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Research Note

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

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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-styles of short-range endemics provide lessons for humanity and sustainable living in old stable landscapes.

Additional keywords: conservation, fragmented landscapes, long-term study, short-range endemism, trapdoor spiders, world-record.

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Introduction

All mygalomorph spiders, except some arboreal species (Pérez-Miles and Perafán 2017), live in burrows constructed by dispersing spiderlings, often close to their maternal burrow (Main 1984). Burrow morphology varies between different mygalomorph spider clades but the species 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.* 2017*a*). The low dispersal of mygalomorph spiders makes for a high diversity of restricted-range species over evolutionary time scales (Rix *et al.* 2017*a*), classifying them as conservation-significant 'short-range endemics' (SREs) (Harvey 2002).

SREs 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.* 2015), 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 species, 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 (Gibson *et al.* 2017).

The life-history traits of mygalomorph spiders demonstrate a successful approach for persistence in old, stable landscapes (Mucina and Wardell-Johnson 2011), which are under threat from novel disturbances such as 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.* 2017*b*). 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 study was 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 it 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. 1*a*). The reserve comprises mixed mallee, heath and thicket vegetation (Fig. 1*b*) (Main 1978).

Monitoring

In 1974, a gridded plot 26 m × 40 m (Fig. 1*b*) 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

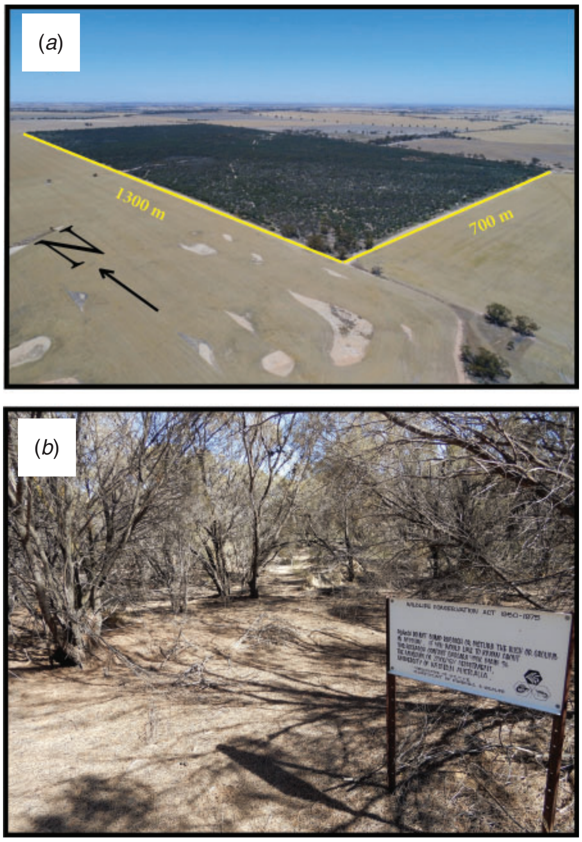

Fig. 1. (*a*) North Bungulla Reserve, south-western Australia, November 2017, the site of a long-term (since 1974) study of mygalomorph spiders. Photograph: Todd Buters. (*b*) The long-term study plot in November 2017. Photograph: Leanda Denise Mason.

sited directly behind burrow hinges to prevent foraging being compromised.

As male and female juvenile spiders are morphologically identical, sex cannot be determined before sexual maturity without genetic verification (Hebert *et al.* 2003). Spiderling emergents were pegged and monitored to determine survivorship and successive recruitment. Adults and associated burrows were monitored at six-monthly intervals or annually to determine age, maturity and reproductive cues.

Males that reach sexual maturity (at ~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 a broken burrow lid seal, together with moults confirms that 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 useful only to estimate ages of juveniles between one and 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. 2*a*), was in the first group of dispersing spiderlings that established a burrow (Fig. 2*b*) pegged by BYM in the first season of the study in March 1974. It was the 16th spider pegged (Fig. 2*c*). By 2016, over 150 spiders had been pegged in the 26 × 40 m study site. The first 15 spiders, and spiders numbered well beyond 16, have died in the interim.

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

On the basis of a diagnostic hole in the burrow lid (Fig. 2*c*), and her burrow falling into disrepair since the previous recording, we recognise that she was 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. 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, and 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 (which will be made available elsewhere).

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 relocate 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 risk in being exposed or above ground, where they are vulnerable to desiccation or predation (Mason *et al.* 2013; Canals *et al.* 2015); and (3) relining 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, defunct burrows of adult spiders are too large to accommodate dispersing spiderlings. Further, the burrow of #16 fell into disrepair soon after the lid had been pierced.

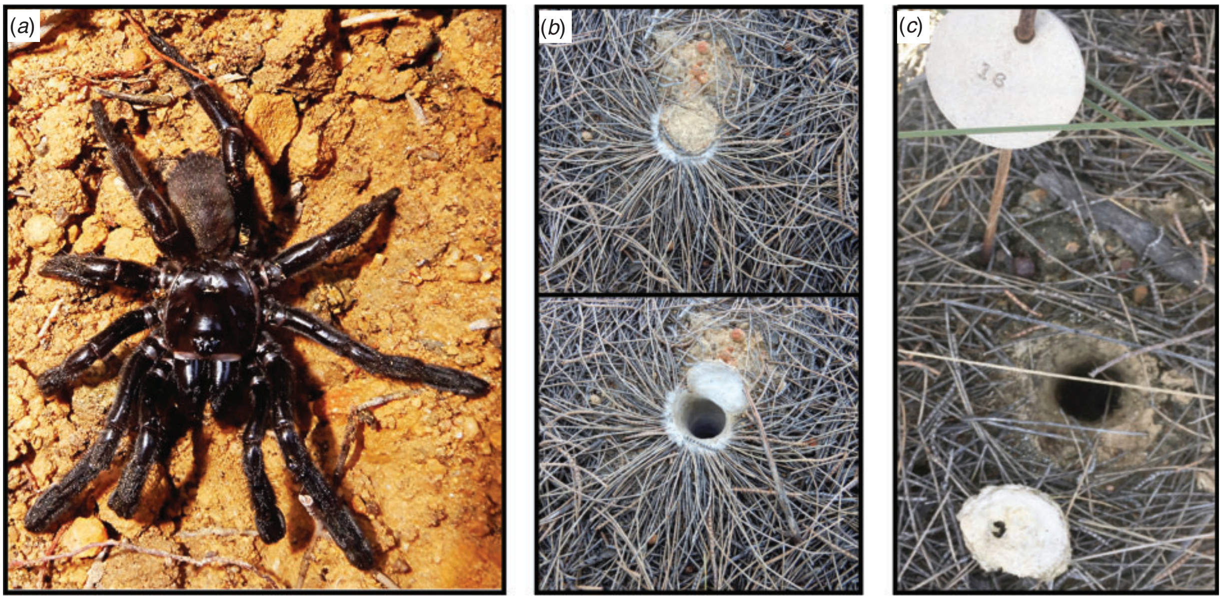

Fig. 2. (*a*) *Gauis villosus* female, (*b*) a typical *G. villosus* burrow and (*c*) burrow of deceased #16 with burrow lid removed showing piercing by parasitic wasp. Photographs: Leanda Denise Mason.

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). SRE invertebrates, such as mygalomorph spiders, represent an unquantified contribution to biodiversity. More than 70% of the native vegetation has been removed from SWA (Wardell-Johnson *et al.* 2015, 2016) and the region was the first Australian global biodiversity hotspot recognised – 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.* 2016). 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.

SWA 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 phosphorus, nitrogen and sulfur. 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, their sedentary nature and poor dispersal ability mean that 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.

Conflicts of interest

The authors have no conflicts of interest to declare.

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