

ISBE – Flexible female choice and the evolution of male sexual ornaments

Organizer: Alexis Chaine (alexis.chaine@ecoex-moulis.cnrs.fr)

Symposium Description:

Classical theory for the evolution of male traits by sexual selection assumes that female choice is fairly consistent. However, a variety of studies have now shown that female choice can be much more complex and that flexibility in choice can yield fitness benefits. Spatial, temporal, and among female variation is likely to have profound consequences on the evolution of exaggerated male ornaments and changes our perspective on the role females play in such selection. The goal of this symposium is to highlight variable selection and flexible female choice through both empirical and theoretical studies and to generate discussion on questions that would be especially fruitful for future studies of flexible female choice. The symposium will be a balance of talks and discussion and participants should be prepared to take an active role in discussions on the topic.

SCHEDULE

9:00-9:25	Alexis Chaine
9:25-9:50	Erik Svensson
9:50-10:15	Tim Fawcett
10:15-10:45	Coffee Break
10:45-11:10	Gerald Borgia
11:10-11:35	Ryan Calsbeek
11:35-12:00	Nathan Bailey
12:00-13:20	Lunch Break
13:20-13:40	Wiebke Schuett
13:40-14:00	Emily Galbraith
14:00-14:20	Petteri Ilmonen
14:20-14:40	Andrea Townsend
14:40-15:00	William Etges

ABSTRACTS

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Studs and Duds: Female Preferences are Altered by Experience of Other Male Signals

Sexual selection theory predicts that female choice can drive the evolution of elaborate male secondary sexual characters. However, the processes maintaining additive genetic variation for male traits and female preferences are elusive. Recent research has focused on the role of non-additive variance in female choice, and in this study I demonstrate how female social experience alters selection pressure on males. I performed mate choice trials with female field crickets (*Teleogryllus oceanicus*), all of which were tested against the same reference playback of a male calling song. However, I manipulated each female's prior acoustic experience of other male calling songs. Female preferences of the reference song depended on the attractiveness of the song they experienced previously, and the shape of the population-level preference function predicts their change in behavior. Females experiencing attractive songs showed decreased preference for the reference song, whereas females experiencing unattractive songs showed increased preference for the reference song. Experience-mediated plasticity in female preferences has important consequences for the trajectory of sexual selection in wild populations; such plasticity may mitigate the loss of genetic variation in male secondary sexual characters under strong directional selection. In the population I studied, a male-silencing mutation has recently swept the population in response to an acoustically-orienting predator, dramatically altering the acoustic environment that females perceive. I discuss the relevance of my findings to the dynamics of sexual selection in this unique population, which has experienced one of the fastest rates of evolutionary change ever documented in the wild.

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Spatial and temporal patterning in mate searching by female satin bowerbirds across individual lifetimes

Most models of mate choice assume an unrestricted pattern of mate sampling of males by females. Spatial separation of displaying males, the costs of mate searching, and female experience can potentially affect female ability to shop for the best mates. Satin bowerbirds have a nonresource-based mating system in which males display at spatially separated bowers. Females are free to choose which male bowers she visits for display and copulation. Our previous studies have shown that females assess relatively few males in a particular season and that past choices influence males chosen in subsequent years. Here we consider shopping patterns for individual female satin bowerbirds over a ten year period. We assess how space affects these patterns over individual female lifetimes, including what factors affect where new females set up their mate searching areas, the extent to which there are shifts in mate searching areas over which females shop and the degree to which these are affected by changes in the quality of male displays and the losses of locally attractive males. We also assess how mate searching patterns change as females gain experience.

Ryan Calsbeek

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Sexual dimorphism and the evolution of Sexual Conflict

Males and females share most of their genomes and express many of the same traits, yet the sexes often have markedly different selective optima for these shared traits. This sexually antagonistic (SA) selection generates intralocus sexual conflict that is thought to be resolved through the evolution of sexual dimorphism. Though studies of sexual conflict are becoming more prominent, we currently know little about the prevalence of SA selection in wild populations, the components of fitness that generate sexual antagonism, or the relationship between sexual dimorphism and current SA selection. Here, using *Anolis* lizards, we demonstrate negative intersexual genetic correlations between parents and offspring for traits important to fitness. Correlations between body size and fitness related traits are opposite between males and females, and the form of natural selection acting on physiological traits significantly differ between the sexes. Though results suggest the potential for sexual conflict, females use sire body size as a cue to sort sperm for the production of sons versus daughters. The data suggest that sexual conflict may be at least partially resolved by post-copulatory fertilization bias. We discuss these results in light of our recent review of published selection studies using a dataset of 424 selection estimates representing 89 traits from 34 species.

Alexis Chaine

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Is flexible female choice wide-spread?

Classic models of sexual selection are based on the presumption that female choice is directional, universal, and consistent. A growing body of evidence suggests that these assumptions may not hold in all systems. Changes in the physical, ecological, and social environment should create shifts in both female needs for direct benefits and the selective environment that offspring will encounter. When such conditions change over shorter time periods, flexible female choice of mates should be favored to take advantage of the best phenotype and genotype under those conditions. This symposium is aimed at calling attention to the possibility that flexible female choice is likely to be much more wide-spread than previously appreciated. In this short introduction, I review a few key examples of flexible female choice, re-interpret some older work on sexual selection that could provide some evidence for flexible choice, and talk about some of the implications that flexible choice is likely to have on our perspective of sexual selection in general.

William J. Etges

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Ecological determinants of sexual isolation between populations.

Female choice in multiply mating species can be strongly influenced by condition dependence and may be plastic across contrasting environments. Genetic influences determining mating success may also be dependent on environmental effects, but understanding of how sensitive genetic effects are to different environments remains poorly understood. We investigated environmental influences on QTLs for mating success based on male courtship song and epicuticular hydrocarbons in the cactophilic species, *Drosophila mojavensis*. Two host cacti were used to rear F2 progeny from a cross of genetically differentiated mainland Mexico and Baja California populations, and QTLs were evaluated for 21 microsatellite loci distributed across the genome. Male mating success with mainland females was assessed in multiple choice mating trials and linear selection gradient analysis revealed that multiple aspects of male courtship songs influenced copulation success, as well as two contrasting groups of epicuticular hydrocarbons. Females showed higher preference for males reared on one of the cactus species, but there was a hydrocarbon by cactus interaction for one group of covarying epicuticular hydrocarbons. QTL results revealed a striking influence of host cactus on detected QTLs for both songs and epicuticular hydrocarbons, as well as a number of GxE interactions. Because populations of *D. mojavensis* can use multiple host cacti in nature, such GxE interactions influencing male mating success can maintain genetic variation in these male traits in populations, but can also slow the rate of trait evolution due to female choice.

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Previous experiences shape optimal mate preferences

Existing models of mate choice assume that individuals have perfect knowledge of their own ability to attract a mate and can adjust their preferences accordingly. However, real animals are typically uncertain of their own attractiveness. A potentially useful source of information on this is the feedback from previous encounters with potential mates. We constructed a dynamic model of mutual mate choice in which both males and females are initially ignorant of their own attractiveness. Individuals sequentially sample potential mates and retain some simple information about the outcome of these encounters (e.g. the number of times they are accepted or rejected). The evolutionarily stable strategy (ESS) we find is one in which individuals are sensitive to this previous experience, adjusting their mate preferences according to the interest received from the opposite sex. In general, experiences of rejection tend to reduce choosiness while experiences of acceptance tend to increase it. This response is favored even when individuals have some prior estimate of their own attractiveness, providing that estimate is not perfectly accurate. Sensitivity to previous experiences allows individuals to exercise a prudent mate-choice strategy in which their preferences are gradually tuned to their prospects on the mating market. This flexibility is based on simple rules and does not require sophisticated cognitive abilities. We are currently testing the predictions of our model in common gobies and humans, by experimentally manipulating the level of interest shown by potential mates.

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The role of context and comparative evaluation in decision-making during mate choice by female wolf spiders

Human decision-making models from Psychology and/or Economics applied to animal behavior often neglect the influence of context, in particular how simultaneous comparison of choices may affect decisions. During mate choice, females may evaluate multiple potential mates simultaneously using multiple criteria (e.g., morphological, physiological, and behavioral traits), and selection is expected to favor females that choose mates based on increasing indicator trait quality. However, male characteristics may differ in the type of information provided to females. In settings where multiple male traits are simultaneously compared and assessed, females may weigh characteristics differentially depending on the choice context (i.e. relative trait levels and number of males present). We examined decision-making in mate choice by female *Schizocosa ocreata* (Hentz) wolf spiders, and tested hypotheses about preference hierarchies, comparative evaluation, and the influence of context for multiple criteria. We used video digitization and playback techniques to modify male traits (courtship vigor and size of male secondary characters) and presented them to females in varied combinations. When given a choice between males with contrasting traits, female preference varied depending on relative levels of different traits, and the number of males presented simultaneously, indicating comparative evaluation of alternatives and context-dependence. Although spiders have served as invertebrate models for studying mate choice as well as cognition, this research is likely the first to address cognitive processes in mate choice. Results support the incorporation of context into future studies of invertebrate mate choice and decision-making. Applications to other fields of study will be discussed.

Petteri Ilmonen, Gloria Stundner, Michaela Thoß, and Dustin J. Penn.

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Heterozygosity as good genes: inbred females prefer outbred males

'Heterozygosity-as-good-genes' models predict that, under certain conditions, females with low heterozygosity should prefer more heterozygous mates to increase offspring heterozygosity and avoid inbreeding. Although previous studies have found that heterozygosity is associated with increased sexual ornamentation, mating success, and reproduction success for males, it is unknown whether females avoid mating with inbred males and whether their own inbreeding status influences their preferences. We tested these questions in wild-derived house mice (*Mus musculus musculus*) and found that females in oestrous showed a preference for scent marks of outbred versus inbred males. Interestingly, only inbred females showed this preference. Our findings help to explain why inbred males have low reproductive success when they must compete for mates, and suggest that mate choice for heterozygosity provides a selective factor against inbreeding and deleterious recessive mutations. Further, they support the idea that studies should consider females' heterozygosity and condition when investigating mating preferences.

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Does personality matter? The role of personality differences in female mate choice

Much of the focus of sexual selection studies has centred on variation in male secondary sexual traits, with variation in female choice receiving much less attention. Similarly, the role of non-sexual behaviour in mate choice has rarely been considered. Here we present the results of an experiment in which we investigated how female zebra finches (*Taeniopygia guttata*) differ in their mate choices - with respect to non-sexual behaviour expressed by males - depending on their own behavioural type or 'personality'. We experimentally manipulated the degree of exploratory behaviour shown by males in order to disentangle behavioural from appearance effects on female choice. After observing two male siblings in a novel environment each, the focal female was allowed to choose between the previously presented males. Results revealed that females of different behavioural types varied not only in their strategy for assessing the males but also in their actual choice. Interestingly, medium explorative females spent the highest proportion of time with males appearing to be explorative, whereas low explorative females spent the least time with males that did explore the environment. We discuss our findings in the contexts of sexual selection and the evolution of personality differences.

Erik Svensson

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Learning and plasticity in mate preferences in insects

Recent studies on animals with parental care, particularly birds, have shown that mate preferences can be phenotypically plastic and influenced by learning. Learning typically takes place early in ontogeny, through imprinting processes during the interactions between parents and their offspring. In animals without parental care, such as insects and fish, there is also increasing evidence for learned mate preferences both in relation to conspecifics and heterospecifics. Recent theoretical models indicate that learned mate preferences can be more efficient in promoting reproductive isolation between taxa than genetic mate preferences, irrespective if the mate preference loci are autosomally or sex-linked. In my talk I will discuss the consequences of learned mate preferences with particular emphasis on insects, illustrating this discussion with data from my own research laboratory and recent research from other laboratories. I will present experimental field data from sympatric and allopatric populations of damselflies (genus *Calopteryx*) which reveals a conflict, at an extremely local scale, between reproductive isolation in sympatry, and female preference for an exaggerated male secondary sexual trait in allopatry. A neural network model and recent experimental data indicate that this pattern of population divergence in mate preference can arise as a by-product of learned mate preferences, resulting in reinforced mate preferences in sympatry and sensory bias in allopatry. These results will be discussed in relation to mechanisms of speciation in insects and the importance of learned mate preferences in other animals without parental care.

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Genetic costs vs. direct benefits of extra-pair paternity in the cooperatively breeding American crow

If extra-pair paternity has an adaptive value for a female, its benefits to her offspring may be genetic (e.g., genetic quality, compatibility, or diversity) or direct. Among cooperative breeders, direct benefits may take the form of offspring provisioning. Simultaneous tests of each of these hypotheses in a single taxon are rare. We test these hypotheses in a population of cooperatively breeding American crows in Ithaca, NY, with a high frequency of inbreeding and well-documented inbreeding depression. We compare survival, body condition, heterozygosity, and disease probability of offspring produced by pair males, extra-pair within-group males, and extra-group males, as well as provisioning rates in broods with and without extra-pair sires. The benefits of extra-pair paternity did not appear to include genetic quality or compatibility: extra-pair offspring, particularly those sired by within-group extra-pair males, were in worse body condition and were less heterozygous than offspring sired by pair males. Likewise, there was no evidence for benefits of genetic diversity: offspring from broods with mixed paternity were more likely to die with disease symptoms than those sired by a single male. The rate of provisioning and fledging success was higher for broods with offspring sired by within-group extra-pair males, however, suggesting that there may be direct benefits to extra-pair paternity when it is shared within group. There was no evidence for “punishment” by cuckolded pair males: provisioning rates by pair males did not vary with the number of extra-pair offspring in their brood. The role of indirect vs. direct selection for extra-pair paternity in this system is discussed.