The longest-lived spider: mygalomorphs dig deep, and persevere

Abstract

We report the longest-lived spider documented to date. A 43 year-old, female *Gaius villosus* Rainbow, 1914 (Mygalomorphae: Idiopidae) has recently died during a long-term population study. This study was initiated by Barbara York Main at North Bungulla Reserve near Tammin, south-western Australia in 1974. Annual monitoring of this species of burrowing, sedentary mygalomorph spider yielded not only this record-breaking discovery but also invaluable information for high-priority conservation taxa within a global biodiversity hotspot. We suggest that the life-style of short-range endemics provide lessons for humanity and sustainable living in old stable landscapes.

Introduction

All mygalomorph spiders, with the exception of some arboreal species (Pérez-Miles and Perafán 2017) live in burrows constructed as dispersing spiderlings and often close to their maternal burrow (Main 1984). Burrow morphology varies between different mygalomorph spider clades but are generally sedentary unless disturbed or requirements are not being met (Main 1984). Mygalomorph spiders are considered 'relictual' having remained in a similar ecological niche since the mid-late Tertiary, despite diversifying genetically (Rix *et al.* 2017a). The low dispersal of mygalomorph spiders makes for a high diversity of restricted range species over evolutionary time scales (Rix *et al.* 2017a), classifying them as conservation significant "short-range endemics" (SREs) (Harvey 2002).

Short range-endemics are animals found in only a small area (entire distribution within 10 000 km^2), due primarily to their low mobility and poor dispersal ability (Harvey 2002). Mygalomorph spiders, as SREs (Rix *et al.* 2014) represent a largely unrecognised contribution to biodiversity. South-western Australia (SWA), the site of this study, hosts 65 described species of mygalomorph spiders (World Spider Catalog, 2018), but also hosts many recorded but unnamed, as well as many yet to be discovered. Many are restricted to narrow ranges and often require specific microhabitats. Short range endemism also adds to the overall diversity of regions through high spatial turnover, a situation also well-recognised for the plants of SWA (Yates *et al*. in review).

The life history traits of mygalomorph spiders demonstrate a successful approach for persistence in old, stable landscapes (Mucina and Wardell-Johnson 2011), but that are under threat from novel disturbances from deforestation, fragmentation, exploitation, and introduced biota (Wardell-Johnson *et al*. 2016). A long-term study established by Barbara York Main in 1974 (Main 1978) enables assessment of the age, longevity and population dynamics of one species of mygalomorph spider - *Gaius villosus* Rainbow, 1914 (Mygalomorphae: Idiopidae) (Rix *et al.* 2017b). Here we report the death of an individual from this long-term population study and outline the significance of this event.

Methods

All methodology for this manuscript is derived from the original study conducted by Main (1978).

Study site

The study site is in the central wheatbelt, SWA. Between 1920 and 1980, this region was subject to substantial clearing for agriculture, and now retains only 7% native vegetation (Jarvis 1981, Deo 2011). North Bungulla Reserve (Area: 104 ha, Latitude: -31.525937, Longitude: 117.591357) is one of few patches of remnant bushland remaining in the region (Fig. 1a). The reserve comprises mixed mallee, heath and thicket vegetation (Fig. 1b)(Main 1978).

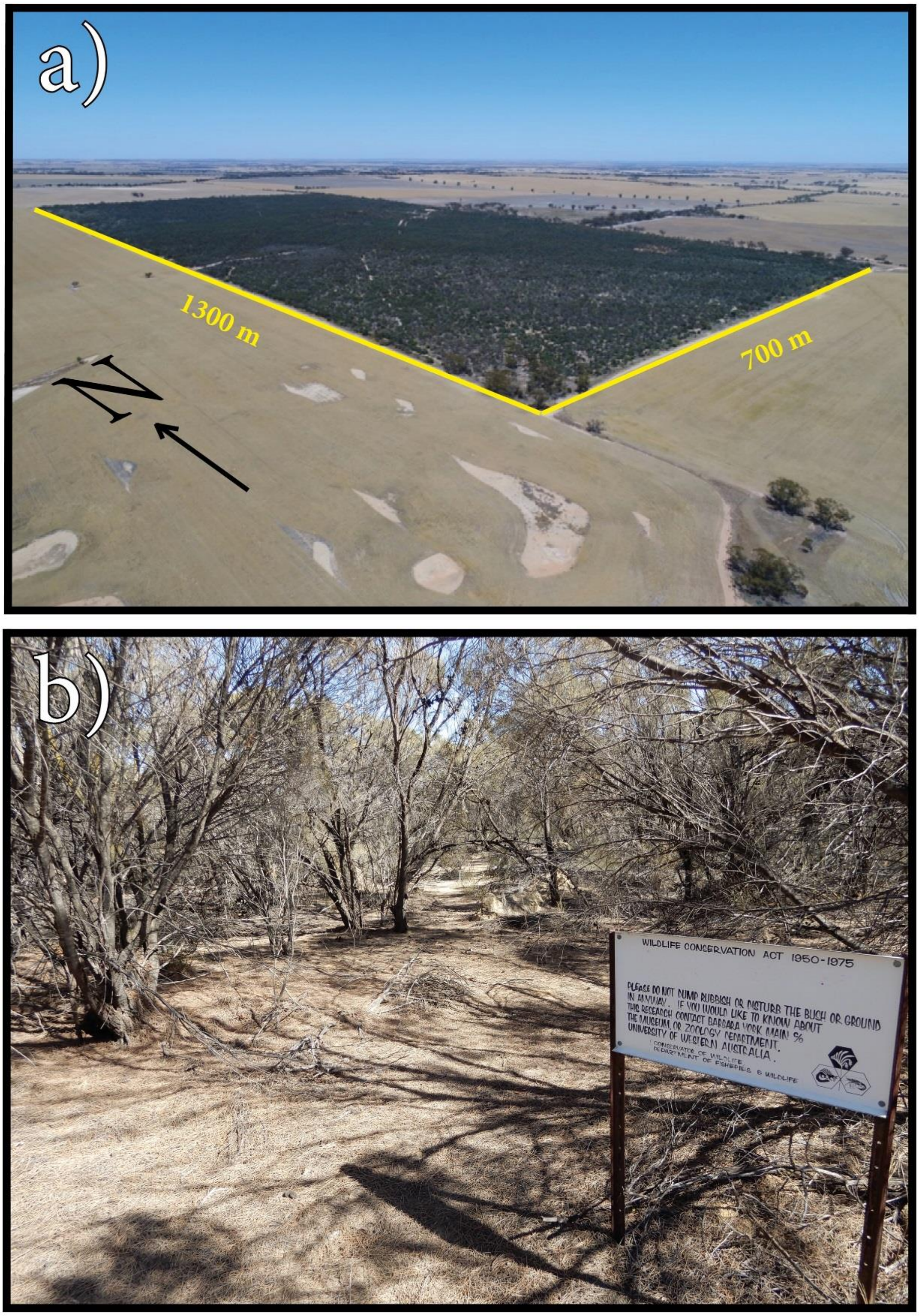

Fig. 1 a) North Bungulla Reserve, south-western Australia, November 2017, the site of a long-term (since 1974) study of mygalomorph spiders. Photo credit: Todd Buters. b) The long-term study plot in November 2017. Photo credit: Leanda Mason

Monitoring

In 1974, a gridded plot 26 m x 40 m (Fig. 1b) was mapped to regularly assess local distribution and demography of a population of *G. villosus*. Permanent numbered tagged pegs were used to identify individuals in subsequent surveys. Pegs were sited directly behind burrow hinges to prevent foraging being compromised.

As male and female juvenile spiders are morphologically identical, gender cannot be determined prior to sexual maturity without genetic verification (Herbert *et al.*, 2003). Spiderling emergents were pegged and monitored to determine survivorship and successive recruitment. Adults and associated burrows were monitored annually to determine age, maturity and reproductive cues.

Males that reach sexual maturity (at approximately 5 years) seal their burrow, and go through a final moult before leaving in search of a female, but perish within the same season. Evidence of the broken burrow lid seal together with moults confirms the burrow had hosted a male, rather than being a now defunct female burrow. Conversely, females always remain in their burrows and when receptive to mating, will put out a silk “doile” thought to attract males through pheromones. Brooding females are recorded from the presence of a mud-plug thought to provide extra protection to the spiderlings.

Thriving populations of these spiders include large and mature active burrows inhabited by aging females, as well as smaller burrows inhabited by juveniles of unknown sex. As spiderlings age, they widen their burrows and moult to grow larger each year until reaching sexual maturity. Widening of burrows can leave silk patterns similar to those of tree rings. However, as they don’t widen their burrow once reaching maturity, this is only useful to estimate ages of juveniles between one to five years old. It was therefore imperative to peg burrows to determine the age of mature spiders.

Results

The oldest spider recorded, a *Gauis villosus* (Fig. 2a), was in the first group of dispersing spiderlings that established a burrow (Fig. 2b) pegged by Barbara in the first season of the study in March 1974. It was the 16th spider pegged (Fig. 2c). By 2016, over 150 spiders had been pegged in the 26 x 40 m study site. The first 15 spiders, and numbers well beyond 16 have died in the interim.

On the 31st October 2016 we found that the lid of the burrow of the oldest spider, #16, had been pierced by a parasitic wasp (Fig. 2c). Having been seen alive in the burrow the previous year, we therefore report the death of an ancient *G. villosus* mygalomorph spider matriarch at the age 43.

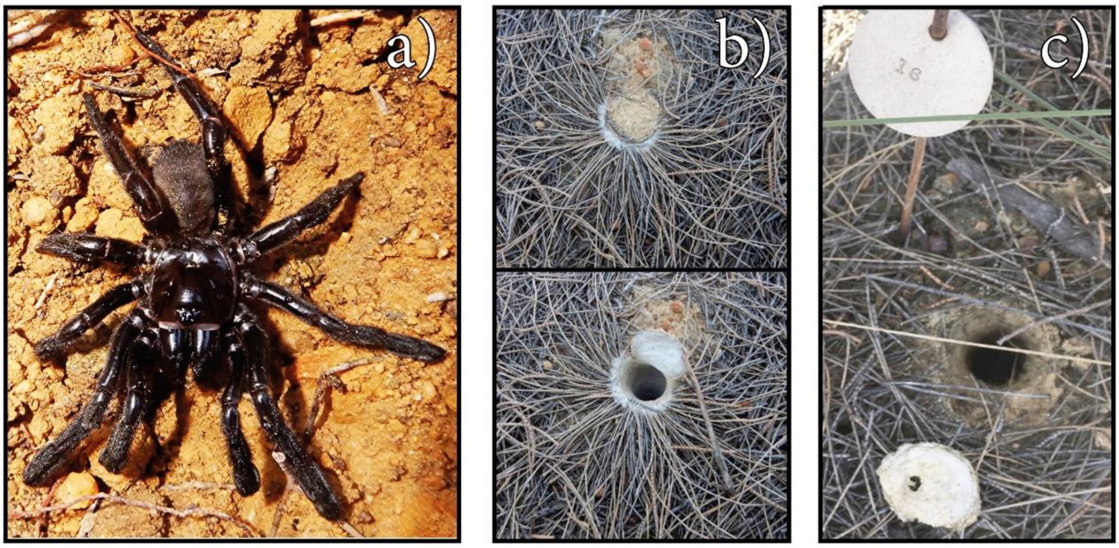

Fig. 2: a) *Gauis villosus* female, b) a typical *G. villosus* burrow and c) burrow of deceased #16 with burrow lid removed showing piercing by parasitic wasp. Photo credits: Leanda Denise Mason

Based on a diagnostic hole in the burrow lid (Fig. 2c), and her burrow falling into disrepair since last years' recording, we recognise that she is either parasitised or already dead. Thus, it is likely that #16 did not die of old age, but rather was parasitised by a spider wasp (Pompilidae - O'Neill 2001). Once the egg hatches, the spider is consumed from the inside, over the course of several weeks. The burrow will be excavated to try find further evidence to confirm wasp parasitisation – such as the presence of a wasp cocoon - in an upcoming study. Detailed data relating to ages, causes of death and life history of the entire population will also be made available.

Discussion

Life history lessons

To our knowledge, #16 is the oldest documented spider recorded, with the Guinness World Record being a 28 year-old Tarantula (Mygalomorphae: Theraphosidae) in captivity, and Tasmanian cave spiders (Araneomorphae: *Hickmania troglodytes*) thought to live 30 - 40 years (Mammola *et al.* 2017).

The findings from the initial years of this long-term study provided invaluable information on spiderling dispersal, sexual maturity, the proportion of males and females (See Main 1978). Continuance of the study has provided more accurate ages, cause of death, and understanding of the life history of this basal group of spiders that will be made available in the future.

There is a high level of certainty that #16 lived for 43 years. Neither males nor females re-use the defunct burrow of another spider (Main 1984). Adult spiders do not re-locate if their burrow is damaged, but repair their existing burrow. There are three likely reasons for this; 1) The chances of locating a suitable defunct burrow at the time of disturbance to their own burrow is low due to mygalomorphs being relatively blind (Willemart and Lacava 2017), 2) There is a high trade-off with being exposed or above-ground, where they are vulnerable to desiccation or predation (Mason *et al.* 2013, Canals *et al.* 2015), and 3) Re-lining the entirety of a burrow with silk and construction of a lid is an exceptionally large energy and time investment (Hils and Hembree 2015). In addition, adult defunct burrows are too large to accommodate dispersing spiderlings. Further, the burrow of #16 fell into disrepair soon after the lid had been pieced.

Sustainability lessons

A deeper appreciation of the place of biodiversity and sustainability in the ancient landscapes of SWA follows from an understanding of life history (Wardell-Johnson and Horwitz 1996, Main 2001). Short-range endemic invertebrates, such as mygalomorph spiders, represent an unquantified contribution to biodiversity. South-western Australia has had more than 70% of its native vegetation removed (Wardell-Johnson *et al*. 2015; 2016) and was the first Australian global biodiversity hotspot recognized – one of the 25 originally defined by Myers et al. (2000). Global biodiversity hotspots are endemic-rich regions that are also under threat. With so much of the landscape having been cleared, we may never know how many species have already been lost.

Historically, sustainability in the old landscapes of SWA has been vastly overestimated with influxes of people in the last 180 years who have transformed the environment and pushed much life to the edge of extinction. The European explorers were impressed by the size of trees and apparent productivity (Wardell-Johnson *et al*. 2015). They would have been better guided by how the Indigenous peoples already dwelling there for tens of millennia were managing, and being managed by these landscapes (Wardell-Johnson *et al*. 2017). For them it was about persistence, low-level impact and frugal resource use. These are the same traits that exemplify the character of those now living sustainably in SWA. It is also the very antithesis of contemporary pressures.

South-western Australia is measured in geological time-scales (Myers 1997), by the time discernible in the wearing down of landscapes, and by the time of deep weathering of landscape profiles (Campbell 1997). This is ample time to lose the essential nutrients for growth, especially phosphorous, nitrogen and sulphur. Old landscapes manage the biota, and the people and societies that come and go.

What follows from the challenges presented by old, deeply weathered, nutrient-poor landscapes where carbon is stockpiled, water thirsted for and nutrients extricated? One successful approach results in a long life-time in a small burrow. Unfortunately, the sedentary nature and poor dispersal ability mean mygalomorph spiders cannot readily break new ground and colonise more broadly. Away from their burrows they are susceptible to desiccation (Mason *et al.* 2013). In addition, many are confined to small areas and often require specific microhabitats. They are therefore highly vulnerable to disturbance that compromises the quality of their habitat (Harvey *et al*. 2011, Mason *et al*. 2016).

Landscapes exemplified by broader SWA may be resilient to disturbances prominent in their evolutionary history such as seasonal instability, fire, and drought (Hopper 2009; Mucina and Wardell-Johnson 2011). However, they are fragile to novel threats. Disturbances such as deforestation, eutrophication, introduced animals, plants and microbes, major substrate disturbance and continued biomass loss transform the landscape into something requiring constant management to be productive (Wardell-Johnson *et al.* 2016).

As we begin rebuilding with more sustainable technologies and improve the management of known threatening processes (Braby 2018), we can be inspired by an ancient mygalomorph spider and the rich biodiversity she embodied.

References

Braby, M. F. (2018). Threatened species conservation of invertebrates in Australia: an overview. *Austral Entomology*

Campbell, E.M. (1997). Granite landforms. *Journal of the Royal Society of Western Australia*. **80**: 101–112.

Canals, M., Veloso, C., and Solís, R. (2015). Adaptation of the spiders to the environment: the case of some Chilean species. *Frontiers in physiology*. ***6*: **220.

Deo, R. C. (2011). Links between native forest and climate in Australia. *Weather* **66**(3): 64-69.

Harvey, M. S. (2002). Short-range endemism in the Australian fauna: some examples from non-marine environments. *Invertebrate Systematics* **16**: 555–570.

Harvey, M. S., Rix, M. G., Framenau, V. W., Hamilton, Z. R., Johnson, M. S., Teale, R. J., Humphreys, G. and Humphreys, W. F. (2011). Protecting the innocent: studying short-range endemic taxa enhances conservation outcomes. *Invertebrate Systematics* **25**(1): 1-10.

Hebert, P. D., Cywinska, A., and Ball, S. L. (2003). Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London B: Biological Sciences* **270**(1512): 313-321.

Hils, J. M., and Hembree, D. I. (2015). Neoichnology of the burrowing spiders Gorgyrella inermis (Mygalomorphae: Idiopidae) and Hogna lenta (Araneomorphae: Lycosidae). *Palaeontologia Electronica* **18**(1): 1-62.

Hopper, S.D. (2009). OCBIL theory: towards an integrated understanding of the evolution, ecology and conservation of biodiversity on old, climatically buffered, infertile landscapes. *Plant and Soil* **322**: 49-86.

Jarvis, N. T. (1981) .*Western Australia: An Atlas of Human Endeavour, 1829-1979.* Education and Lands and Surveys Departments of Western Australia, Perth, Western Australia

Main, B. Y. (1978). Biology of the arid-adapted Australian trapdoor spider *Anidiops villosus* (rainbow). *Bulletin of the British Arachnological Society* **4**: 161-175.

Main, B. Y. (1984). 'Spiders'. Sydney, (William Collins Pty Ltd.)

Main, B.Y. (2001). Historical ecology, responses to current ecological changes and conservation of Australian spiders. *Journal of Insect Conservation* **5**(1): 9-2.

Mammola, S., Michalik, P., Hebets, E. A., and Isaia, M. (2017). Record breaking achievements by spiders and the scientists who study them. *PeerJ*, **5**, e3972.

Mason, L., Tomlinson, S., Withers P. and Main B. (2013). Thermal and hygric physiology of Australian burrowing mygalomorph spiders (Aganippe spp.). *Journal of Comparative Physiology B* **183**(1): 71–82.

Mason, L. D., Wardell-Johnson G. and Main B. Y. (2016). Quality not quantity: conserving species of low mobility and dispersal capacity in south-western Australian urban remnants. *Pacific Conservation Biology* **22**(1): 37-47.

Mucina, L. and Wardell-Johnson, G (2011). Landscape age and soil fertility, climate stability, and fire regime predictability: beyond the OCBIL framework. *Plant and Soil* **341**: 1-23.

Myers, J.S. (1997). Geology of granite. *Journal of the Royal Society of Western Australia*. **80**: 87–100.

Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* **403**(6772): 853-858.

O'Neill, K. M. (2001). 'Solitary wasps: behavior and natural history', (Cornell University Press.)

Pérez-Miles, F., and Perafán, C. (2017). Behavior and Biology of Mygalomorphae. In *Behaviour and Ecology of Spiders* (pp. 29-54). Springer, Cham.

Rix, M. G., Edwards, D. L., Byrne, M., Harvey, M. S., Joseph, L. and Roberts, J. D. (2014). Biogeography and speciation of terrestrial fauna in the south-western Australian biodiversity hotspot. *Biological Reviews,* **90**(3), 762-793.

Rix, M. G., Cooper, S. J., Meusemann, K., Klopfstein, S., Harrison, S. E., Harvey, M. S. and Austin, A. D. (2017a). Post-Eocene climate change across continental Australia and the diversification of Australasian spiny trapdoor spiders (Idiopidae: Arbanitinae). *Molecular phylogenetics and evolution* **109**: 302-320.

Rix, M. G., Raven, R. J., Main, B. Y., Harrison, S. E., Austin, A. D., Cooper, S. J. B. and Harvey, M. S. (2017b). The Australasian spiny trapdoor spiders of the family Idiopidae (Mygalomorphae : Arbanitinae): a relimitation and revision at the generic level. *Invertebrate Systematics* **31**(5): 566-634.

Wardell-Johnson, G. and Horwitz, P. (1996). Conserving biodiversity and the recognition of heterogeneity in ancient landscapes: a case study from south-western Australia. *Forest Ecology and Management* **85**(1): 219-238.

Wardell-Johnson, G., Calver, M., Burrows, N. and Virgilio, G. D. (2015). Integrating rehabilitation, restoration and conservation for a sustainable jarrah forest future during climate disruption. *Pacific Conservation Biology* **21**(1-11)

Wardell-Johnson, G., Wardell-Johnson, A., Bradby, K., Robinson, T., Bateman, P. W., Williams, K., Keesing, A., Braun, K., Beckerling, J. and Burbridge, M. (2016). Application of a Gondwanan perspective to restore ecological integrity in the south-western Australian global biodiversity hotspot. *Restoration Ecology* **24**(6): 805-815.

Willemart, R. H., and Lacava, M. (2017). Foraging Strategies of Cursorial and Ambush Spiders. In *Behaviour and Ecology of Spiders* (pp. 227-245). Springer, Cham.

Yates, C. J., Robinson, T., Wardell-Johnson, G. W., Keppel, G., Byrne, M., Hopper, S. D., Niel, K. V. and Schut, A. G. T. (IN REVIEW). Plant diversity on granite inselbergs exemplifies high species richness and turnover in multiple habitats in the Southwest Australian Floristic Region (SWAFR). *Diversity and Distributions.*

Authors have no conflicts of interest to declare.