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Lizards, ticks and contributions to Australian parasitology: C. Michael Bull (1947–2016)

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ABSTRACT

Professor C. Michael Bull was a great scientist and mentor, and an Associate Editor of this journal. While his research career spanned the fields of behavioural ecology, conservation biology and herpetology, in this article, we pay tribute to his major contribution to Australian parasitology. Mike authored more than eighty articles on host-parasite ecology, and revealed major insights into the biology and ecology of ticks from his long term study of the parapatric boundary of two tick species (*Amblyomma limbatum* and *Bothriocroton hydrosauri*) on the sleepy lizard (*Tiliqua rugosa*). In this article, we provide an overview of how this research journey developed to become one of the longest-running studies of lizards and their ticks, totalling 35 years of continuous surveys of ticks on lizards, and the insights and knowledge that he generated along that journey.

Professor C. Michael Bull (hereafter referred to as Mike) was a renowned ecologist, with a strong research focus on the ecology, behaviour and conservation of lizards. His major discovery was long-term monogamy in the sleepy lizard (*Tiliqua rugosa*) which sparked much subsequent research into lizard sociality (Bull et al., 2017). However, his career path was strongly shaped by his initial research into ticks on lizards; a research theme that continued throughout his entire career. Here, we provide a brief overview of his contributions to the field of Australian parasitology.

As a young biologist, Mike was interested in the ecological processes maintaining parapatric boundaries; a phenomenon where species have distributions that meet abruptly, with very little overlap (if any) between them. He completed a PhD investigating this occurrence in two species of frogs in Western Australia; *Crinia pseudosignifera* and *C. insignifera* (Bull, 1975) before moving back to Adelaide to begin researching a similar phenomenon in three tick species that infest a common Australian lizard (*Tiliqua rugosa*), which was initially discovered by Michael Smyth at Adelaide University (Smyth, 1973), Mike's honours supervisor. *Bothriocroton* (*Aponomma*) *hydrosauri* has a southerly distribution while *Amblyomma limbatum* has a northerly distribution, and *A. albolimbatum* had a westerly distribution on its lizard host (Fig. 1). Where any pair of tick species met, they had abrupt species boundaries, overlapping by one to 2 km at most (Smyth, 1973). The question that drove Mike at the time was what influences the shape and maintenance of this abrupt species boundary?

Ticks are particularly sensitive to desiccation in the off-host environment, so environmental conditions can play a major role in shaping their distributional patterns. Early work revealed that *B. hydrosauri* experienced more rapid water loss and had a lower critical temperature than either of the two *Amblyomma* species (Bull and Smyth, 1973). Thus, climate could broadly explain the species distributions; *B. hydrosauri* was physiologically limited in how far north it could move (Bull and Smyth, 1973). However, *A. limbatum* had no such physiological constraints, so why did it not move further south and overlap the distribution of *B. hydrosauri*?

To more closely examine this question, Mike initiated a study in the mid-north of South Australia in 1982, at a site known as Mt Mary/Bundey Bore, which is located roughly half-way between the townships of Burra and Morgan, and is situated on the boundary of *A. limbatum* and *B. hydrosauri* (Fig. 1). Unbeknown to Mike at the time, this study was to become one of the longest-running studies of a lizard in the southern hemisphere, and quite possibly the longest running study of wildlife ticks anywhere in the world. These surveys continued year after year, with Mike passing away only a few days after completing his 35th year of field work.

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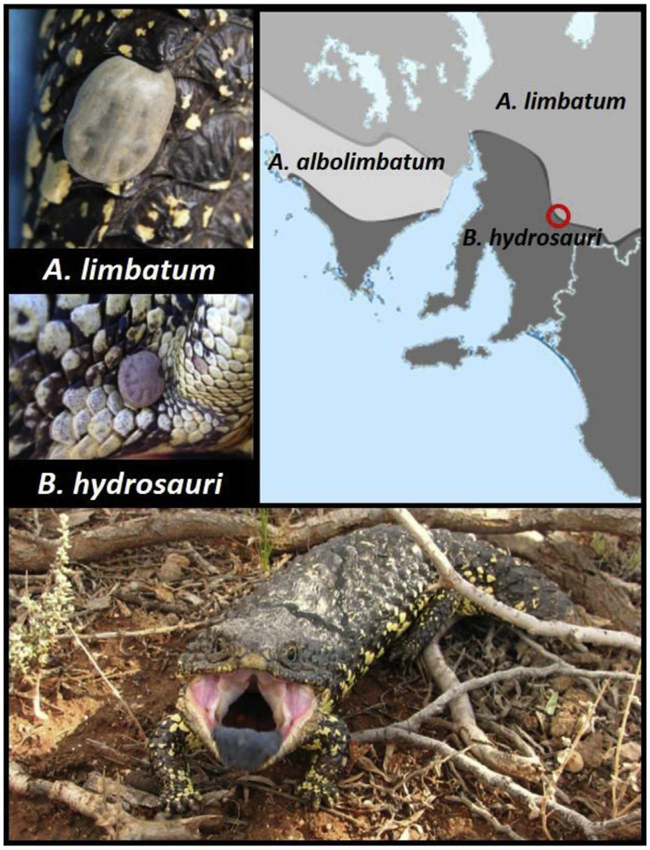

Fig. 1. Photographs of the two tick species (*Amblyomma limbatum* and *Bothriocroton hydrosauri*), their host (*Tiliqua rugosa*) and a map indicating the approximate parapatric distribution of these two ticks (and additionally, *Amblyomma albolimbatum*), with the location of the long-term study site 'Bundey Bore/Mt Mary' circled. The parapatric distributions are taken from Smyth (1973).

Mike and his long-running research assistant - Dale Burzacott - would drive along the dirt roads in the study area, catching lizards and recording the identity of the lizard, its sex and body size, along with the species and number of ticks, lifecycle stages, where they were located on their lizard host, and whether they were engorged, with their methods being consistent across the years (Fig. 2). Between the two of them, they collated more than 56,000 captures of lizards, recording attributes of the lizards, their ticks and their location. Sadly, Dale also passed away unexpectedly, only a few months after Mike in early 2017.

Mike and his students carried out analyses on this growing dataset, and conducted a range of experiments to understand what factors could maintain such an abrupt species boundary. This research made numerous contributions to our understanding of the biology and ecology of ticks, including host-seeking behaviour (e.g. Belan and Bull, 1995), competition between tick species (Bull et al., 1989), and the impacts of predation on tick populations (Chilton and Bull, 1996), resulting in over 40 publications on tick biology and ecology alone. From these numerous studies, the only promising factor that emerged in terms of explaining the parapatric boundary was the possibility of reproductive interference between the two tick species. Andrews et al. (1982) reported the inability of either tick species to reproduce in the presence of the other. However, a later repeat of this work using ticks and lizards in outdoor enclosures refuted these findings (Bull and Burzacott, 1994), meaning the mechanism maintaining the parapatric boundary remains unknown to this day.

As the yearly surveys continued, Mike began to notice that the same male-female individuals would pair up each spring time, across consecutive years. The sleepy lizard is a common lizard across the southern half of Australia, so Mike assumed this behaviour would have been documented somewhere. Instead, he discovered that no one had reported this kind of long-term pairing behaviour in any other lizard species, anywhere else in the world (Bull, 1988). A recent analysis of these data by Leu et al. (2015) revealed more than 30 pairs had remained together for 15 years or more, with one pair still together after 27 years (and counting). Mikes attention was drawn towards this unique behaviour in a system where the normal benefits of monogamy (e.g. joint parental care) were absent. However, the tick surveys continued, and remained a constant theme through his research in the years that followed.

Through this long-term dataset, Mike discovered that tick loads had an impact on this long-term pairing behaviour. Some females would occasionally switch partners between years, and those males that became 'divorced' had higher average tick loads than males that were retained as a partner from one year to the next (Bull and Burzacott, 2006). This suggested that parasites (and specifically ticks) could influence this long-term pairing behaviour, and perhaps play a role in shaping mate selection in this species. Conversely, Mike also discovered that behaviour could influence parasite transmission. Kerr and Bull (2006) found a positive relationship between the temperature under bushes (that lizards use as a refuge), and lagged tick load (2 weeks later). Specifically, the highest tick loads were seen when temperatures reached above 30 °C under bushes (Kerr and Bull, 2006). This coincides with when temperatures under bushes become too hot for thermoregulatory purposes, and lizards seek deeper, cooler refuges, such as wombat burrows. Several lizards simultaneously can be observed using these refuges during heat waves, and these refuges are likely to provide an ideal environment for tick development, as well as the relocation of a new host.

This started an investigation into the influence of refuge sharing on the transmission of parasites. At the time, significant advances had been made in technology that allowed detailed insights into the movement patterns of lizards using micro-GPS loggers. Using these loggers, Leu et al. (2010) could identify which refuges lizards were using and their temporal sequence of use, to build a picture of potential tick transmission pathways represented by a social network. This analysis revealed that tick loads were higher in lizards that shared refuges (within a time window that allowed for the moulting of the tick into its next lifecycle stage) with more neighbouring individuals (Leu et al., 2010). Similar patterns were found in studies of networks of other reptile species that Mike was involved with (e.g. gidgee skinks, *Egernia stokesii* (Godfrey et al., 2009); tuatara, *Sphenodon punctatus* (Godfrey et al., 2010); pygmy blue-tongue lizards, *T. adelaidensis* (Fenner et al., 2011)), indicating this phenomenon is widespread, and suggests a significant role for host behaviour in the transmission of parasites in wildlife populations.

Mike provided major contributions to our understanding of parasites and their interactions with hosts in the context of behaviour, ecology and biology, that we have only touched on here. Other contributions include the description of two new parasite species; a tick (*Amblyomma vikirri*) from the gidgee skink (*Egernia stokesii*) (Keirans et al., 1996), and an oxyurid nematode (*Pharyngodon wandillahensis*) from the endangered pygmy bluetongue lizard (*Tiliqua adelaidensis*) (Fenner et al., 2008). He has left an enormous legacy, both in expanding our understanding of the ecology of host-parasite interactions, and in the long-term insights that his lizard study has enabled, and likely will continue to provide in the years to come. This is significant, both in terms of the rarity of