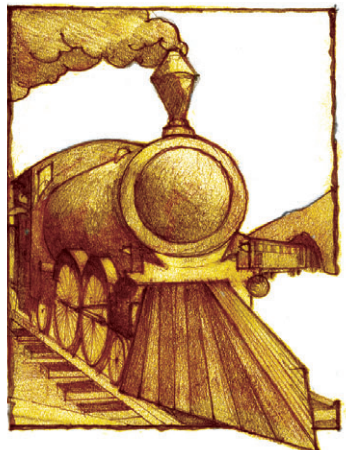
Keeping track of the literature isn't easy, so Outside JEB is a monthly feature that reports the most exciting developments in experimental biology. Short articles that have been selected and written by a team of active research scientists highlight the papers that JEB readers can't afford to miss.

Outside JEB

LARVAL LOCOMOTION



CATERPILLARS MOVE LIKE PISTONS

Many larval stages of insects that metamorphose – caterpillars, maggots and the like – are shaped like a tube with the gut running through the middle. In a recent hi-tech study, a group of US researchers led by Michael Simon of Tufts University set out to discover how caterpillars move, with surprising results.

First they stuck some crawling hawkmoth caterpillars at the business end of a synchrotron and bombarded them with X-rays, which were then converted to visible light and recorded. The resultant X-ray movies showed that the movement of the caterpillar's internal structures could be measured by following the trachea – the slender tubes that connect the insect's insides with the outside and enable it to respire. Some of these trachea are connected to muscles, others are connected to the gut.

To the researchers' surprise, video analysis revealed that at the beginning of each crawling motion, shortly before the caterpillar's middle prolegs began to move, its gut moved forward within the body, in time with the rear prolegs and ahead of all the external structures with which it had previously been in line. The back half of the body would then catch up, sliding over the gut. At some points in the movement cycle, the middle of the gut would be about 1 s 'ahead' of the middle of the external body.

To study whether this bizarre piston-like motion applied to the whole gut, the researchers moved to a smaller, earlier caterpillar stage, which also had the advantage of being transparent, and could be studied directly under a light microscope. They found that although the overall movement of the gut was linked with that of both the head end and the rear of the caterpillar, it was not connected with the movement of the outside body wall. In other words, different bits of the caterpillar stretch and contract at different times, with the outside sliding over the inside.

The fact that the gut swings forward inside the animal as it begins to move might be thought to give added momentum to the caterpillar (the gut and its contents can represent over 1/3 of a caterpillar's body mass). However, this appears not to be the case and it remains unclear why this odd form of locomotion has evolved.

It seems probable that other larval insects and even animals like leeches will turn out to move in the same way. Even more tantalizingly, the authors suggest that studies of biomechanics on animals with stiff skeletons should turn their attention to the soft bits of our bodies – there may be pistons there, too.

10.1242/jeb.049577

Simon, M. A., Woods, W. A., Serebrenik, Y. V., Simon, S. M., van Griethuijsen, L. I., Socha, J. J., Lee, W.-K. and Trimmer, B. A. (2010). Visceral-locomotory pistoning in crawling caterpillars. *Curr. Biol.* **20**, 1458-1463.

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DIETARY EFFECTS

DIET AFFECTS *DROSOPHILA* SLEEP PATTERNS

We all need sleep. Miss a night and you really feel the consequences. Sleep contributes to the health and survival of most organisms and sleep disorders contribute to a wide range of physical disturbances. However, studying sleep patterns in mammals is challenging, for subjects and scientists alike. Fortunately, sleeping *Drosophila* share a lot of similarities with sleeping mammals: they arouse in response to dopamine and have intrinsic circadian rhythms. James Catterson and colleagues from the University of Edinburgh, have looked at the effect of diet on sleep–wake patterns in *Drosophila*. By examining the effect of various foods on sleep, the important relationship between what we eat and how we sleep can be unravelled.

Setting about testing the sleep-wake patterns of *Drosophila*, the team used an automated system that measured activity by recording the number of times flies crossed a laser beam. Adult *Drosophila* held in the lab are usually fed a standard diet made up of agar and a little bit of sucrose. The team wanted to see whether adding yeast to the standard diet would change the fly's sleep patterns, and what effect additional sugar may have.

Male flies fed a yeast-supplemented diet slept less often, for shorter times, and were more active during the day and the night than flies on a conventional lab diet. This may be because increased nocturnal activity is advantageous to male flies that have an increased sex drive at night. However, the female flies slept more often during the day when they ate the diet with added yeast. The team suspect that these sex-based differences may be due to differences in insulin signalling between males and females.

Looking at flies fed a sugar-supplemented diet, the team found no sex-specific differences, but the additional sugar had altered their sleep patterns. Both sexes stayed up longer during the day and night, which resulted in higher activity levels. However, when the flies were asleep, the sucrose diet did not affect how long they slept, suggesting a disconnection of sleep from exercise.

Next, the team investigated the possible mechanism of yeast-induced arousal in male flies by administering a drug that inhibited dopamine synthesis (responsible for arousal from sleep) to males on the standard lab diet and males on the yeast-supplemented diet. Catterson and his colleagues suspected that reducing dopamine would cause the flies to sleep more and be less susceptible to arousal. Looking at the activity levels of the insects on the normal diet, the team found that they were sleepier; however, the effect was diminished when the flies consumed yeast, suggesting that yeast limited the sleep-inducing effect of decreased dopamine levels.

As dietary sugar caused increased activity but not increased sleep, the team investigated whether flies that were less active would require less sleep. This time, they gave the flies a drug that decreased the amount of energy that the insects' muscles could produce and ultimately how much activity they were capable of. As seen with the sucrose diet, the amount of time that the flies slept was independent of their activity level, as the flies showed reduced locomotion but they did not sleep less. The team suspect that fly sleep does not contribute to metabolic balance, and suggests that food intake and locomotor activity are better regulators of energy balance than sleep.

So yeast in the diet aroused male flies during the day and night, while female flies became sleepier during the day. In contrast, sucrose promoted activity in both sexes but did not make them sleep more; meaning that the amount of sleep required by flies appears to be independent of their energy levels and previous activity. Ultimately, this study illustrates the complex nature of physiology, highlighting that diet has far reaching impacts beyond that of gastrointestinal physiology.

10.1242/jeb.049593

Catterson, J. H., Knowles-Barely, S., James, K., Heck, M. M. S., Harmar, A. J. and Harley, P. S. (2010). Dietary modulation of *Drosophila* sleep–wake behaviour. *Plos One* **5**, e12062.

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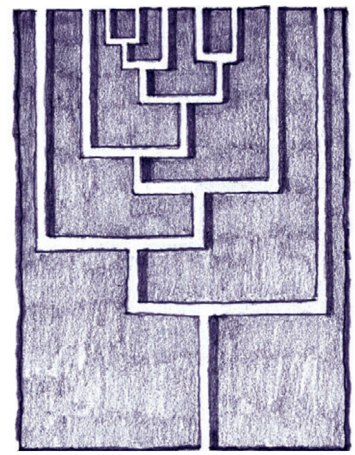
SOCIAL METABOLISM



ANT COLONIES OBEY THE ¾ POWER 'LAW' OF METABOLIC RATE SCALING

While some geometric characteristics (length, surface area) of animals don't increase in direct proportion to any given mass increases, one would feel safe to assume that biochemical interactions (i.e. metabolic rate, MR) scale isometrically (10 times size=10 times metabolic rate). Mathematically expressed as $MR=mass^{1}$, the exponent (1) indicates this direct proportionality (isometry). However, for individual organisms ranging in size from unicellular animals to mega-mammals, multiple studies have indicated that larger animals have lower than proportional (hypometric) metabolic rate increases with a consensus exponent of 0.75 – $MR=mass^{0.75}$. While several (sometimes controversial) hypotheses have been formulated, we still lack clear agreement as to the underlying mechanisms of this ¾ power 'law'. It does, however, suggest intricate cooperative interactions among cells, tissues and organs of individual organisms. Similarly, colonies of social organisms also show intricate interactions and non-centralized emergent properties. This raises the question of whether this level of social organization would extend to colony metabolic rate scaling comparable to that of individual organisms.

James Waters and colleagues, from Arizona State University, investigated the scaling relationships among 13 seed-harvester ant (*Pogonomyrmex californicus*) colonies ranging from 95 to 659 ants, all 10 months old. Using flow-through respirometry they measured metabolic rates of these fully functional lab-reared colonies. For comparison, Waters and colleagues then developed additive mathematical models to predict the collective metabolic rates, and the resultant scaling, of 13 hypothetical colonies, taking into account colony demographics such as numbers and masses of castes and developmental stages. They also measured metabolic rates of 20 groups of workers (1–225 ants) extracted from the lab colonies. In addition they determined individual sizes of all colonies, quantified worker activity in various sized colonies, and calculated the colonies' net growth rates.

The metabolic rate scaling for the additive models and also the extracted worker groups were isometric ($MR=mass^{1}$), as expected, based on the direct proportional increases inherent in the additive models and from similar results obtained by previous authors working on isolated ant groups. The fully functional colonies, however, showed metabolic rate scaling indistinguishable from that of various sized individual organisms ($MR=mass^{0.75}$)!

Waters and colleagues discuss a number of factors that could not explain this disparity, including colony composition and net growth rates. According to the team a greater proportion of 'layabout' ants in larger colonies only partly explained the reduction in the colonies' metabolic rate. The team showed that when activity is factored into the additive models, active individuals would need to increase their metabolic rate 25-fold to achieve the 0.75 scaling coefficient; however, Waters only measured a 6-fold increase between the ants' resting and running metabolic rates. Other factors that might contribute to the colony's reduced metabolic rate are reduced maintenance costs and/or metabolic rates that may vary relatively among colonies, and the fact that these colony size-independent metabolic rates may determine colony growth rates and effective sizes.

The team also speculates that individuals in insect colonies may integrate in a similar way to physically connected cells, tissues and organs in individual organisms and physically connected individuals such as sea squirts that show ¾ power scaling. Nevertheless, these findings clearly demonstrate that a colony of eusocial organisms behave metabolically like a single organism, possibly through networked behavioural interactions leading to patterns of resource and information transfer that influence metabolic scaling, and this lends more credence to the concept of the superorganism.

10.1242/jeb.049585

Waters, J. S., Holbrook, C. T., Fewell, J. H. and Harrison, J. F. (2010). Allometric scaling of metabolism, growth, and activity in whole colonies of the seed-harvester ant *Pogonomyrmex californicus*. *Am. Nat.* **176**, 501-510.

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NEURAL CIRCUITRY

FRUITFUL SEARCH FOR SEX CIRCUITS IN FLIES

In most animals, males and females show different (dimorphic) patterns of behaviour. But we know relatively little about how the neural circuits that underlie sexually dimorphic behaviours are organized. Jai Yu and colleagues at the Research Institute of Molecular Pathology in Austria, in collaboration with Greg Jefferis at the MRC Laboratory of Molecular Biology in Cambridge, UK, recently attempted to untangle sex-specific neural circuitry in fruit flies. In a recent paper published in *Current Biology*, they attempted to map out connectivity among the neurons that control how male flies court female flies.

In the presence of females, male fly brains integrate sensory cues and produce complex motor output in the form of stereotyped leg, abdomen and wing movements (including an audible courtship 'song' generated by the wings). The behaviours are innate, and a male version (splice variant) of the gene *fruitless* controls the entire behavioural sequence. Females expressing the male version of the gene behave like males; males without the male version behave like females. The gene is expressed in ~1500 neurons throughout the fly brain. How does this constellation of neurons control a complex sequence of sex-specific behaviours? Yu and colleagues reasoned that the essential first step was to simply examine how *fruitless* expressing neurons connect to one another in male and female brains. To begin with, they developed a genetic technique that allowed them to systematically visualize the anatomy of small numbers of *fruitless* expressing neurons throughout the brain. After generating hundreds of genetic lines with different groups of *fruitless* neurons labelled, they then charted where individual groups of neurons were in relation to each other and common structural landmarks.

Examination of the overlap among cellular processes from different groups allowed the team to make predictions about how *fruitless* expressing cells are connected to one another in males and females.

First the group showed that multiple *fruitless* expressing sensory pathways converge on one part of the fly brain (lateral protocerebral complex), suggesting that this area is the core site for integration of sensory cues during courtship. Next they identified pathways for motor output from the lateral protocerebral complex. Surprisingly, when they compared dimorphisms between males and females, they only found 11 anatomical dimorphisms in the circuit. Interestingly, they also uncovered a general rule: neurons that are present in both sexes but have dimorphic arborizations tend to be in primary sensory pathways or motor pattern generating circuits, whereas sex-specific neurons are usually in areas postulated to be involved in higher order information processing (e.g. lateral protocerebral complex). These results suggest that anatomical dimorphisms are actually not that common in the circuit, and are concentrated primarily in areas of the brain that are involved in making decisions.

Overall, Yu and co-workers have done something in flies that is very difficult to do in most animals. They have constructed a comprehensive potential wiring diagram for a large circuit controlling complex sex-specific behaviours. That said, it is important to remember that this work only predicts where connections could be – it does not actually prove the presence of any synapses. But this is what makes this paper great; it generates a large number of testable hypotheses and opens up new opportunities to study how neural circuits give rise to sexually dimorphic behaviour.

10.1242/jeb.049601

Yu, J. Y., Kanai, M. I., Demir, E., Jefferis, G. S. and Dickson, B. J. (2010). Cellular organization of the neural circuit that drives *Drosophila* courtship beahvior. *Curr. Biol.* **20**, 1602-1614.

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