EVOLUTION AND THE IMPACT OF INVASIVE SPECIES: CANE TOADS AND SNAKES IN AUSTRALIA

A thesis submitted to The University of Sydney for the degree of Doctor of Philosophy
by
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August 2004
DECLARATION

I hereby declare that the work contained in this thesis is my own and contains no materials previously written by another person, except where specifically acknowledged. I have not submitted a similar thesis at another university.

Ben Phillips

March 2005
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At the end of each chapter, I have listed specific acknowledgments, thanking people who helped with the execution of the science. I am grateful to all listed there, for their help. Without them, this thesis would not be.

Almost without fail, however, these people have provided more than technical or logistical help. Others still, are not mentioned in relation to any specific piece of work but have helped in less direct and more important ways; with love, friendship and support. Without some of these people, I would not be.

But where does one start? The beginning seems sensible but is, of course, impossible to identify; something like this has no beginning, although it might have an end. When in doubt, start somewhere and see where it ends…

Firstly then, to the great and lustrous Herpes (aka Richard Shine), god of the reptiles and my supervisor in this enterprise. Rick took me on as a student despite the fact that I refused to move to Sydney and that I couldn’t be talked out of a thesis on snakes and toads. After accepting my idiocy, he lent the full weight of his knowledge and experience to the identification of avenues that might be navigable. Throughout the project he has been a constant source of encouragement, humour, and useful advice. As a writer and scientist, he still manages to be inspirational. Rick also provided a chance to play with LOTS of snakes in Canada (a trip that doubled as a crash-course in science, Shine style), for which I am very grateful. I am probably grateful for the wrong reasons however; the trip gave me a dirty little insight into Rick’s bovine proclivities, a piece of information that has kept me entertained ever since.

And what is Rick without Melanie Elphick? My guess would be a man drowning in his own output. Mel keeps the lab oiled, effortlessly wears her heart on her sleeve, and has gone well beyond the call of duty for me on several occasions. I have always offered to repay her in beer but I suspect (for health reasons) that it might be better not to at this point.

Greg “King” Brown, president of the Beatrice Hill Venomous Snake-Lovers’ Society, and my associate supervisor, also deserves special mention; mostly for his excellent hospitality and generous help. Greg is also the custodian of many empirically-perfected recipes, an encyclopaedic knowledge of the blues tradition, a wicked sense of humour and – in a pattern disturbingly similar to Rick – an unhealthy fascination with calves; all of which add greatly to the joy of field work in Darwin.

Whilst on the subject of Beatrice Hill, I have also taken great enjoyment in the company of Slim Dusty, “Fuck’n” Eric Cox and Jason Stephens. Watching Slim destroy a coconut and Eric and Jase muster goannas have become memories to warm the heart.

Much of my time has been spent off campus. In particular, the first year was spent in Lismore. Peter Baverstock, the PVC at Southern Cross University kindly provided me with an office and constant intellectual challenge (I lost count of the number of times I heard him say “that’s bullshit!”) for which I am very grateful. Among friends made in the Bav Lab, Anthony Moore was the ultimate friend-in-need and walked a delicate line with incredible poise. He does however, have what can only be described as an unhealthy fascination with fish.
Early work in Lismore was also given endless, selfless assistance from Jeff Hayter and Eric Bateman; two guys that took serious risks with their health removing large, dangerous snakes from people’s homes, simply because “someone has to do it” – no ego, no posing, no fuss. I gained a new appreciation of Jeff’s 300 brown snakes a year (with no bites) average after spending 15 terror-soaked minutes in a small swimming pool with a large, cranky brown. These guys are heroes!

Further north, Ian Jenkins was a major source of snakes from toad-exposed areas. As well as running a farm, caring for wildlife and helping Barb raise the kids, Ian manages to run an excellent snake show for tourists in Childers and, like Jeff and Eric, rescues hundreds of snakes that would otherwise be cut or shot in half. Ian and Barb’s hospitality has also been fantastic, although I probably visit them less than I should, as a consequence of their small, but deeply psychotic parrot.

Virginia McGrath, Ingham’s “snake lady”, provided unstinting hospitality and endless conversation about wildlife (snakes in particular); company that was, on occasion, sorely needed. Several times she let me turn up, almost unannounced, and take over large sections of her back verandah with that bloody swimming pool.

In Sydney, Michael “Dwayne” Kearney was instrumental in sliding the doors that led to this thesis. He has since become a great friend and a highly-respected colleague. How anyone maintains his obscene levels of enthusiasm and energy on a diet consisting almost entirely of chocolate milk and sardines is one of the greatest unanswered questions I have encountered during the course of this research. But deep perplexity aside, there is no-one I would rather watch prancing down the road, gaily sweeping a butterfly net from side to side, catching low-flying frogs. Poetry in motion.

Dwayne also introduced me to Dr James Smith; a hairy, fishy-smelling, mud-loving, mozzie-swatting, crazy man who also happens to be a consummate musician and a great friend. Sadly, James’ commitment to extreme fieldwork has led to a nasty case of recurring finger gout that may one day spread, causing his genitals to fall off. I hope that before this inevitable tragedy, he finds it in his heart to forgive me for leaving him to dangle upside-down in the bamboo over that crocodile. It was an accident, I swear.

For unceasing entertainment throughout the course of the project, Amanda “Magic Pants” Lane deserves special mention. Irrespective of my geographical locality and state of mind, she managed to find me and make me laugh, occasionally to the point of tears. There were times this perpetual silliness kept me functioning and reminded me how it felt to laugh when I had forgotten. The Pants is also, I believe, the silent inspiration for the ROAM list (details of which – for reasons of security – I am unable to divulge). Such concepts as Gristle and Byte the death metal band, chameleon spunk and the ultimate email raspberry indicate to me a mind wasted doing biology on the gorgeous beaches of New Caledonia. All I can say is pthththththththblbltht!

Miss Magic Pants, gets me to thinking about Adnan Moussalli and Devi Stuart-Fox; luminous friends, inspirational company and currently lost somewhere in the wilds of Johannesburg. Adnan introduced me to drumming, a sport from which I have gained immense pleasure. More importantly however, Adnan and Devi supplied the last piece for my reworked existential jigsaw puzzle, whilst we squatted amongst pieces of used toilet paper and other unsavoury rubbish on the side of the road in Botswana; an unlikely place for an epiphany, but not unlikely company.

On the subject of epiphanies, there have been a few over the last several years, and most of the important ones have been personal. I ended an eight-year relationship
with my first love and in the process somehow lost contact with the fabric of life. I am, however, deeply grateful for the time I spent with Julie and she deserves special thanks for encouraging me to embark on this project. Without her initial encouragement it wouldn’t have happened (the alternative plan, equally ambitious but a lot less scientific, was to grow a garden).

Clare “No-nerves” Morrison also provoked a few epiphanies, taught me the incalculable value of English breakfast tea and accompanied me on the first marshes trip – we came back with more skulls than snakes, as I recall. Despite deserting me for a tropical island, Clare still manages to be responsible for my intimate knowledge of Giardia and the fact that everything I cook whilst camping nowadays tastes like metho.

In my mind at least, Clare leads effortlessly to the Gold Coast Mob; Luke Shoo, Marc Hero, Naomi Doak and Narinder Virdee – good friends and beautiful people all. Luke of the immensely unflappable wa, in particular has been an excellent friend and even managed to find time to attend a portion of one of my field trips. I have been promising to reciprocate for years but his insane penchant for climbing large, ominous mountains keeps me daunted. Besides, I have a feeling there won’t be too many lonely mountaintops in his foreseeable future. May they both be blessed.

Luke leads me to David Fouche, random American guy and all round funny bastard. After a ten-minute conversation on a beach in Fiji (the extent of our relationship to that point), I offered him (somewhat hesitantly) a ride up the Queensland coast – just as long as he didn’t mind that we were going to be stopping on the way to catch snakes. Apparently he didn’t, and I fear I may have created a monster. He spent the rest of his six months in Australia catching various reptiles and sending me the photos. The only living witness to the taipan catching incident (one of my more reckless moments), he was last seen in Florida; mild mannered engineer by day, mud-stained gecko wrestler by night.

I think this brings us to Sydney and The Last Eleven Months (sighs of relief, murmurs of approval, increased levels of attention). Settle down, I am only just getting started. Despite initial reservations about living in the big city, my time in Sydney has been deeply satisfying, if somewhat tiring, and filled to overflowing with excellent company. There is something, poorly-defined but incredibly important about balancing work and play and it is the Sydney Mob that I hold responsible for my relative sanity at this point.

Mike “damn you!” Wall and “Marauding” Audrey Ching kindly put me up when I first moved down, and have since become valued friends. I suspect that when the time comes to part ways I will feel that I haven’t spent enough time with either of them. But at least Mike and I will always have the Terror of Eumungerie to bind us… Oh, dear.

My fantastic office mate, Dan “the Jacky Man” Warner has proven to be ridiculously forgiving. Considering that the first time we met I was mostly naked, under the influence of way too many capirinhas and may have been wearing a napkin on my head, things have worked remarkably well, particularly given that I have probably done nothing to dispel those initial impressions. But we will see him breakdance, oh yes, we will.

And with Dan comes Tonia Warner, who along with Tracy Langkilde has the most immense ability to drag joy from the depths of your soul simply by saying hello. Time spent in such smiley company is time well spent.
On the subject of smiley company, how could we forget **Jacquie “The Jackster” Herbert**? Again, another smile nut, but the Jackster combines the love of smiling with the love of mirrorballs, glitter, dancing and fast-talking. I feel that so far I have been terribly clever about avoiding a night of dancing at that bloody retro place, but I am fast running out of excuses and she simply doesn’t give up.

This brings me to my comrades in the belly of the beast, **Mathew “Cronjer” Crowther** and **Jai/Darko Thomas**. Cronjer hides his warm-hearted, intelligent, and incredibly caring nature behind the guise of a slightly deranged lunatic. As a consequence, he is endlessly funny, often in stunningly inappropriate ways and is always ready to launch into a lecture on random topics (probably the Irish blood). Few of us in Sydney will ever forget the “sneaky fucking fairy-wrens” or the “sex life of the male echidna” addresses. Magic stuff.

Jai on the other hand, is more your quiet, incredibly perceptive, watch the crowd type. Curiously enough, Darko inhabits the same body, often emerging after dark to sing like an angel, dance like a demon, do impressions, and generally make comedy. Jai has all the willpower, intelligence and strength necessary to chase his dreams, Darko has the confidence to make it happen. As well as being a good mate, Jai (as Mel’s 2IC) helped with the snake husbandry and a couple of cunning ideas.

In addition to these folks, **Jon Webb, Sam Vine, Andrew Sunter, Pedro Range, Raju Radder, The Limpards, Julia Jones, Sebastian Iglesias, Simon Hudson** (we couldn’t have done it without you, scarecrow), **Clare Holleley, Beth Hammond, Team Haggis, Matt Greenlees, Al Glen, Hamlet “Hammers” Giragossyan, Paul Fox, Helena Forsman, Mark Fitzgerald, Weiguo Du, Yvonne Davila, Juan Jose Cruz, Emilie Cameron, Alana Burley, Chin Liang Beh, Gavin Bedford, Dave Allsop and Scott and Wendy Agnew, all provided friendship, help, or both during the course of this project. **Semra Yetke and Suzan Ramsay** saved my administratively retarded arse on a number of occasions, and **Debbie Erikson and Ina Fine** at the library were incredibly helpful, particularly in getting papers to me while I was off campus.

But no acknowledgements would be complete without mentioning my family. **Mum, Dad** and my sister, **Ché**, have provided endless support, understanding, and love, as well as wise counsel. Their company continues to be simultaneously eccentric, inspirational and deeply enjoyable, such that they are among my best friends, as well as being my family. Mum and Dad also gave me (and the snakes) a place to stay when the shit hit the fan (losing a large portion of their shed in the process) and continue to provide an unparalleled sanctuary at The Storrin.

Long acknowledgements? Lots of fantastic people. Thanks all.
Evolution can occur rapidly, along timescales that are traditionally regarded as “ecological”. Despite growing acceptance among biologists of rapid evolution, a strong paradigm of contemporary evolution is still absent in many sub-disciplines. Here I apply a contemporary evolution viewpoint to conservation biology.

Specifically, I examine the impact of cane toads (*Bufo marinus*) on Australian snakes. Toads were introduced into Australia in 1935, have spread rapidly and represent a novel, extremely toxic prey item to naïve Australian predators (including snakes). Based on dietary preferences and geographic distributions I find that 49 species of Australian snake are potentially at risk from the invasion of the toad. Furthermore, examination of physiological resistance to toad toxin in 10 of these “at risk” species strongly suggests that most species of Australian snake are poorly equipped to deal with a likely dose of toad toxin. Even species that are highly resistant to toad toxin (such as the keelback, *Tropidonophis mairii*) face indirect fitness costs associated with consuming toads.

Within a population of snakes however, the impact of toads is unlikely to be random. For example, the examination of several component allometries describing the interaction between snakes and toads revealed that, within a species, smaller snakes are more likely to ingest a fatal dose of toad toxin than are larger snakes.
Further consideration of the interaction between snakes and toads suggests that toads will not only be exerting differential impact on snakes based upon morphology, but also exert non-random selection on prey preference and resistance to toad toxin in snake populations. To examine the possibility of a morphological response by snakes to toads, I examined changes in the body size and relative head size of four species of snake as a consequence of time since exposure to toads. Two of the species (green treesnakes and red-bellied blacksnakes) are predicted to face strong impacts from toads. These two species showed an increase in mean body size and a decrease in relative head size as a consequence of time since exposure to toads; both changes in an adaptive direction. In contrast, the other two species (keelbacks and swampsnakes) are predicted to face much lower impact from toads, and these two species showed little or no evidence of morphological change associated with time since exposure to toads. These results indicate an adaptive change in morphology at a rate that is proportional to the predicted level of impact for each species, strongly suggesting an evolved response.

Red-bellied blacksnakes (a toad-vulnerable species) were further assessed for evolved responses in prey preference and toxin resistance. Comparisons between toad-exposed and toad-naïve populations of blacksnakes revealed that snakes from toad-exposed populations exhibited slightly higher resistance to toad toxin and a much-reduced tendency to eat toads, when compared with toad-naïve snakes. Naïve snakes exhibited no tendency to learn avoidance of toxic prey, nor were they able to acquire resistance to toxin as a
result of several sub-lethal doses, suggesting that the observed differences between populations is evolved rather than acquired. Together, these results strongly suggest that blacksnakes are exhibiting an evolved shift in prey preference and toxin resistance as a consequence of exposure to toads.

Thus, it appears that snakes are exhibiting adaptation at multiple traits in response to exposure to toads. Given the high likelihood that these adaptive shifts have an evolved basis, it appears that the impact of toads will decrease with time in many snake populations. But what about toads? Because the outcome of the interaction between a toad and a snake is also mediated by the body size and relative toxicity of toads, it is important to understand how these traits vary in space and time. Exploratory analysis revealed that toads exhibit a decrease in body size and a decrease in relative toxicity as a consequence of time since colonisation, indicating that their impact on native predators decreases with time. Additionally, there appears to be meaningful spatial variation in toad relative toxicity, indicating that some populations of native predators are facing higher impact from toads than others.

Overall, these results clearly indicate the importance of assessing the potential for rapid evolutionary response in impacted systems. Doing so may provide evidence that some species are in less trouble than originally thought. Additionally, and as more data accumulate, it may be possible to characterise certain categories of environmental impact by their potential for eliciting adaptive response from “impacted” species. This approach has strong
implications for the way conservation priorities are set and the way in which conservation dependent populations are managed.
It was with some surprise that I put all these chapters together and noticed that they formed a reasonably themed, focussed piece of work. The progression of ideas and data presented herein has only a weak association with real time. Often, for either logistical or no apparent reason, horses went before carts and good ideas came along after they were needed. I suspect this is a normal part of the discovery process. Well, it’s normal for me, anyway.

I also suspect that the loose association between time and logic’s arrow is not necessarily a problem. Someone famous once remarked that a scientific paper is one of the most contrived instruments imaginable and I suspect, in most cases, they were right. This thesis thus consists of eight, highly contrived pieces of writing as, for pragmatic reasons, each data chapter has been written in the format of a paper. Another outcome of a thesis presented in such a manner is redundancy. Many chapter introductions and discussions repeat previous chapters and one may get the impression that one is being harped at. This was not my intention and I hereby express sincere apologies to any reader sensitive about finger waggling.

The work and ideas presented here are almost entirely my own. Spending most of my time off campus reduced my chances for active collaboration but did allow me relative freedom to develop and test ideas. Occasionally, by either design or accident, I got lost and my supervisor, Richard
Shine, provided useful guidance. Rick and others have also made many useful corrections to my, occasionally rambling, prose.

Unfortunately, endless hours were spent bogged down in administration with the net result that animals were collected under permits S10769 and B2272 (NSW), SF004029 (WA), W4/002711/01/SAA, WISP00947103, WITK00946503 and ATH03/017 (Qld), and 15292, 15225, 12460 and 11195 (NT). The record for the state with the longest permit approval time goes to Queensland, with an administration time of eight months, during which time I could do nothing but develop ulcers. The project was approved by the Animal Care and Ethics Committee of the University of Sydney (protocols L04/4-2003/2/3737 and L04/9-2003/3/3192).