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Contents

Conflict, communication and choice in anuran mating systems.

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Amplexus (male clasping of females) is a key reproductive behaviour in anuran amphibians (frogs and toads). I focussed on amplexus behaviour in the cane toad (*Chaunus marinus*, formerly Genus *Bufo*) to investigate costs of reproduction, inter- and intrasexual communication and the role of mate choice and body size in anuran mating systems. Sprint and swim trials indicated that females have reduced locomotor performance in amplexus and that male size influences performance (suggesting possible size-assortative mating). Likewise, solitary males and females fed more (and more rapidly) compared to when they were in amplexus. I confirmed intersexual differences in signalling capabilities. Males vibrate their flanks and give a release call when clasped by another male (precipitating dismount) while females can only give the flank vibrations. Acoustic playback experiments (using pre-recorded male release calls) revealed that the call (and not the vibration, or sexually dimorphic skin texture) is the primary element of the release signal and that males can identify the source of the call. This may leave (mute) females at a disadvantage when inappropriately amplexed, as their signal does not precipitate dismount. Mate choice experiments revealed the influence of body size in mediating amplexus (males were more likely to amplex larger conspecifics). Body size was also important in determining male tenacity (strength in clasping) and ability to maintain amplexus when challenged by other males. In both instances, large males had the advantage. My study suggests conflicting selection pressures for body size. Females may benefit indirectly from mating with larger males, but may also suffer the increased costs of amplexus with a larger male. Furthermore, while there is a large-male advantage in terms of tenacity and fighting ability, large males in high density mating scenarios are more likely to be inappropriately amplexed by other males than their smaller conspecifics. This indicates the importance of an unambiguous signal for amplexus termination, which males (alone) possess in the release call.

Toads: Gods of rain or loyal disciples?

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Toads have been associated with rain for as long as humans have observed them. This culminated in the belief within Western civilisation that toadlets were spawned in clouds and literally fell to the earth with raindrops. Pursuing this idea was the likes of 'The Academy on the Raining of Toads' in Paris, 1859. In New York in 1869 it was pronounced 'a question for philosophers'. By 1940 in Chicago, ‘toad showers’ were declared a myth.

In the latter half of this century, investigations of the spatial and temporal distribution of toads has tended to depart from environmental causation. In 2006, as a member of 'Team Bufo', the aim of my project is to combine the scientific framework with the historical correlation between toads and rain to investigate the spatial and temporal distribution of metamorph cane toads.

Fighters, drifters and cheats: intraspecific aggression in an Australian stingless bee

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The Australian stingless bee *Trigona carbonaria* can form dense swarms of workers, amidst which hundreds of individuals pair on the wing, drop to the ground and wrestle til their death. Microsattellite analysis of eight of these 'fighting swarms' indicate two colonies are predominantly involved, one of which is located close to the swarm. Four colonies which were repositioned to receive large numbers of incoming workers from another nest all exhibited rapid swarm responses. These results are consistent with the theory that 'fighting swarms' arise from attempted intraspecific robbery or nest usurpation.

Further manipulations allowed just 100 non-nestmate workers (1% average colony population) to enter experimental colonies within a one-hour period and caused 5 out of 6 receiver colonies to swarm. When 100 non-nestmates entered over 3 hours, only 2 out of 6 receiver colonies swarmed. High levels of worker drift in native bee apiaries may explain the high incidence of 'fighting swarms' in these environments.

Worker reproduction, in which workers rather than queens produce the males of a colony, occurs in many stingless bees and can make colonies vulnerable to egg-dumping from drifted workers. Over 1000 males from 10 *T. carbonaria* colonies were genotyped to determine maternity and all were consistent with queen origin. Thus reproductive worker parasitism is unlikely to be a threat in this species.

A new parasite of *T. carbonaria* from west Brisbane is also described. The euphorinae wasp (Hymenoptera; Braconid) is an endoparasitoid of adult worker bees and is the first record of the genus *Syntretus* from Australiasia.

Peer-pressure; examining the expression of density-dependent behavioural phenotypic plasticity in *Chortoicetes terminifera*, the Australian Plague Locust.

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Locusts are infamous for forming devastating swarms. Central to the seeding of swarms is density-dependent behavioural phenotypic plasticity. Typically, locusts occur at low population densities throughout their habitats – generally semi-arid ecosystems. At low densities, locusts express a solitarious behavioural phenotype (or phase) characterised by avoidance of conspecifics and the undertaking of short-distance journeys. As is well known, arid-ecosystems are subject to boom-and-bust cycles of rainfall-driven primary production, and in the event of prevalent localised grass-growth, resident locusts will capitalise on the opportunity for reproduction. Experiencing the resultant increase in the population's size and density drives a change in the behavioural phenotype expressed by resident locusts from the solitarious to gregarious phase. Unlike solitarious locusts, gregarious individuals display heightened levels of activity and strong attraction to conspecifics – culminating in their ability to undertake cohesive mass-migrations following the exhaustion of locally available food.

My study is the first to examine the expression of behavioural phenotypic plasticity in the Australian plague locust (APL), our most economically important locust. By developing a novel automated video-tracking behaviour assay, I observed, quantified and compared the behaviours displayed by crowd- and isolated-reared APLs - establishing that the species does express classic solitarious and gregarious phenotypes contrary to prior opinion. Next, I demonstrated that crowding solitarious locusts for 72 h, and isolating gregarious locusts for 72 h shifted the expression of behavioural phenotypes from solitarious to gregarious and vice-versa. Strikingly homologous behavioural patterns are also displayed by the extensively studied African desert locust. It has been identified that mechanosensory stimulation of the hind-femur, provided by buffeting against other locusts in a dense crowd, induces the shift from solitarious to gregarious. I discovered that in APLs too, repetitively stimulating (for 6 h) the hind femur of solitarious locusts (in this case with a paint-brush) evokes gregarious behaviours.

Central nervous system (CNS) serotonin and dopamine levels are known to change in concert with gregarisation and solitarisation (respectively) in the desert locust, suggesting that phase change is neurochemcially mediated. Via high-performance liquid chromatography, I compared the levels of CNS serotonin and dopamine between gregarious and solitarious APL, finding no baseline differences between the phases. There were also no changes in the neurotransmitter's levels following 72 h crowding of solitarious locusts, the 72 h isolation of gregarious locusts, or following 6 h of mechanosensory stimulation of solitarious locust's hind femora.

Given the similarities in the life history and phase change patterns between APLs and desert locusts it will be worthwhile to continue examining the role played by CNS neurotransmitters in phase change. Of particular interest would be the discovery of differing physiological mediators of phase change between the two species, perhaps offering unique insights into the evolution of behavioural phenotypic plasticity.

Keeping the Peace: The reproductive mechanisms maintaining a stable hybrid zone between two invasive African honeybee subspecies

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Hybrid zones occur where genetically distinct groups of organisms come into contact and produce viable hybrid offspring. I studied a unique hybrid zone between two African honey-bee subspecies: *Apis mellifera scutellata* and *A. m. capensis*. The stability of this hybrid zone is unexpected as *A. m. capensis* workers are able to reproduce clonally and become a lethal social parasite within *A. m. scutellata* populations. *Capensis* workers can do so because of a suite of behavioural and physiological traits, known as the '*Capensis* complex', which allow them to bypass colony defence mechanisms and become reproductively active. On the other hand, *A. m. scutellata* is an extremely successful invasive species outside its natural range, usurping resident honeybee populations through reproductively dominant behaviour of queens and drones. I tested the hypothesis that the behavioural mechanisms observed outside the natural ranges of *capensis* and *scutellata* also operate within, and contribute to the stability of, the natural hybrid zone. To do so I examined three aspects of *capensis* and *scutellata* reproductive biology through field experiments in South Africa and laboratory analysis in Sydney; drone flight behaviour, inheritance pattern of the '*Capensis* complex' upon hybridisation, and the prevalence of parasitic clonal reproduction within the *capensis* population. Two further experiments examining *scutellata* drone and queen behaviour could not be completed due to adverse circumstances.

Capensis and *scutellata* drone mating flight times overlapped, indicating that hybridisation between the two subspecies may occur. Further, examination of the inheritance pattern of the '*Capensis* complex' revealed that these traits were under polygenic control. Thus, upon hybridisation, the traits necessary for effective parasitism segregate, rendering hybrid *capensis* offspring ineffective parasites. Finally, using microsatellite parentage analysis, I detected parasitic clonal reproduction occurring in *capensis* queen cells. This final result challenges the paradigm that the honeybee queen is solely responsible for new queen production, and confirms that clonal worker reproduction occurs on both sides of the hybrid zone.

Negative associations between *Rhabdias* cf. *hylae* (Nematoda) infection and metamorph performance in invasive cane toads (*Bufo marinus*)

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Parasites significantly influence population viability. The cane toad (*Bufo marinus*) and the lung nematode (*Rhabdias* cf. *hylae*) provide an appropriate model system to study the effects of a common anuran parasite on an invasive species.

I aimed to investigate the effect of *R. hylae* infection on the performance of metamorph cane toads. I exposed 50 metamorphs to 30 infective larvae and 50 metamorphs to distilled water. Fourteen (±1) days post-infection I calculated their growth rates and raced them to exhaustion to measure sprint speed and endurance (total distance and time ran before exhaustion). Fifty (±10) days post-infection toads were offered 15 crickets and total number eaten over 10 minutes was recorded as a measure of feeding rate. Toads were videoed in their enclosures for 90 minutes and activity levels were calculated by counting total number of movements made and total time spent in the different areas of the enclosure (sand, dry refuge, water). Overall mortality was measured as the proportion of all metamorphs to die during the course of the experiment.

Infected toads had reduced growth rates, feeding rates, running speeds and endurance (total distance and time ran) compared to non-infected toads. General activity levels were similar between treatment and control groups but overall mortality was higher for the infected toads.

Reduced growth rates in infected toads may reflect increased energy demands associated with replacing lost blood, repairing lung damage and mounting an immune response. Additionally, the apparent decrease in food intake would further disadvantage growth rates and may be a secondary effect of the lethargy induced by the costs of infection. Decreased locomotor performance could reflect energy conservation and limited aerobic capacity in infected toads. With apparent differences found in utilisable energy between the treatment and control groups, it was surprising that general daily activity levels were similar. It is possible that the infected toads were more active than expected because their infection and associated infected larvae in their enclosure induced discomfort and restlessness. Increased mortality in infected toads may be a by product of invasion, with burrowing infective larvae breaching protective barriers throughout the body and causing infection.

Conclusively, *R. hylae* negatively influences metamorph cane toads by reducing both growth and locomotor performance and increasing mortality.

Anti-predator behaviour of small mammals to the introduced Red fox

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The red fox *Vulpes vulpes* has been implicated in the decline of a variety of mammals in Australia. Implementation of the NSW Fox Threat Abatement Plan in Ku-ring-gai National Park has resulted in a decrease in the activity of foxes in baited areas. Within this system I examined the anti-predator behaviour of the brown antechinus *Antechinus stuartii* and the bush rat *Rattus fuscipes* in baited and unbaited areas.

Capture-mark-recapture data showed that small mammal abundances did not vary significantly between areas of different fox activity. The application of odours to traps to examine whether faecal scents deterred trap entry resulted in Antechinus and young (<60g) bush rats exhibiting strong aversion to fox odour. Adult bush rats indiscriminately entered predator and non-predator odour traps.

A series of foraging experiments using a giving-up-density (GUD) design found that Antechinus foraged less from trays with fox odour applied. GUD values were also higher for bush rats at fox-scented trays, indicating that this species exhibits caution. Spool and line tracking of Antechinus and bush rats displayed no significant difference between habitat and structure use between baited and unbaited areas for either species. However, some habitat features were used proportionally more than they were available.

The results of this study indicate no effect of decreased fox activity on the behaviour of small mammals. However, Antechinus and bush rats do exhibit anti-predator behaviour in response to fox faecal olfactory cues. The life history characteristics may explain the variation of anti-predator behaviour in the bush rat. These results provide insight into the ability of small mammals to identify and react appropriately to the threat of an alien predator, with which these mammals have co-existed for over 100 years.

Interactions between generalist herbivores and plants: foraging behaviour and plant responses

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Generalist herbivores feed on a variety of plants. The vulnerability of any particular plant species to browsing by these generalists depends on the physical and chemical characteristics of that species. The vulnerability may also be affected by the characteristics of neighbouring plants. Neighbouring plant hypotheses consider the vulnerability a focal plant as a function of its own characteristics compared with those of its neighbours. While herbivores respond to plants, at the same time, plants are not simply passive to herbivory and may respond to it using chemical and physical strategies. This project investigated interactions between plants and two herbivores, introduced Rusa deer (*Cervus timorensis*) and native swamp wallabies (*Wallabia bicolor*), in the sandy heathland in Royal National Park. Browse levels of 31 plant species were determined using a survey; and deer preferences (relative consumption) for nine plant species were measured in a field trial. *Allocasuarina distyla*, an evergreen shrub species, was of intermediate preference to the deer and was used as a focal plant to examine the role of neighbouring vegetation in a separate experiment. Plots of *A. distyla* were placed adjacent to one of five plant species which had been browsed at high, low and equal levels (relative to *A. distyla*) in the survey and preference trials. Swamp wallabies were the dominant visitor in this trial and the results showed that there was a neighbouring plant effect. Chemical and physical responses of *A. distyla* seedlings to herbivory were studied using a factorial design for presence/absence of saliva and extent of artificial browsing (0, 5, 50 %). Six weeks after treatment, new growth was harvested and various growth parameters measured and chemical assays conducted. Saliva did not significantly affect the physical characteristics of seedlings or the fibre levels. New growth of branchlets (as % of total branchlet biomass) was greatest with a high (50 %) level of browsing (0 % and 5 % no difference). The number and lengths of new growth, and the percentage of fibre, all increased from 0 % to 5% browsing (5 % and 50 % no difference). This suggests that the mechanical action of herbivory triggers various physical and primary chemistry responses in plants regardless of the amount of biomass removed. The phenolic levels showed a significant interaction between browsing and saliva, indicating that the presence of saliva changes the plant response to browsing. My results demonstrate that these generalist herbivores show preferences for different plant species, and that neighbouring vegetation affects the extent to which each plant species is eaten. I have also demonstrated for the first time, that *A. distyla*, which uses mainly branchlets for photosynthesis, responds to herbivory by altering growth, chemical and physical characteristics.