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Insect Book Review
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Insect Behaviour

Illness-induced anorexia may reduce trade-offs between digestion and immune function

Shelley A. Adamo a, Amy Bartletta, Jeffrey Le, Nora Spencer and Kenneth Sullivan

a Department of Psychology and Neuroscience, Dalhousie University, Canada

Animals from across the animal kingdom decrease feeding during an infection. Superficially this response seems maladaptive because the decline in food intake occurs at the same time as immune activation increases energy expenditure. However, illness-induced anorexia could be beneficial by decreasing trade-offs between the immune system and digestion. For example, in insects (i.e. crickets) there is a trade-off between lipid transport and immune function. We predicted that increasing the need for lipid transport (e.g. when digesting a high fat meal) would reduce immune function. After consuming a high fat meal, crickets (Gryllus texensis) showed an increase in haemolymph lipid concentration. Crickets also showed a decrease in resistance to bacterial infection (Serratia marcescens). After an immune challenge, crickets not only ate less, they also preferred foods containing less fat. This occurred whether the target food was an ecologically valid food item (dead cricket), natural foods (e.g. lettuce and ground meat) or an artificial diet containing different amounts of lipid. Therefore, the change in feeding behaviour after an immune challenge is consistent with the need to reduce lipid transport in order to maximize immune function. Illness-induced anorexia may be one method by which animals can bias physiological pathways towards enhanced immune function. Some behaviours may be adaptive because they can bias the direction of physiological trade-offs.

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Extreme cost of male riding behaviour for juvenile females of the Zeus bug

Therésa M. Jones, Mark A. Elgar and Göran Arnqvist

a Department of Zoology, University of Melbourne, Australia
b Animal Ecology, Department of Ecology and Evolution, University of Uppsala, Sweden

Precopulatory male mate guarding is predicted to occur close to the female's fertile period. However, in many species mate guarding commences when females are juveniles and may be several moults from sexual maturity. Such behaviour is inconsistent with the above prediction. In the Zeus bug, Phoreticovelia disparata, sexual size dimorphism is very pronounced and adult males commence riding on the backs of juvenile fourth-instar females. Males derive direct benefits from this association but the fitness consequences of precopulatory male riding behaviour for females are unknown. We investigated the effect of male presence during juvenile development for female Zeus bugs. We found a dramatic cost of male riding for females allocated a mate from the fourth instar: they were less likely to survive to adulthood and had substantially reduced adult longevity. These costs were significantly reduced for females allocated a mate during their fifth instar or as adults. We found no evidence that male presence affected female development time, adult size, body shape or the number of melanized dorsal scars present on their abdomen. Our study indicates that adult females and older juvenile females (fifth instar) are adapted to bear the costs imposed by riding males but that sexual conflict is likely to be intense between males and fourth-instar females. We suggest that the Zeus bug mating system originates from both sexes striving to make the best of a bad job: males ride immature females in the absence of unguarded adult females and females permit riding males as a form of convenience polyandry.
(E)-Methylgeranate, a chemical signal of juvenile hormone titre and its role in the partner recognition system of burying beetles

Wolf Haberera, Sandra Steigera, and Josef K. Müllera

Faculty of Biology, Department of Evolutionary Biology and Ecology, University of Freiburg, Germany
Behavior, Ecology, Evolution and Systematics Section, School of Biological Sciences, Illinois State University, USA

In recent years, studies have shown that animals can communicate their physiological state or condition by means of chemical signals. However, as the chemicals involved in the condition-dependent signals have rarely been identified, evolutionary mechanisms that ensure their reliability are not well understood. We identified a volatile chemical signal that may serve as a reliable indicator of hormonal state in burying beetles, and is involved in their partner recognition system. Burying beetles reproducing on carcasses are able to distinguish between their breeding partners and infanticidal conspecifics. This discrimination depends on breeding status, which is positively linked to juvenile hormone III (JH III) titre. Breeding Nicrophorus vespilloides beetles, in contrast to nonbreeding ones, emitted considerable amounts of (E)-methylgeranate. The amount of emitted (E)-methylgeranate was positively correlated with juvenile hormone titres known from other burying beetle studies. Moreover, our behavioural experiments showed that dummies treated with methylgeranate induced tolerant behaviour, whereas control dummies were treated aggressively. The fact that (E)-methylgeranate and JH III share a conspicuous structural similarity and the same biosynthetic pathway may explain how the reliability of the signal for JH titre is ensured. We discuss the implications of our results in the light of theoretical work on the evolution of chemical communication, particularly on the origin of chemical signals.

Recruiter or recruit: who boosts the recruitment in starved nests in mass foraging ants?

Anne-Catherine Mailleux, Aurelie Buffin, Claire Detrain and Jean-Louis Deneubourg

Unit of Ecology and Biogeography, Université Catholique de Louvain, Louvain-la-Neuve, Belgium
Unit of Social Ecology, Université Libre de Bruxelles, Belgium

In social insects, each behavioural group holds information that may be crucial for the colony’s functioning and regulation. We investigated which behavioural group plays the key role in the regulation of recruitment and how it manages to tune the foraging effort according to the level of starvation in the colony. We focused on recruiters and recruits: Recruiters hold information concerning the characteristics of the food source whereas domestics and potential recruits may be better informed about the colony's needs because of the constant contact that they have with their recruits and/or larvae. We imposed different starvation levels on nest-workers and recruiters and observed their interactions. The level of starvation did not alter the behaviour of the recruiters. However, we observed a change in the recruits' response to the recruiter’s signal if the starvation level increased. This induced more recruits and thus more workers foraging in starved colonies. In nonstarved colonies, recruiters did not respond to the recruitment signal and no recruitment occurred. Our results suggest that the recruits' response is the major key to the regulation of the recruitment process. This study has deciphered how individuals assess the colony’s needs and integrate all the information to build up an optimal food exploitation strategy adjusted to starvation.
**Crickets groom to avoid lethal parasitoids**

Crystal M. Vincent and Susan M. Bertram

Department of Biology, Carleton University, Ottawa, Canada

Hosts that are infected by parasitoids pay the ultimate cost: death. Here we investigate whether hosts can combat the lethal effects of parasitoids by enhancing their grooming behaviour and removing the parasitoids before they have a chance to enter the host's body. Many field cricket species are stalked and parasitized by gravid females of the parasitoid fly *Ormia ochracea*. Female parasitoids lay live first-instar larvae (planidia) on and around the cricket. Planidia burrow into the cricket host where they feed and grow. Because parasitism invariably results in host death, there should be strong selection for crickets to avoid being parasitized. We investigated whether field-caught Texas field crickets, *Gryllus texensis*, groom to avoid parasitism by *O. ochracea*. We quantified grooming behaviour of crickets when they were in the same area as *O. ochracea* adults or larvae (proximity avoidance), and following contact between the cricket and *O. ochracea* adults or larvae (contact avoidance). Crickets did not adjust grooming behaviour when in close proximity to adult gravid female *O. ochracea*, nor did they avoid planidia-laden grass. Crickets did, however, substantially increase their grooming activity when placed in an arena filled with planidia-laden grass. Furthermore, crickets that groomed more were much less likely to succumb to parasitoid infestation, compared to crickets that groomed less. Our findings suggest that grooming in *G. texensis* may function as a strong defence against parasitism by *O. ochracea*.

**Reproductive hierarchies and status discrimination in orphaned colonies of *Pachycondyla apicalis* ants**

Pierre Blachera, Dominique Fresneau and Elise Nowbahari

Laboratoire d’Ethologie Expérimentale et Comparée, Université Paris 13, Villetaneuse, France

In group-living animals where dominance hierarchies occur, aggression can be reduced if individuals are able to recognize each other. To do this, and to adapt their behaviour suitably when faced with a rival, individuals may rely on two nonmutually exclusive recognition means: they could recognize group members individually and/or their social status. Within insect societies, although conflicts over reproduction resulting in hierarchy establishment are widespread, relatively little is known about the cognitive abilities involved in the regulation of agonistic interactions. We tested whether low-ranking workers of *Pachycondyla apicalis* ants are able to discriminate each other individually and/or if they can discriminate the status of their nestmates. We found no evidence of individual discrimination among subordinates whereas they were able to discriminate their nestmates on the basis of their social and reproductive status. Such a skill may allow them to regulate worker reproduction in queenright colonies efficiently. By considering the structure of the hierarchy and the nature of the dominance relationships in *P. apicalis* societies, we discuss the existence of a more accurate recognition system among the high-ranking workers.
Antipredatory properties of an animal architecture: how complex faecal cases thwart arthropod attack

Christopher G. Browna and Daniel J. Funk,b
a Department of Biological Sciences, Vanderbilt University, U.S.A.

Animals create a wide variety of structures to deal with abiotic and biotic challenges. We evaluated an intriguing structure whose function has never been thoroughly tested. Specifically, we evaluated the hypothesis that the body-enclosing ‘faecal case’ created and lived in by the immature stages of Neochlamisus leaf beetles reduces their risk of predation. We especially focus on the case of N. platani, which is externally covered with host-plant trichomes, and includes a distinct trichome-filled chamber (‘attic’) in the case apex. Here, we separately evaluated the effects of case, trichomes and attic on each of several behavioural stages of predator attack using N. platani and N. bimaculatus larvae and pupae. Three generalist predators (crickets, soldier bugs and lynx spiders) that represent different feeding strategies were used in our individual-level repeated observation behavioural trials. Results strongly demonstrated that the faecal case itself greatly reduced predation risk for all combinations of beetle species, life history stage and predator. Additional evidence indicated that both trichomes and attics further and independently reduced predation risk. Variation in results among treatments was also informative. For example, the capacity of faecal case components to reduce predation sometimes varied markedly among predators and between larval versus pupal life stages. Patterns of predator behaviour provided no evidence that caseless larvae have alternative means of defence. This study further presents a rare example of the co-option of a physical plant defence (trichomes) by an herbivore.

Sexual harassment by males reduces female fecundity in the alfalfa leafcutting bee, Megachile rotundata

Benjamin H. Rossia, Peter Nonacsa and Theresa L. Pitts-Singerb
a Department of Ecology and Evolutionary Biology, University of California, Los Angeles, U.S.A.
b USDA-ARS Bee Biology & Systematics Laboratory, Utah State University, Logan, U.S.A.

Under sexual conflict, males evolve traits to increase their mating and reproductive success that impose costs on females. Females evolve counteradaptations to resist males and reduce those costs. Sexual harassment is a form of sexual conflict in which males make repeated, costly attempts to mate. Costs to female foraging or predation risk have been measured in several species, but quantitative measurements of direct fitness costs are rare. In the alfalfa leafcutting bee, Megachile rotundata (Fabricius; Hymenoptera: Megachilidae), males harass females, and females resist all mating attempts. We placed bees in large, outdoor cages with various male-biased sex ratios. Harassment rate, nest progression, offspring production, temperature, and food availability were measured daily for 7 days. Harassment rates were highest at intermediate sex ratios. Harassment reduced the number of foraging trips and increased the duration of foraging trips made by females. Females produced offspring at a slower rate when subjected to higher rates of harassment. This shows a direct link from sex ratio to harassment to female fitness under natural conditions. We also discuss an alternative explanation that female resistance is a mechanism for mate choice for high-quality males, which would require that indirect benefits accrue through either daughters or grandsons, because all sons in haplodiploid species arise from unfertilized eggs.
Female reproductive success is affected by selective male harassment in the damselfly *Ischnura senegalensis*

Yuma Takahashi\(^a\) and Mamoru Watanabe\(^a\)

\(^a\) Conservation Biology Laboratory, Graduate School of Life and Environmental Sciences, University of Tsukuba, Japan

In animals without any courtship behaviour, persistent mating attempts by males are frequently observed. Male harassment affects female reproductive success in the laboratory, but few studies have evaluated the costs of male harassment in the wild. In the damselfly *Ischnura senegalensis*, females exhibit colour dimorphism (andromorph and gynomorph), and the morph frequency varies between local populations. In two populations where gynomorphs were common, we found that males harassed more gynomorphs than andromorphs throughout their daily foraging and oviposition activity period. Gynomorphs excreted less faeces than andromorphs, indicating that preferential harassment of gynomorphs decreased their food intake. Gynomorphs also produced fewer eggs than andromorphs. As a result, gynomorphs laid 35% fewer eggs per day than andromorphs, suggesting that male harassment decreased their reproductive success.

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The moment before touchdown: landing manoeuvres of the honeybee *Apis mellifera*

C. Evangelista\(^1,3\), P. Kraft\(^1,3\), M. Dacke\(^1,3,4\), J. Reinhard\(^1\) and M. V. Srinivasan\(^1,2,3,\ast\)

\(^1\) Queensland Brain Institute, The University of Queensland, St Lucia Campus, Brisbane QLD 4072, Australia
\(^2\) School of Information Technology and Electrical Engineering, The University of Queensland, St Lucia Campus, Brisbane QLD 4072, Australia
\(^3\) Australian Research Council Centre for Excellence in Vision Science, Research School of Biology (Building 46), The Australian National University, ACT 0200, Australia
\(^4\) Department of Cell and Organism Biology, Lund University, Box 117, S-22100 Lund, Sweden

Although landing is a crucial part of insect flight, it has attracted relatively little study. Here, we investigate, for the first time, the final moments of a honeybee's (*Apis mellifera*) landing manoeuvre. Using high-speed video recordings, we analyse the behaviour of bees as they approach and land on surfaces of various orientations. The bees enter a stable hover phase, immediately prior to touchdown. We have quantified behaviour during this hover phase and examined whether it changes as the tilt of the landing surface is varied from horizontal (floor), through sloped (uphill) and vertical (wall), to inverted (ceiling). The bees hover at a remarkably constant distance from the surface, irrespective of its tilt. Body inclination increases progressively as the tilt of the surface is increased, and is accompanied by an elevation of the antennae. The tight correlation between the tilt of the surface, and the orientation of the body and the antennae, indicates that the bee's visual system is capable of inferring the tilt of the surface, and pointing the antennae toward it. Touchdown is initiated by extending the appendage closest to the surface, namely, the hind legs when landing on horizontal or sloping surfaces, and the front legs or antennae when landing on vertical surfaces. Touchdown on inverted surfaces is most likely triggered by a mechanosensory signal from the antennae. Evidently, bees use a landing strategy that is flexibly tailored to the varying topography of the terrain.
Insect Biocontrol

Host-seeking behavior and parasitism by Spathius agrili Yang (Hymenoptera: Braconidae), a parasitoid of the emerald ash borer

Xiao-Yi Wang, Zhong-Qi Yang, Juli R. Gould, Hui Wu and Jian-Hai Ma

The Key Laboratory of Forest Protection, State Forestry Administration, Research Institute of Forest Ecology, Environment and Protection, Chinese Academy of Forestry, Beijing 100091, China
Animal and Plant Health Inspection Service, Department of Agriculture, Otis ANGB, MA 02542 5008, USA
Forestry Bureau of Sanming City in Fujian Province, Sanming, Fujian 365000, China
Forest Pest Control Station of Qinghai Province, Xining, Qinghai 810000, China

Spathius agrili Yang (Hymenoptera: Braconidae) is a newly described and important idiobiont ectoparasitoid of the emerald ash borer (EAB) that has excellent potential as a biological control agent against EAB populations in the USA. In order to understand the ecological factors involved in the search and discovery of concealed hosts by S. agrili, we investigated the behavioral responses of adult female wasps to potential semiochemicals from host plants, hosts, and host frass as well as to vibration signals from host feeding and movement. Using a bioassay, we showed that S. agrili first finds the host’s habitats by detecting the volatile compounds emitted by ash. In the second phase of host location and acceptance, the parasitoids detect the mechanical vibrations produced by host feeding and movement under the surface of the bark and then probe to find the EAB larvae. Contact chemicals seem to play little or no role in short-range host finding. Female wasps avoided laying eggs on EAB larvae already parasitized and thus paralyzed. We hypothesized that female wasps were not attracted to these larvae due to their lack of feeding or movement. While an induced paralysis in the host is instrumental in avoiding superparasitism, we cannot rule out that S. agrili females also use an oviposition pheromone to deter conspecific females. Together, these results suggest that vibration and olfactory cues play significant roles in distinct phases of S. agrili host habitat and host location behaviors.

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Effects of six sugars on the longevity, fecundity and nutrient reserves of Microplitis mediator

Shuping Luo, Jiancheng Li, Xiaoxia Liu, Ziyun Lu, Wenliang Pan, Qingwen Zhang and Zhangwu Zhao

Department of Entomology, College of Agronomy and Biotechnology, China Agricultural University, Beijing 100193, China
Institute of Plant Protection, Hebei Academy of Agriculture and Forestry Sciences, Baoding 071001, China

Parasitoid adults can directly feed on floral nectar and honeydew containing monosaccharides and disaccharides. Oligosaccharides such as maltose, melezitose and raffinose are also found in honeydew but are rare in floral nectar. The effects of six different sugar resources on the longevity, fecundity and nutrient reserves of Microplitis mediator, a larval endoparasitoid in the cotton bollworm Helicoverpa armigera (Hübner) were determined in our laboratory. The results showed that both food and sex affected longevity of this wasp. Females and males of M. mediator fed with 1 M sucrose solution survived longer than controls fed with water (5.7- and 3.7-fold longer, respectively). When provided with sucrose, glucose or fructose solutions, the parasitoid generated 3.6-
to 3.7-fold more offspring than controls, and 60–75% of these progenies were produced during the first 5 days. When separately given fructose, sucrose or glucose, this wasp accumulated fructose and total sugar at the highest level, which means a high sugar levels might lead to prolonging longevity and more offspring in *M. mediator*. In addition, compared with organisms fed galactose or raffinose, *M. mediator* fed sucrose or fructose accumulated high glycogen levels. Furthermore, in *M. mediator*, the lipid content declined with the advancing age. Females showed the slowest lipid metabolic rates when fed with sucrose, glucose, fructose, mannose and galactose solutions versus when fed with raffinose and control. In addition, only sucrose had a significant effect on lipid levels in males nearing the end of life.

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http://www.sciencedirect.com/science?_ob=ArticleURL&_udi=B6WBP-4X65S4B-1&_user=10&_coverDate=01%2F31%2F2010&_rdoc=1&_fmt=high&_orig=browse&_sort=d&_docanchor=&_acct=C000050221&_version=1&_userid=10&md5=55de1b237f113475d4738b329a5ba58d43

Insect Cell Biology

The nuclear cofactor DOR regulates autophagy in mammalian and *Drosophila* cells

Caroline Maucvezin1,2,3, Meritxell Orpinell1,2, Víctor A Francis1,2,3, Francisco Mansilla4, Jordi Duran1,2,3, Vincent Ribas1,2,4, Manuel Palacin1,2, Patricia Boya5, Aurelio A Teleman6 & Antonio Zorzano1,2,3
antonio.zorzano@irbbarcelona.org

Institute for Research in Biomedicine (IRB Barcelona), C/Baldri Reixac 10, Barcelona 08028, Spain
Department of Bioquímica i Biologia Molecular, Facultat de Biologia, Universitat de Barcelona, Avenida Diagonal 645, Barcelona 08028, Spain
CIBER de Diabetes y Enfermedades Metabólicas Asociadas (CIBERDEM), Calle Mallorca 183, Barcelona 08036, Spain
Department of Molecular Medicine, Center for Molecular Clinical Cancer Research, Aarhus University, 8200 Aarhus N, Denmark
3D Lab (Development, Differentiation & Degeneration), Department of Cellular and Molecular Physiopathology, Centro de Investigaciones Biológicas, CSIC, 28040 Madrid, Spain
Structural and Functional Genomics Program, German Cancer Research Center (DKFZ), Im Neuenheimer Feld 580, D-69120 Heidelberg, Germany

The regulation of autophagy in metazoans is only partly understood, and there is a need to identify the proteins that control this process. The diabetes- and obesity-regulated gene (DOR), a recently reported nuclear cofactor of thyroid hormone receptors, is expressed abundantly in metabolically active tissues such as muscle. Here, we show that DOR shuttles between the nucleus and the cytoplasm, depending on cellular stress conditions, and re-localizes to autophagosomes on autophagy activation. We demonstrate that DOR interacts physically with autophagic proteins Golgi-associated ATPase enhancer of 16 kDa (GATE16) and microtubule-associated protein 1A/1B-light chain 3. Gain-of-function and loss-of-function studies indicate that DOR stimulates autophagosome formation and accelerates the degradation of stable proteins. CG11347, the *Drosophila* homologue, has been predicted to interact with the *Drosophila* Atg8 homologues, which suggests functional conservation in autophagy. Flies lacking CG11347 show reduced autophagy in the fat body during pupal development. All together, our data indicate that DOR regulates autophagosome formation and protein degradation in mammalian and *Drosophila* cells.

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An actomyosin-based barrier inhibits cell mixing at compartmental boundaries in *Drosophila* embryos

Bruno Monier1,2, Anne Pélissier-Monier1,2,3, Andrea H. Brand1,2 & Bénédicte Sanson1 bm343@cam.ac.uk
bs251@cam.ac.uk
Partitioning tissues into compartments that do not intermix is essential for the correct morphogenesis of animal embryos and organs\textsuperscript{1,2,3}. Several hypotheses have been proposed to explain compartmental cell sorting, mainly differential adhesion\textsuperscript{1,2,3,4,5,6,7,8,9}, but also regulation of the cytoskeleton\textsuperscript{10,11}, or of cell proliferation\textsuperscript{10,12}. Nevertheless, the molecular and cellular mechanisms that keep cells apart at boundaries remain unclear. Here we demonstrate, in early \textit{Drosophila melanogaster} embryos, that actomyosin-based barriers stop cells from invading neighbouring compartments. Our analysis shows that cells can transiently invade neighbouring compartments, especially when they divide, but are then pushed back into their compartment of origin. Actomyosin cytoskeletal components are enriched at compartmental boundaries, forming cable-like structures when the epidermis is mitotically active. When MyoII (non-muscle myosin II) function is inhibited, including locally at the cable by chromophore-assisted laser inactivation (CALI)\textsuperscript{13,14}, in live embryos, dividing cells are no longer pushed back, leading to compartmental cell mixing. We propose that local regulation of actomyosin contractility, rather than differential adhesion, is the primary mechanism sorting cells at compartmental boundaries.

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\text{http://www.nature.com/ncb/journal/v12/n1/abs/ncb2005.html?lang=en}

\textbf{Insect Chemoecology}
\textbf{Eating chemically defended prey: alkaloid metabolism in an invasive ladybird predator of other ladybirds (Coleoptera: Coccinellidae)}

J. J. Sloggett\textsuperscript{1,*} and A. J. Davis\textsuperscript{2} johnsloqgett@yahoo.co.uk
\textsuperscript{1} Tussen Beide Markten 45, 9712 CC Groningen, The Netherlands, Beutenberg Campus, Hans-Knöll-Straße 8, D-07745 Jena, Germany
\textsuperscript{2} Max Planck Institute for Chemical Ecology, Beutenberg Campus, Hans-Knöll-Straße 8, D-07745 Jena, Germany

By comparison with studies of herbivore physiological adaptation to plant allelochemicals, work on predator physiological adaptation to potentially toxic prey has been very limited. Such studies are important in understanding how evolution could shape predator diets. An interesting question is the specificity of predator adaptation to prey allelochemicals, given that many predators consume diverse prey with different chemical defences. The ladybird \textit{Harmonia axyridis}, an invasive species in America, Europe and Africa, is considered a significant predatory threat to native invertebrates, particularly other aphid-eating ladybirds of which it is a strong intraguild predator. Although ladybirds possess species-specific alkaloid defences, \textit{H. axyridis} exhibits high tolerance for allospecific ladybird prey alkaloids. Nonetheless, it performs poorly on species with novel alkaloids not commonly occurring within its natural range. We examined alkaloid fate in \textit{H. axyridis} larvae after consumption of two other ladybird species, one containing an alkaloid historically occurring within the predator's native range (isopropyleine) and one containing a novel alkaloid that does not (adaline). Our results indicate that \textit{H. axyridis} rapidly chemically modifies the alkaloid to which it has been historically exposed to render it less harmful: this probably occurs outside of the gut. The novel, more toxic alkaloid persists in the body unchanged for longer. Our results suggest metabolic alkaloid specialisation, in spite of the diversity of chemically defended prey that the predator consumes. Physiological adaptations appear to have made \textit{H. axyridis} a successful predator of other ladybirds; however, limitations are imposed by its physiology when it eats prey with novel alkaloids.
Insect Development

The Drosophila nuclear receptors DHR3 and βFTZ-F1 control overlapping developmental responses in late embryos

Anne-Françoise Ruaud, Geannette Lam and Carl S. Thummel*
carl.thummel@genetics.utah.edu
Department of Human Genetics, University of Utah School of Medicine, 15 N 2030 E Room 2100, Salt Lake City, UT 84112-5330, USA

Studies of the onset of metamorphosis have identified an ecdysone-triggered transcriptional cascade that consists of the sequential expression of the transcription-factor-encoding genes DHR3, βFTZ-F1, E74A and E75A. Although the regulatory interactions between these genes have been well characterized by genetic and molecular studies over the past 20 years, their developmental functions have remained more poorly understood. In addition, a transcriptional sequence similar to that observed in prepupae is repeated before each developmental transition in the life cycle, including mid-embryogenesis and the larval molts. Whether the regulatory interactions between DHR3, βFTZ-F1, E74A and E75A at these earlier stages are similar to those defined at the onset of metamorphosis, however, is unknown. In this study, we turn to embryonic development to address these two issues. We show that mid-embryonic expression of DHR3 and βFTZ-F1 is part of a 20-hydroxyecdysone (20E)-triggered transcriptional cascade similar to that seen in mid-prepupae, directing maximal expression of E74A and E75A during late embryogenesis. In addition, DHR3 and βFTZ-F1 exert overlapping developmental functions at the end of embryogenesis. Both genes are required for tracheal air filling, whereas DHR3 is required for ventral nerve cord condensation and βFTZ-F1 is required for proper maturation of the cuticular denticles. Rescue experiments support these observations, indicating that DHR3 has essential functions independent from those of βFTZ-F1. DHR3 and βFTZ-F1 also contribute to overlapping transcriptional responses during embryogenesis. Taken together, these studies define the lethal phenotypes of DHR3 and βFTZ-F1 mutants, and provide evidence for functional bifurcation in the 20E-responsive transcriptional cascade.

http://dev.biologists.org/content/137/1/123.abstract

Drosophila growth cones: A genetically tractable platform for the analysis of axonal growth dynamics

Natalia Sánchez-Soriano1, Catarina Gonçalves-Pimentel1,2, Robin Beaven3, Ulrike Haessler1,4, Lisa Ofner-Ziegenfuss1,5, Christoph Ballestrem1, Andreas Prokop1Andreas.Prokop@manchester.ac.uk
1Faculty of Life Sciences, Wellcome Trust Centre for Cell-Matrix Research, Manchester M13 9PT, United Kingdom
2PhD Programme in Experimental Biology and Biomedicine, Center for Neuroscience and Cell Biology, University of Coimbra, 3004-517 Coimbra, Portugal

The formation of neuronal networks, during development and regeneration, requires outgrowth of axons along reproducible paths toward their appropriate postsynaptic target cells. Axonal extension occurs at growth cones (GCs) at the tips of axons. GC advance and navigation requires the activity of their cytoskeletal networks, comprising filamentous actin (F-actin) in lamellipodia and filopodia as well as dynamic microtubules (MTs) emanating from bundles of the axonal core. The molecular mechanisms governing these two cytoskeletal networks, their cross-talk, and their response to extracellular signaling cues are only partially understood, hindering our conceptual understanding of how regulated changes in GC behavior are controlled. Here, we introduce Drosophila GCs as a suitable model to address these mechanisms. Morphological and cytoskeletal
readouts of *Drosophila* GCs are similar to those of other models, including mammals, as demonstrated here for MT and F-actin dynamics, axonal growth rates, filopodial structure and motility, organizational principles of MT networks, and subcellular marker localization. Therefore, we expect fundamental insights gained in *Drosophila* to be translatable into vertebrate biology. The advantage of the *Drosophila* model over others is its enormous amenability to combinatorial genetics as a powerful strategy to address the complexity of regulatory networks governing axonal growth. Thus, using pharmacological and genetic manipulations, we demonstrate a role of the actin cytoskeleton in a specific form of MT organization (loop formation), known to regulate GC pausing behavior. We demonstrate these events to be mediated by the actin-MT linking factor Short stop, thus identifying an essential molecular player in this context.

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**Insect Ecology**

**Seasonal variation in the trophic structure of a spatial prey subsidy linking aquatic and terrestrial food webs: adult aquatic insects**

Jeff Scott Wesner, jeffwesner@ou.edu

Dept of Zoology, Univ. of Oklahoma, 730 Van Vleet Oval, Room 314, Norman, OK 73019, USA.

Research over the past decade has established spatial resource subsidies as important determinants of food web dynamics. However, most empirical studies have considered the role of subsidies only in terms of magnitude, ignoring an important property of subsidies that may affect their impact in recipient food webs: the trophic structure of the subsidy relative to in situ resources. This may be especially important when subsidies are composed of organisms, as opposed to nutrient subsidies, because the trophic position of subsidy organisms may differ from in situ prey. I explored the relative magnitude and trophic structure of a cross-habitat prey subsidy, adult aquatic insects, in terrestrial habitats along three streams in the south-central United States. Overall, adult aquatic insects contributed more than one-third of potential insect prey abundance and biomass to the terrestrial habitat. This contribution peaked along a permanent spring stream, reaching as high as 94% of abundance and 86% of biomass in winter. Trophic structure of adult aquatic and terrestrial insects differed. Nearly all adult aquatic insects were non-consumers as adults, whereas all but one taxon of terrestrial insects were consumers. Such a difference created a strong relationship between the relative contribution of the prey subsidy and the trophic structure of the prey assemblage: as the proportion of adult aquatic insects increased, the proportion of consumers in the prey assemblage declined. Specific effects varied seasonally and with distance from the stream as the trophic structure of the subsidy changed, but general patterns were consistent. These findings show that adult aquatic insect subsidies to riparian food webs not only elevate prey availability, but also alter the trophic structure of the entire winged insect prey assemblage.

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**Insect Heredity**

**Rapid evolution of Wolbachia density in insecticide resistant *Culex pipiens***

P Echaubard\(^1\), O Duron\(^2\), P Agnew\(^1\), C Sidobre\(^1\), V Noël\(^1\), M Weill\(^2\) and Y Michalakis\(^1\)

\(^1\)Génétique et Évolution des Maladies Infectieuses (CNRS/IRD—UMR 2724), Montpellier, France

\(^2\)Institut des Sciences de l'Évolution, CNRS - Université Montpellier 2, Montpellier, France

yannis.michalakis@mpl.ird.fr

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The maternally inherited symbiotic *Wolbachia* have been previously shown to have much greater densities in insecticide-resistant *Culex pipiens* mosquitoes than in insecticide-susceptible individuals. These high densities were shown to be at least partially responsible for the costs related to insecticide resistance in this species. We report here the rapid evolution, on the order of 50 generations, of bacterial densities both in laboratory and field populations. Along with other recently published studies, this report shows that *Wolbachia*–host interactions are very dynamic.

Heredity (2010) 104, 15–19
http://www.nature.com/hdy/journal/v104/n1/abs/hdy2009100a.html

*Response to selection and realized heritability of sperm length in the yellow dung fly (Scathophaga stercoraria)*

R Dobler and D J Hosken
Zoology Museum, University of Zürich, Zürich, Switzerland
Centre for Conservation and Ecology, University of Exeter, Cornwall Campus, UK

Sperm length shows considerable phenotypic variation both inter- and intra-specifically, but a general explanation for this variation is lacking. In addition, our understanding of the genetic variation underlying sperm length variation is also limited because there have been few studies on the genetics of sperm size. One factor that could explain the variation in sperm length is that length influences sperm competitiveness, and there is some evidence for this. However, in yellow dung flies (*Scathophaga stercoraria*), microevolutionary responses to experimental variation at levels of sperm competition indicate that sperm length does not influence sperm competitiveness, although this lack of response may simply indicate sperm length lacks evolutionary potential (that is, it is constrained in some way), in spite of evidence that sperm length is heritable. Here we report on a laboratory study, in which we artificially selected upwards and downwards on sperm length in *S. stercoraria*. We found that sperm length significantly diverged after four generations of selection, but the response to selection was asymmetrical: upward selection generated a rapid response, but downward did not. We estimated the realized heritability of sperm length to be approximately 50%, which is consistent with previous sire–son estimates. We also assessed the fertility of males from upward and downward lines and found they did not differ. Results are discussed in the context of sperm competition.

http://www.nature.com/hdy/journal/v104/n1/abs/hdy200993a.html

**Insect Molecular Ecology**

*Cryptic differences in dispersal lead to differential sensitivity to habitat fragmentation in two bumblebee species*

B. DARVILL, S. O’CONNOR, G. C. LYE, J. WATERS, O. LEPAIS and D. GOULSON
School of Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, UK

dave.goulson@stir.ac.uk

Habitat loss has led to fragmentation of populations of many invertebrates, but social hymenopterans may be particularly sensitive to habitat fragmentation due to their low effective population sizes. The impacts of fragmentation depend strongly on dispersal abilities, but these are difficult to quantify. Here, we quantify and compare dispersal abilities of two bumblebee species, *Bombus muscorum* and *Bombus jonellus*, in a model island system. We use microsatellites to investigate population genetic structuring, dispersal and spatial patterns in genetic diversity. Populations of both species showed significant structuring, and isolation by distance, but this was markedly greater in
Insect Morphology

Morphological variation in the forelegs of the Hawaiian Drosophilidae. I. The AMC clade

Julian B. Stark1 2*, Patrick M. O’Grady3 stark@amnh.org
1Department of Biological and Geological Sciences, Queensborough Community College, Bayside, New York
2Department of Invertebrate Zoology, American Museum of Natural History, New York, New York
3Department of Invertebrate Zoology, Policy, & Management, Division of Organisms and the Environment, University of California, Berkeley, California

The Hawaiian Drosophilidae possess spectacular diversity in male foreleg modifications, many of which are unknown in other Diptera. The greatest diversity in foreleg morphology is in the antopocerus, modified tarsus, and ciliated tarsus clade (AMC Clade), a group of 95 species. The modified tarsus flies are divided into the bristle, ciliated, split, and spoon tarsus subgroups. The bristle tarsus species feature one or two rows of thickened setae on the basitarsus. The split tarsus species are characterized by only having four tarsal segments, in contrast to five tarsomers in the remainder of Diptera. Based on comparisons of the apparent ground state of ventral setal rows across the Hawaiian Drosophila, we suggest that it is the second tarsal segment which has been lost. The spoon tarsus species are characterized by having the second tarsomere modified into a setae-filled, concave-shaped spoon. The ciliated tarsus species, all of which possess one or more elongate setae on the tarsus of males, are probably not monophyletic with respect to the bristle tarsus subgroup. The antopocerus flies are characterized by a long basitarsus, with extensive setation on the tibia and basitarsus of some species. The use of these foreleg modifications in courtship behavior has been previously described and it is suggested that they represent the results of sexual selection. The current work expands on previous morphological analyses, presenting a level of detail not previously possible without SEM images. The new characters revealed will figure prominently in future cladistic studies.

Insect Neuroethology

Behavioural state affects motion-sensitive neurones in the fly visual system

R. Rosner*, M. Egelhaaf and A.-K. Warzecha rosner@staff.uni-marburg.de
Lehrstuhl für Neurobiologie, Universität Bielefeld, Bielefeld, Germany

The strength of stimulus-induced responses at the neuronal and the behavioural level often depends on the internal state of an animal. Within pathways processing sensory information and eventually controlling behavioural responses, such gain changes can originate at several sites. Using motion-sensitive lobula plate tangential cells (LPTCs) of blowflies, we address whether and in which way information processing changes for two
different states of motor activity. We distinguish between the two states on the basis of haltere movements. Halteres are the evolutionarily transformed hindwings of flies. They oscillate when the animals walk or fly. LPTCs mediate, amongst other behaviours, head optomotor responses. These are either of large or small amplitude depending on the state of motor activity. Here we find that LPTC responses also depend on the motor activity of flies. In particular, LPTC responses are enhanced when halteres oscillate. Nevertheless, the response changes of LPTCs do not account for the corresponding large gain changes of head movements. Moreover, haltere activity itself does not change the activity of LPTCs. Instead, we propose that a central signal associated with motor activity changes the gain of head optomotor responses and the response properties of LPTCs.

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Insect Neuroscience
Lineage-specific effects of Notch/Numb signaling in post-embryonic development of the Drosophila brain

Suwei Lin1,*, Sen-Lin Lai1,†, Sen-Lin Lai1,*,†, Sen-Lin Lai1,†, Huang-Hsiang Yu2,†, Takahiro Chihara3,‡, Liqun Luo3 and Tzumin Lee1,2,§ leet@janelia.hhmi.org
1Department of Neurobiology, University of Massachusetts Medical School, Worcester, MA 01605, USA
2Howard Hughes Medical Institute, Janelia Farm Research Campus, Ashburn, VA 20147, USA
3Howard Hughes Medical Institute, Department of Biology, Stanford University, Stanford, CA 94305, USA

Numb can antagonize Notch signaling to diversify the fates of sister cells. We report here that paired sister cells acquire different fates in all three Drosophila neuronal lineages that make diverse types of antennal lobe projection neurons (PNs). Only one in each pair of postmitotic neurons survives into the adult stage in both anterodorsal (ad) and ventral (v) PN lineages. Notably, Notch signaling specifies the PN fate in the vPN lineage but promotes programmed cell death in the missing siblings in the adPN lineage. In addition, Notch/Numb-mediated binary sibling fates underlie the production of PNs and local interneurons from common precursors in the IAL lineage. Furthermore, Numb is needed in the lateral but not adPN or vPN lineages to prevent the appearance of ectopic neuroblasts and to ensure proper self-renewal of neural progenitors. These lineage-specific outputs of Notch/Numb signaling show that a universal mechanism of binary fate decision can be utilized to govern diverse neural sibling differentiations.

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Role of Notch signaling in establishing the hemilineages of secondary neurons in Drosophila melanogaster

James W. Truman*,§, Wanda Moats, Janet Altman*, Elizabeth C. Marin† and Darren W. Williams‡
trumanj@janelia.hhmi.org
Department of Biology, Box 351800, University of Washington, Seattle, WA 98195, USA

The secondary neurons generated in the thoracic central nervous system of Drosophila arise from a hemisegmental set of 25 neuronal stem cells, the neuroblasts (NBs). Each NB undergoes repeated asymmetric divisions to produce a series of smaller ganglion mother cells (GMCs), which typically divide once to form two daughter neurons. We find that the two daughters of the GMC consistently have distinct fates. Using both loss-of-function and gain-of-function approaches, we examined the role of Notch signaling in establishing neuronal fates within all of the thoracic secondary lineages. In all cases, the ‘A’ (NotchON) sibling assumes one fate and the ‘B’ (NotchOFF) sibling assumes another, and this relationship holds throughout the neurogenic period, resulting in two major
Neural correlates of odor learning in the honeybee antennal lobe

Michael Denker 1,*, Robert Finke 2,*, Frank Schaupp 1, Sonja Grün 1,2,3 and Randolf Menzel 1,2,3
mdenker@brain.riken.jp
1 RIKEN Brain Science Institute, Wako-Shi, 351-0198 Saitama, Japan
2 Freie Universität Berlin, Institut für Biologie – Neurobiologie, Berlin, Germany
3 Bernstein Center for Computational Neuroscience, Berlin, Germany

Extracellular spiking activity and local field potentials (LFP) were recorded via tetrodes at the output of the antennal lobe (AL) in the honeybee brain during olfactory conditioning. Odors induce reliable rate responses that consist of either phasic-tonic responses, or complex responses with odor-specific profiles. In addition, odors evoke consistent responses of LFP oscillations in the 50-Hz band during the phasic ON-response to odor stimulation, and variable LFP responses at other frequency bands during the sustained response. A principal component analysis of the ensemble activity during differential conditioning consistently indicates the largest changes in response to the learned odor (conditioned stimulus; CS+). Relative LFP power increases for CS+ in the 15–40-Hz frequency band during the sustained response, and decreases for frequencies above 45 Hz. To quantify the relationship between these population responses given by the ensemble spiking activity and LFP, we show that for CS+ the learning-related changes in the degree of the phase-locked spiking activity correlate with the power changes in the corresponding frequency bands. Our results indicate associative plasticity in the AL of the bee leading to both enhancement and decrease of neuronal response rates. LFP power changes and the correlated changes in the locking between spikes and LFP at different frequencies observed for the learned odor serve as further evidence for a learning-induced restructuring of temporal ensemble representations.

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Dissecting differential gene expression within the circadian neuronal circuit of Drosophila

Emi Nagoshi1,2,4, Ken Sugino2, Ela Kula1,2,4, Etsuko Okazaki3, Taro Tachibana3, Sacha Nelson2 & Michael Rosbash1,2,4
1. Howard Hughes Medical Institute, Brandeis University, Waltham, Massachusetts, USA.
2. National Center for Behavioral Genomics, Department of Biology, Brandeis University, Waltham, Massachusetts, USA.
3. Department of Bioengineering, Graduate School of Engineering, Osaka City University, Osaka, Japan.
4. Present addresses: Institute of Cell Biology, University of Bern, Bern, Switzerland (E.N.) and Department of Neurobiology and Physiology, Northwestern University, Evanston, Illinois, USA (E.K.).

Behavioral circadian rhythms are controlled by a neuronal circuit consisting of diverse neuronal subgroups. To understand the molecular mechanisms underlying the roles of
neuronal subgroups within the *Drosophila* circadian circuit, we used cell-type specific gene-expression profiling and identified a large number of genes specifically expressed in all clock neurons or in two important subgroups. Moreover, we identified and characterized two circadian genes, which are expressed specifically in subsets of clock cells and affect different aspects of rhythms. The transcription factor Fer2 is expressed in ventral lateral neurons; it is required for the specification of lateral neurons and therefore their ability to drive locomotor rhythms. The *Drosophila melanogaster* homolog of the vertebrate circadian gene nocturnin is expressed in a subset of dorsal neurons and mediates the circadian light response. The approach should also enable the molecular dissection of many different *Drosophila* neuronal circuits.


**Insect Pathology**

Sigma viruses from three species of *Drosophila* form a major new clade in the rhabdovirus phylogeny

Ben Longdon1, Darren J. Obbard1 and Francis M. Jiggins2
b.longdon@ed.ac.uk
Institute of Evolutionary Biology, University of Edinburgh, Ashworth Laboratories, Kings Buildings,
West Mains Road, Edinburgh EH9 3JT, UK
Department of Genetics, University of Cambridge, Cambridge CB2 3EH, UK

The sigma virus (DMelSV), which is a natural pathogen of *Drosophila melanogaster*, is the only *Drosophila*-specific rhabdovirus that has been described. We have discovered two new rhabdoviruses, *D. obscura* and *D. affinis*, which we have named DObsSV and DAffSV, respectively. We sequenced the complete genomes of DObsSV and DMelSV, and the L gene from DAffSV. Combining these data with sequences from a wide range of other rhabdoviruses, we found that the three sigma viruses form a distinct clade which is a sister group to the Dimarhabdovirus supergroup, and the high levels of divergence between these viruses suggest that they deserve to be recognized as a new genus. Furthermore, our analysis produced the most robustly supported phylogeny of the *Rhabdoviridae* to date, allowing us to reconstruct the major transitions that have occurred during the evolution of the family. Our data suggest that the bias towards research into plants and vertebrates means that much of the diversity of rhabdoviruses has been missed, and rhabdoviruses may be common pathogens of insects.

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http://rspb.royalsocietypublishing.org/content/277/1678/35.abstract

**Insect Pharmacology**

Postembryonic development of centrally generated flight motor patterns in the hawkmoth, *Manduca sexta*

Ricardo Vierk2, Carsten Duch1 and Hans-Joachim Pflüger1
r.vierk@uke.uni-hamburg.de
carsten.duch@asu.edu pflueger@neurobiologie.fu-berlin.de
(1) Institute of Biology/Neurobiology, Freie Universität, Königin-Luise-Str. 28-30, 14195 Berlin, Germany
(2) Institute of Anatomy I: Cellular Neurobiology, University Medical Center, 20246 Hamburg, Germany
(3) School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA

This study analyses the maturation of centrally generated flight motor patterns during metamorphosis of *Manduca sexta*. Bath application of the octopamine agonist chlordimeform to the isolated central nervous system of adult moths reliably induces fictive flight patterns in wing depressor and elevator motoneurons. Pattern maturation is investigated by chlordimeform application at different developmental stages.
Chlordimeform also induces motor patterns in larval ganglia, which differ from fictive flight, indicating that in larvae and adults, octopamine affects different networks. First changes in motoneuron activity occur at the pupal stage P10. Rhythmic motor output is induced in depressor, but not in elevator motoneurons at P12. Adult-like fictive flight activity in motoneurons is observed at P16 and increases in speed and precision until emergence 2 days later. Pharmacological block of chloride channels with picrotoxin also induces fictive flight in adults, suggesting that the pattern-generating network can be activated by the removal of inhibition, and that proper network function does not rely on GABA_A receptors. Our results suggest that the flight-pattern-generating network becomes gradually established between P12 and P16, and is further refined until adulthood. These findings are discussed in the context of known physiological and structural CNS development during Manduca metamorphosis.

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Cellular mechanisms of acid secretion in the posterior midgut of the larval mosquito (Aedes aegypti)

U. Jagadeshwaran*, H. Onken†, M. Hardy, S. B. Moffett and D. F. Moffett
urmil@wsu.edu
School of Biological Sciences, Washington State University, Pullman, WA 99164-4236, USA

The gut contents of larval mosquitoes are alkalinized by the anterior midgut and reacidified by the posterior midgut. In the present study the cellular mechanisms of reacidification were studied in isolated, perfused posterior midgut by measuring the transepithelial voltage (V_te) and the rate of acid secretion as indicated by the color change of m-cresol purple during intervals of perfusion stop. The lumen-positive V_te and reacidification were significantly increased by serotonin (0.2 µmol l⁻¹). The V-type H⁺-ATPase inhibitor concanamycin A (10 µmol l⁻¹) on the luminal side inhibited acidification and decreased V_te. On the hemolymph side the carbonic anhydrase (CA) inhibitor acetazolamide (1 mmol l⁻¹) almost abolished V_te, but had no effect on acidification. Similarly, hemolymph-side DIDS (0.1 mmol l⁻¹), DPC (0.5 mmol l⁻¹), amiloride (1 mmol l⁻¹) and ouabain (2.5 mmol l⁻¹) significantly reduced V_te, whereas Ba²⁺ (5 mmol l⁻¹) was without effect. DPC and amiloride also reduced V_te when applied to the luminal side of the epithelium. Unilateral substitution of gluconate for Cl⁻ affected V_te in a way consistent with a greater permeability for Cl⁻ versus Na⁺. Cl⁻ replacement in the lumen decreased V_te, whereas replacement on the hemolymph side increased it. Bilateral replacement left the control voltage unaffected. Na⁺ replacement on either side of the tissue reduced V_te to different degrees. Omission of luminal amino acids was followed by a significant decrease in V_te. Except for concanamycin A, none of the above manipulations impaired acidification, indicating that acidification requires only the apical proton pump. However, the chemical source of secreted H⁺ is still unknown and needs to be investigated.

http://jeb.biologists.org/cgi/content/abstract/213/2/295

Insect Photoreception

Photoreceptor responses of fruitflies with normal and reduced arrestin content studied by simultaneous measurements of visual pigment fluorescence and ERG

Gregor Belušič¹, Primož Pirih² and Doekele G. Stavenga²
gregor.belusic@bf.uni-lj.si
(1) Department of Biology, Biotechnical Faculty, University of Ljubljana, Večna pot 111, 1000 Ljubljana, Slovenia
(2) Department of Neurobiophysics, University of Groningen, Nijenborgh 4, 9747 AG Groningen, The Netherlands
We have simultaneously measured the electroretinogram (ERG) and the metarhodopsin content via fluorescence in white-eyed, wild-type *Drosophila* and the arrestin2 hypomorphic mutant (*w−; arr2−*) at a range of stimulus wavelengths and intensities. Photoreceptor response amplitude and termination (transition between full repolarization and prolonged depolarizing afterpotential, PDA) were related to visual pigment conversions and arrestin concentration. The data were implemented in a kinetic model of the rhodopsin-arrestin cycle, allowing us to estimate the active metarhodopsin concentration as a function of effective light intensity and arrestin concentration. Arrestin reduction in the mutant modestly increased the light sensitivity and decreased the photoreceptor dynamic range. Compared to the wild type, in the mutant the transition between full repolarization and PDA occurred at a lower metarhodopsin fraction and was more abrupt. We developed a steady-state stochastic model to interpret the dependence of the PDA on effective light intensity and arrestin content and to help deduce the arrestin to rhodopsin ratio from the sensitivity and PDA data. The feasibility of different experimental methods for the estimation of arrestin content from ERG and PDA is discussed.

Insect Vision
First evidence of fine colour discrimination ability in ants (Hymenoptera, Formicidae)

Y. Camliitepe* and V. Aksoy yilmazc@trakya.edu.tr
Department of Biology, Faculty of Arts and Sciences, Trakya University, 22030, Edirne, Turkey

In the present study, we report the first evidence that ants discriminate and learn perceptually close colour stimuli. Foragers of the ant species *Cataglyphis aenescens* and *Formica cunicularia* were trained in a Y-maze choice apparatus to monochromatic light stimuli of a constant intensity associated with a food reward. Two stimuli, with a mean wavelength of 40 nm perceptual distance, were chosen from the UV (340 nm vs 380 nm) and the green (510 nm vs 550 nm) range because these species are UV–green dichromats. Foragers were trained with two conditioning paradigms [absolute conditioning (AC) and differential conditioning (DC)]. In the UV range, *C. aenescens* foragers failed to discriminate when presented with a small colour difference in both training procedures. Foragers also failed in the green range when trained with AC but showed significant bias towards the rewarded stimulus when trained with DC. *Formica cunicularia* foragers achieved the task in the UV range when trained with DC only. In the green range, *F. cunicularia* foragers showed clear preference for the rewarded stimulus in both training conditioning procedures. Foragers never failed in choosing the rewarded stimulus in DC even when the intensity of the rewarded stimulus was reduced by one log unit. This clearly indicates that DC is of paramount importance to discriminate perceptually close colour stimuli.

Insect Review
Ecological speciation in phytophagous insects

Kei W. Matsubayashi ¹, Issei Ohshima ² & Patrik Nosil ³,⁴* patrik.nosil@colorado.edu
¹ Department of Natural History Sciences, Hokkaido University, Sapporo 060-0810, Japan , ² Department of Evolutionary Biology, National Institute for Basic Biology, Okazaki 444-8585, Japan , ³ Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA , and ⁴ Wissenschaftskolleg, Institute for Advanced Study, Berlin, 14193, Germany
Divergent natural selection has been shown to promote speciation in a wide range of taxa. For example, adaptation to different ecological environments, via divergent selection, can result in the evolution of reproductive incompatibility between populations. Phytophagous insects have been at the forefront of these investigations of ‘ecological speciation’ and it is clear that adaptation to different host plants can promote insect speciation. However, much remains unknown. For example, there is abundant variability in the extent to which divergent selection promotes speciation, the sources of divergent selection, the types of reproductive barriers involved, and the genetic basis of divergent adaptation. We review these factors here. Several findings emerge, including the observation that although numerous different sources of divergent selection and reproductive isolation can be involved in insect speciation, their order of evolution and relative importance are poorly understood. Another finding is that the genetic basis of host preference and performance can involve loci of major effect and opposing dominance, factors which might facilitate speciation in the face of gene flow. In addition, we raise a number of other recent issues relating to phytophagous insect speciation, such as alternatives to ecological speciation, the geography of speciation, and the molecular signatures of speciation. Throughout, we aim to both synthesize what is known, as well as highlight areas where future work is especially needed.

A plethora of discoveries relating to sex influences on brain function is rapidly moving this field into the spotlight for most areas of neuroscience. The domain of molecular or genetic neuroscience is no exception. The goal of this article is to highlight key developments concerning sex-based dimorphisms in molecular neuroscience, describe control mechanisms regulating these differences, address the implications of these dimorphisms for normal and abnormal brain function and discuss what these advances mean for future work in the field. The overriding conclusion is that, as for neuroscience in general, molecular neuroscience has to take into account potential sex influences that might modify signalling pathways.

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Insect Book Review
Far from simple: insect immune defences
Joachim Kurtz
University of Münster, Institute for Evolution & Biodiversity, Hüfferstrasse 1, D-48149 Münster, Germany

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