally, this approach allows for continued comparison of preferences of other livebearing fishes.

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### **Sperm Traits and Sexual Ornaments in the Great Tit**

Socially monogamous birds commonly engage in extra-pair copulations. This exposes males to two different kinds of sexual selection: 1. pre-copulatory competition, in which males attempt to persuade females to copulate with them through sexual ornaments and displays, and 2. post-copulatory competition of the sperm cells to fertilise eggs. Males' reproductive fitness depends on both forms of selection, which may act on different male traits, e.g. ornamentation and sperm traits. Males, however, are limited in their resources to invest in traits. We measured levels of extra-pair paternity (EPP) in a wild population of great tits (*Parus major*). Each males' plumage ornamentation (black breast band width) and sperm traits were analysed. Sperm samples were obtained via cloacal massage and sperm morphology and vitality, indicators of male fertility, were measured. Males with a more pronounced ornamentation had a lower sperm vitality. This hints at a trade-off between investment in pre- and post-copulatory competition. Our study uncovers the extent to which female choice of ornaments and sperm quality contribute to both within-pair and extra-pair fertilisation success, and can shed light onto why males might choose a reproductive strategy.

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### **The baculum – what morphological variation can tell us about sexual selection**

The baculum is a heterotopic bone within the glans penis of many mammalian species. The extreme morphological variation of the baculum, within and between taxa, is probably its most remarkable feature. While, traditionally, this variation has been used for phylogenetic studies, recent literature focusses on the evolution and function of this bone. Sexual selection is probably the reason for the morphological diversity of the baculum, which in turn shapes the erect penis. The mechanisms, however, of how sexual selection could shape the baculum, are more uncertain. In this ongoing study on baculum functional morphology, we are testing hypotheses on mice (C57BL/6J) by either allowing males to mate or keeping them in all-male groups and comparing bone remodelling between groups. One hypothesis is, that baculum shape, symmetry, and

size are honest signals about body condition and previous mating experience of the male. This idea is based on the knowledge, that long bones react to strain by growing in width. A wider baculum might thus be a signal of previous mating activity. Postcopulatory female choice probably plays a vital role in sexual selection, especially in species with greater intraspecific baculum variation.

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### **New approaches to the study of courtship displays**

A number of species show very elaborate courtship displays. Few studies have investigated how sexual selection shapes the evolution of these complex and often costly behaviours. In this poster we present a new approach to study the elaborate “jump-snap” display of male golden collared manakin (*Manacus vitellinus*). The males of this species perform an acrobatic courtship dance that is so fast that it cannot be studied using standard consumer video cameras. We collaborated with a company to develop a new system composed of multiple, synchronized cameras for recording behaviour at high-speed. Calibration of the cameras in the field allows then to annotate videos and reconstruct 3D visualizations of the behaviour. In a first step, we described the courtship dances of several males in 3D to evaluate individual variability of the dance parameters. Future studies will investigate how dance choreography and parameters such as speed or accuracy play an important role in determining male success.

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### **The contribution of sexual traits to simultaneous inter and intra sexual selection in pheasants, *Phasianus colchicus*.**

Sexual selection leads to the most extravagant sexual traits of polygynous males (Anderson 1994). In sexually dimorphic species in which males have elaborate sexual traits, especially those where they appear to exhibit multiple ornamentation, it is often unclear whether these traits function in intrasexual contests or in intersexual choice, or both. The pheasant, *Phasianus colchicus*, offers a system in which males compete with one another to establish territories and females subsequently assess males, leading to reproductive skew. Males are sexually dimorphic, multi-ornamented and possess features inferred to be important in sexual selection. However, it is unclear whether these morphological characteristics function in intrasexual or intersexual selection. We tested how morphological traits predicted: a) female choice in a binary choice test; b)

female choice expressed as copulation rate in a semi-natural environment; c) the rate of male sexual display behaviours; and d) male dominance rank in a naturalistic multi-male: multi-female group. We will compare contributions that traits make to inter and intrasexual selection and so explore how elaborate multimodal displays may have arisen and evolved in this polygynous mating system.

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### **Sexual selection in changing environments in a butterfly**

The understanding of adaptation of long-lived species to natural, ecologically-relevant environmental settings may allow explaining the maintenance of genetic variability in adaptive traits under strong directional selection such as sexually selected traits. We tested whether sexually selected signals produced at different life stages provided complementary information to females about male lifetime adaptation to its fluctuating environment in a model lab-reared butterfly *Bicyclus anynana*. In *B. anynana*, two male sexually-selected traits affect mate choice: the UV-reflectance of forewing eyespot centers (UV-EC) and male sex pheromone composition (MSP). While UV-EC is fixed at adulthood, MSP varies with age and should be sufficiently plastic to track environmental heterogeneity. Using a full-factorial family design, we tested whether a food stress at larval or adult stages affected male condition, sexually-selected traits, and mating success. We found that MSP, but not UV-EC, signaled male phenotypic quality -namely past developmental and current adult feeding conditions- to females, as well as potentially male genetic quality (e.g. 'good' genes). Indeed, we detected weak genotype-by-environment interactions in MSP, suggesting these may not be the main mechanism maintaining genetic variation of MSP or most likely that the species is adapted to the levels of food stress we applied.

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## **Fine-scale vocal behaviour and movement patterns in bottlenose dolphin reproductive interactions**

Reproductive behaviour is notoriously difficult to study in cetaceans, and detailed information on their reproductive interactions is largely lacking. Recent high-resolution animal-borne tags offer unprecedented details on the behaviour of these wide-ranging, elusive animals, but so far they have been mainly used to study foraging and sensory ecology. Here we describe a novel approach to investigate fine-scale reproductive behaviour of free-ranging common bottlenose dolphins (*Tursiops truncatus*), combining movement and acoustic Dtag data from simultaneous deployments on socially bonded animals, and behavioural data from focal-follows. In the mating system of bottlenose dolphins, males form long-term alliances, and they associate with females in brief encounters interpreted as forms of sexual coercion or mate guarding. We provide insights on male-female interactions, including: 1) fine-scale use and function of male acoustic signals, and associated female behavioural response; 2) fine-scale movements of allied males; 3) cooperative within-alliance communication for coordinating male movements. By unveiling details of vocalizations and movements used to mediate agonism and cooperation, this method may direct future dedicated studies on the sexual selection pressures that have shaped communication and mating strategies in bottlenose dolphin reproduction.

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## **Securing paternity by mutilating female genitalia in spiders**

Competition between males and their sperm over access to females and their eggs has resulted in manifold ways by which males try to secure paternity. Male adaptations to sperm competition manipulate females by altering not only female behaviour or physiology, but also female morphology. In the orb-weaving spider, *Larinia jeskovi*, mating may entail mutilation of external structures of the female genitalia. We show that external female genital mutilation prevents the female from remating with subsequent males due to mechanical coupling difficulties. In the field, male-inflicted genital damage is very prevalent since all female *L. jeskovi* were found to be mutilated at the end of the mating season. External genital mutilation is an overlooked but widely spread phenomenon since 80 additional spider species were found for which male genital manipulation can be suspected. Interlocking genital structures provide an evolutionary platform for the rapid evolution of this highly effective mechanism to secure paternity, and we suspect that other animal groups with such genitalia might reveal similarly drastic male adaptations.

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### **Does sexual selection influences the persistence of dung beetle species after the modification of tropical rainforest?**

Understanding how species adapt and persist within altered environments is a major concern within our rapidly changing world. Sexual selection is ubiquitous in sexually reproducing species and the strength of sexual selection has previously been suggested to potentially increase adaptation rates, but also possibly increase risk of extinction within novel environments. Within the current study dung beetle communities were surveyed across a gradient of habitat modification in Sabah, Malaysian Borneo, and the intensity of sexual selection experienced by each species estimated from morphological traits. We find that as habitat disturbance increases species richness and the abundance of species found in old-growth rainforest decreases. Horned species and those species with relatively large horns however, tend to persist and maintain high abundances across the disturbance gradient compared to hornless species and those species with relatively small horns. There was little or no effect of testes mass and sexual size dimorphism on the abundance of species. These results suggest that male contest competition and the strength of competition between males may drive adaptation to novel environments and increase the ecological niche width of species.

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### **Male violence and sexual intimidation in wild chacma baboon**

Sexual violence occurring in the context of long-term heterosexual relationships, such as sexual intimidation, is widespread across human populations. However, its evolutionary origins remain speculative because few studies have investigated the existence of comparable forms of sexual coercion in animals, where repeated male aggression towards a female provides the aggressor with delayed mating benefits. Here, we tested whether male aggression towards females functions as sexual coercion in wild chacma baboons (*Papio ursinus*). We found that male aggression (1) is greatest against cycling females, (2) is costly and represents the main source of injuries for cycling females, and (3) increases male mating success with their victims in the future. Detailed analysis of chronological sequences between aggression and matings further showed that aggression and matings are temporally decoupled. This decoupling may explain why

some forms of sexual violence have been largely overlooked in well-studied animal populations despite their likely impact on the fitness of both sexes. This study of sexual intimidation in a wild primate suggests that it may be widespread across mammalian societies, with important implications for understanding the evolution of mate choice and sexual conflict in mammals.

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### **From individual to population- measuring mate preferences for fitness benefits.**

Under sexual selection, mate preferences can evolve for traits advertising fitness benefits. Observed mating patterns are often assumed to represent preference, even though they result from the interaction between preference, sampling strategy and environmental factors. Therefore correlating fitness with mate choice (realised pairs), instead of preference, may lead to confounded conclusions about the role of preferences in sexual selection. Instead, to understand the evolution and consequences of mate preferences, preference and choice should be studied as two distinct processes. In this study we uniquely combined mate preference tests with a field offspring cross-fostering experiment to study the fitness benefits of the measured preferences and realised pairs. We tested 139 wild great tits (*Parus major*) for their preferences in a six-choice test setup. Preference functions were calculated for several phenotypic and genetic traits, including plumage ornaments, personality and heterozygosity. Using different approaches to analyse preferences, from population wide to on an individual level, we were uniquely able to compare preferences with choice, and the reproductive benefits of choice. With these results we show that individuals differ in their mate preferences depending on their own traits and that, despite constraints on mate choice, finding a compatible mate can increase reproductive success.

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### **Differences in potential reproductive rates of adults determine the operational sex ratio (OSR) in ladybird, *Menochilus sexmaculatus* (Coleoptera: Coccinellidae).**

Literature on mate choice and sex ratio had revealed that mating occurs as the result of OSR which is the ratio of sexually active males and females present at a given time. It is

influenced directly or indirectly by several factors. We evaluated the impact of potential reproductive rate (PRR) on OSR and found, OSR will be more biased towards the sex with higher PRR. In second study, we evaluated the impact of nutritional plasticity of males on life attributes of *Menochilus sexmaculatus* (Fabricius) (Coleoptera: Coccinellidae) kept in three male-biased sex ratio treatments i.e. no (1♀:1♂), limited (1♀:2♂), and intense (1♀:5♂) competition. Males were reared on three food regimes (abundant, alternate and scarce). Females used in experiment were well fed. Results revealed that the time to commence mating was shortest and copulation duration was longest when adults were reared on abundant diet. Number of eggs in the first clutch and their percent egg viability was also highest of the adults with abundant diet. Among male-biased sex ratio treatments, performance of males in intense competitive treatment surpassed the other two in spite of their food regimes which can be concluded that the surrounding environment probably enhances the performance of these beetles.