

The natural history of the Australian garden orb-weaving spiders *Hortophora biapicata* and *H. transmarina* (Araneae: Araneidae)

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Abstract. Australia is home to an incredible diversity of spiders, but much of their biology remains unstudied. The orb-weaving spiders (family Araneidae) are especially diverse and frequently encountered, yet the ecology of very few species has been explored. The common name “Australian garden orb-weaver” refers to several species, including *Hortophora transmarina* (Keyserling, 1865), found mostly along Australia’s east coast, and *Hortophora biapicata* (L Koch, 1871), found mostly along Australia’s south and south-eastern coasts. These two similar species are large, nocturnal orb-weavers that occupy a wide range of both natural and anthropogenically disturbed habitats. Here, I describe the general morphology, habitat use, diet and foraging behavior, key predators, laboratory rearing, and mating dynamics of these common but understudied spiders. This information was gathered via field observations, laboratory experiments, and literature reviews. These spiders provide a useful system for studying a number of aspects of spider biology, including mating systems, predation, anti-predator defences, and nocturnal behaviors.

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Australian orb-weaving spiders (in the family Araneidae) are a speciose group comprised of several hundred described species. They have a broad distribution over Australia, ranging from isolated natural habitats to heavily urbanized areas. However, despite their abundance, and considerable variation in morphology, behavior, and ecology, orb-weavers in Australia remain largely understudied apart from the genera *Argiope* Audouin, 1826 and *Trichonephila* Dahl, 1911 [e.g., 1–4]. This bias likely stems from the fact that *Argiope* and *Trichonephila* are large and diurnal, whereas smaller species and nocturnal species are largely ignored, an issue that pervades other fields of biology (Gaston 2019). In addition to this taxonomic bias, the Australian araneid literature is also largely methodologically confined to taxonomy, descriptive rather than functional morphology, and mating behaviors (e.g., Elgar et al. 2000; Elgar & Jones 2008; Framenau 2019; Framenau et al. 2021; Henneken et al. 2015; Scharff et al. 2020). Thus, we have a poor understanding of other aspects of their biology, and relatively little is known about the behavior of the nocturnal foragers (but see Ceballos et al. 2005; Willmott et al. 2018, 2019; Peng et al. 2020).

The Australian garden orb-weaving spiders, genus *Hortophora* Framenau & Castanheira, 2021, are medium to large, nocturnal araneids found all over Australia in a variety of habitats. Primarily, two species have been studied: the larger of the two, *Hortophora transmarina* (Keyserling, 1865) (body length: females 30 mm, males 25 mm), is found mostly along the east and north coasts, with some records in Papua New Guinea and on Norfolk Island; and *Hortophora biapicata* (L Koch, 1871) (females 21 mm, males 17 mm), found primarily along the south and east coasts but with some records throughout the rest of mainland Australia (Davies 1980). Both species occur in habitats ranging from dry sclerophyll forest to riparian habitats to wet forests, and *H. biapicata* have been found in dry shrubby habitats in central Australia. Perhaps because of their ability to occupy such a diverse range of habitats, both species are also common in urban parks and gardens. Previous records describe *H. transmarina* (formerly synonymous with *H. biapicata*) as common and abundant in orchards, as well as parks and backyards, and thus these spiders occupy the equivalent niche to the European garden spider, *Araneus diadematus* Clerck, 1757 (Dondale 1966). Importantly, *Hortophora* possess traits that differentiate them from the better-studied *Argiope*

and *Trichonephila*, including their morphology and development, and their mating and foraging behaviors.

Hortophora females are larger than males, but these spiders do not show the extreme sexual size dimorphism typical of *Argiope* and *Trichonephila* – females are on average 60% heavier, but male body length is only slightly shorter, and males have relatively longer legs. Females of both species have hardened plates where the genital opening is located and an epigyne scape, which is an elongated process extending from the epigyne (Framenau et al. 2021). This structure facilitates the male’s attachment to the female during copulation (Framenau et al. 2021), and may act as a barrier to interspecific mating (Ah-King et al. 2014). The tibiae of the second legs in males possess exaggerated, thickened spines, allowing the male to clasp the front two pairs of legs of the female with his front two pairs of legs during copulation. *Hortophora* are annual species and mature in summer. At maturity, males stop constructing webs and instead search for females. The lack of extreme female-biased sexual size dimorphism has important implications for mating dynamics and the risk of sexual cannibalism (Elgar 1991; Elgar & Jones 2008). Mating was briefly described in *H. transmarina*, and involves a fixed sequence of stages and specific behaviors by both the male and female (Brunet 1994). However, much of the dynamics of mating in these spiders has remained undescribed.

These orb-weavers usually construct their circular orb-web around 30–45 minutes after sunset, forage throughout the night, and dismantle and consume their web before dawn. On rare occasions, spiders may steal webs from conspecifics, either by occupying abandoned webs or by dislodging or even cannibalising the host (Brunet 1994). Some individuals have been recorded using thick sticks or pebbles as counterweights to hold the web taut when it can’t be attached securely to the ground (McKeown 1936). Male foraging behavior as adults remains unobserved in the wild, but they will capture house flies in laboratory enclosures. Like many Australian orb-weavers, and unlike *Argiope* and *Trichonephila*, *Hortophora* are nocturnal, meaning they forage for a different set of prey compared with the diurnal spiders. Lepidoptera, followed by Diptera and Coleoptera, are major prey of *Hortophora* (Herberstein & Elgar 1994). However, this can vary: these spiders can use artificial light sources to increase their foraging success, but in artificially lit habitats like these, Lepidoptera may be caught less frequently (Willmott et al. 2019).

In contrast to studies of the diets of *Hortophora*, there has been no formal investigation or description of their predators or defenses against these predators. There are disparate records across the literature found in descriptions of the behaviors and diets of predators – this includes the araneophagic assassin bug, *Stenolemus bituberus* Stål, 1874, found on the webs of *H. biapicata* (Wignall & Taylor 2008), remains of *Hortophora* found in the gizzards of the southern boobook (*Ninox boobook* (Latham, 1801)) (Penck & Queale 2002), and diurnal predation on *Hortophora* in their webs by birds such as the honeyeaters (family Meliphagidae) (Brunet 1994). However, based on ecologically-similar spiders such as *Eriophora ravilla* (CL Koch, 1844), wasps in the families Pompilidae, Sphecidae, and Ichneumonidae are likely to be major predators of *Hortophora* (Chadwick & Nikitin 1975; Evans et al. 1980; Kurczewski 1981; Austin 1985; Brunet 1994; Mason et al. 2018; Scharff et al. 2020). A potential defense against these predators is visual camouflage. Many spiders exhibit variation in coloration and patterning both between and within individuals, which can function to reduce predation risk or increase prey capture success (Graf & Nentwig 2001; Anderson & Dodson 2015). Variation within individuals may occur rapidly or ontogenetically (Graf & Nentwig 2001; Anderson & Dodson 2015), but little is known about these processes. A melanic form of *Hortophora transmarina* was described in 1966, along with melanic forms of other Araneidae, with this coloration affording camouflage against dark tree bark (Mascord 1966). Highly color-variable spiders such as *Hortophora* provide an interesting model for studying these patterns under different conditions.

Here I provide the first comprehensive description of the natural history of *H. biapicata*, with comparisons to *H. transmarina*. First, I begin by describing the morphology and development of these species, with a particular focus on variation among individuals. Second, I describe the mating behaviors of *H. biapicata*, with comparisons to other species. Third, I detail their foraging behaviors and diet, under both natural conditions in the field and artificial conditions in the lab. Fourth, I outline the limited information on the predators and parasitoids that attack *Hortophora*, and describe potential anti-predator traits that require further research. Throughout, I outline key knowledge gaps and future avenues for research, in order to highlight the value of these spiders as models for answering important biological questions.

METHODS

General overview.—To collect information about these spiders, I used field and laboratory observations and experiments, literature reviews, database and library searches, and correspondence with Australian arachnologists and collections managers. This genus and both species have been renamed on several occasions, thus much of the historical biological knowledge of these species is disparately recorded. Further, the previous classification of *H. transmarina* and *H. biapicata* in the genus *Eriophora* was based on superficial similarities to northern hemisphere species such as *E. ravilla*, and they have only recently been placed in the new genus *Hortophora* based on genetic evidence (Scharff et al. 2020; Framenau et al. 2021). For literature searches, I used synonyms from the historical literature: the genus names *Hortophora*, *Eriophora*, *Araneus*, and *Epeira*; and the specific names *transmarina*, *transmarinus*, *viridis*, *producta*, *thyridota*, *capitalis*, *productus*, and *biapicata* are synonyms for *Hortophora transmarina* and *Hortophora biapicata*. Between February 2016 and March 2021, I performed observations and

several collections of *Hortophora biapicata* ($n > 700$ spiders used in behavioral observations) from multiple urban, suburban, and natural habitats around Melbourne. Between October 2018 and March 2021 I observed and collected *Hortophora transmarina* ($n = 30$) from similar sites around Sydney. These collections included juvenile and adult *H. biapicata*, and adult *H. transmarina*; I used these spiders for the observations and experiments described below. Spiders in the field were primarily observed on and collected from their webs after sunset, using headtorches to increase visibility, although diurnal observations were occasionally made. For laboratory rearing, spiders were housed in inverted plastic cups (12.5 cm tall, 9.5 cm diameter; with mesh-covered ventilation holes) and in large Perspex frames (58 cm tall, 58 cm wide, and 15 cm deep) for web-building. Juveniles were fed with a pollen-based paste and live vinegar flies (*Drosophila melanogaster* Meigen, 1830), and transitioned to house flies (*Musca domestica* Linnaeus, 1758) and crickets (*Acheta domesticus* (Linnaeus, 1758)) as they matured. Further details for laboratory rearing of *H. biapicata* are described elsewhere (Willmott et al. 2018, 2019).

Development and morphological variation.—During rearing experiments in the lab, I tracked rates of molting, growth, and mortality. After the mating experiments described below, the production of eggsacs and the number of spiderlings in each eggsac were recorded. I used color photography and microscopy to record and describe the morphological traits and variation among individuals and across development in *H. biapicata* ($n = 276$). In particular, I captured the variation in dorsal coloration of the opisthosoma and the legs ($n = 138$), which are highly variable among individuals in both females (Fig. 1) and males (Fig. 2), and measured morphometric traits such as leg length and the number and size of spines on the tibiae of adult males ($n = 138$). For morphometric analyses, I photographed spiders with a scale bar, and used ImageJ (Troschianko & Stevens 2015) to calculate lengths and count spines.

For a subset ($n = 130$) of spiders from a rearing experiment in 2020, I measured their capacity to change color by modifying the color of the substrate on which they rested during the day. This substrate, which consisted of a strip of gaffer (cloth) tape on one side of the plastic cups, was colored either black ($n = 69$) or light brown ($n = 61$) (see Supplemental Fig. S1, online at <https://doi.org/10.1636/JoA-S-22-061.s1>). I photographed the spiders after each molt until maturity, and categorized their color (as light, medium, or dark) while blind to their tape-color group. I then scored their transition from juvenile to adult coloration as “lighter” (change from dark to medium, dark to light, or medium to light), “unchanged” (light to light, medium to medium, dark to dark), or “darker” (light to medium, light to dark, medium to dark). This was based on a qualitative assessment of coloration as technical difficulties prevented standardized measurements, and spiders were classified as unchanged unless there was an obvious difference. I used a Chi-squared test to compare the color transition (between the juvenile starting point and the adult endpoint) between the two background color groups. These morphological, along with behavioral, measures allowed me to describe potential anti-predator traits that may protect *H. biapicata* from its natural enemies.

Mating dynamics.—During December 2016 – May 2017 and January – March 2020, I observed mating dynamics in *H. biapicata* under laboratory conditions ($n = 116$ mating pairs). I recorded the process of mate assessment by both sexes, the ensuing courtship behaviors, the mechanics of copulation, and the behaviors related to sexual conflict at each stage, including frequencies of attempted sexual cannibalism. To observe mating, females were placed in large



Figure 1.—Photo series depicting variation in colouration and patterning among individual adult females of *H. biapicata*.

Perspex frames ($58 \times 58 \times 15$ cm) for several nights to build webs. Between one and three hours after sunset, a male was introduced to one of the support strands of the female's web. The pair was then observed for up to three hours, until two complete copulations occurred, or until the female attempted to cannibalize the male. Females were kept in the lab under the same conditions to allow them to produce eggsacs, and the number of viable offspring produced per eggsac was counted. Prior to mating trials, females were fed crickets (*A. domesticus*) *ad libitum*, and female and male body mass (using a 4 decimal scale), body length, and leg length (photos with rulers measured in ImageJ) were recorded on the same day as the mating trial. I used Pearson correlation tests in R (R Core Team 2022) to test for significant correlations between body mass, tibia length, and tibia spine length and number. I then used generalized linear models to test for the effects of these morphological traits on copulation duration (normal regression: response variable was copulation duration in seconds) and the likelihood of a cannibalism attempt by females (logistic regression: response variable was binary, cannibalism attempt or not).

Diet and foraging behavior.—Diet information was derived from literature searches and personal communication with other

arachnologists (described above), my previous research (Willmott et al. 2018, 2019), and additional field and laboratory experiments. Laboratory observations included placing housefly (*M. domestica*) pupae in the bottom of their enclosures weekly during late juvenile development, and holding crickets (*A. domesticus*) in front of the spiders by forceps during subadult and adult instars, to determine if these were effective and efficient ways of feeding these spiders under laboratory conditions.

Predators and parasitoids.—I collated a list of the predators and parasitoids of these spiders using my own observations, communications with other arachnologists, and a literature search including diet analyses of birds, mammals, reptiles, wasps, and other predators.

RESULTS

Development and morphological variation.—The following data are derived from my field observations and laboratory rearing experiments. *Hortophora* are annual species, maturing in summer. During lab rearing of *H. biapicata*, under a natural 12:12 light dark cycle, males ($n = 40$) reached maturity in 300.28 ± 6.22 (mean \pm SE) days (~ 13 instars), and females ($n = 32$) in 334.91 ± 7.12 days



Figure 2.—Photo series depicting variation in colouration and patterning among individual adult males of *H. biapicata*.

(~14 instars). Although it has previously been reported that these spiders lay about 200 eggs in an eggsac (Brunet 1994), eggsacs produced by lab-reared females ($n = 225$ eggsacs) contained an average of 626.40 ± 28.94 spiderlings, and a female collected post-mating from the field laid a single eggsac with over 2500 viable eggs.

In both species, these spiders do not survive beyond their first breeding season; under a natural 12:12 light dark cycle at 22°C under laboratory conditions, males survived for 83.35 ± 6.46 (mean \pm SE; $n = 40$) days after maturing, and females for 129.63 ± 8.66 days ($n = 32$) post-maturity. Males and females are easily distinguished as subadults and adults: subadult females have a small epigyne scape (Fig. 3a) and adult females possess an elongated scape (Fig. 3b); subadult males exhibit enlarged palps (Fig. 3c) and adult males exhibit drastically different palp morphology (Fig. 3d). There is extreme individual variation in coloration and patterning in *H. biapicata* (frequencies of different patterns are described in Fig. 4). These species have a folium (leaf-like) pattern with a stencilled margin on the dorsum of the abdomen (Fig. 4). This folium pattern often has different coloration to the rest of the abdomen, or pigmentation may be lacking in the folium (Main 1999). A small proportion (~5%) of individuals possess UV-reflective guanidine deposits, which show through as vibrant white stripes, blotches, or cross-shaped markings on the dorsal surface of their abdomen (Fig. 4). They are also able to change the coloration of this dorsal abdomen pattern over successive molts (Fig. 5). For spiders on a black background, 34.8% became darker, 10.1% lighter, and 55.1% unchanged. In contrast, for spiders on a brown background, 8.2% became darker, 21.3% lighter, and 70.5% unchanged. Hence, spiders on dark backgrounds were more likely to become darker, and spiders on light backgrounds were more likely to become lighter ($\chi^2 = 14.12$, $df = 2$, $n = 130$, $P < 0.001$). Their ventral coloration and red femurs

do not camouflage against their substrate, but these structures are only visible while the spider is on its web or when it is walking.

Mating dynamics.—The following description of mating is based on my observations of *H. biapicata* ($n = 116$ mating pairs). When a male locates a female's web, he tastes the silk, and then plucks at the radii of the web. At this stage, hungry or unreceptive females may rapidly and aggressively approach the male. The usual outcome of this interaction is that the male will drop off the web, although the female may cannibalize the male. However, if the female is receptive, she will in turn pull on the radii in the direction of the male before returning to her position at the hub of the orb web. In this case, the male constructs a safety line between nearby scaffolding and the edge of the web (under laboratory conditions, this happens 1813 ± 218 (mean \pm SE) seconds after finding the female web, median = 1220 seconds). He then reinforces this line with at least one more silk thread – often two or three threads – forming the mating strand. The construction of a mating strand was not included in a previous description of mating in *H. transmarina* (Brunet 1994), but is a necessary step during courtship for *H. biapicata*. At any of the stages described above or below, males may remain motionless for periods ranging from minutes to hours (3129 ± 254 seconds from finding the web to copulation, median = 2686 seconds), or may groom the legs with the mouthparts, usually prior to plucking the mating strand.

Once the mating strand is constructed, he strums the mating strand with all eight legs, following what appears to be a regular pattern, alternating between left and right legs (cumulative duration of strumming before a successful mating is 95 ± 14 seconds, median = 55 seconds). During strumming, the female orients towards the male. If the female is receptive, she will approach the male by travelling along her web radii before moving onto the male's mating strand.



Figure 3.—Four views of *Hortophora biapicata*: (a) ventral subadult female showing the developing epigyne scape; (b) ventral adult female showing elongated scape; (c) ventral subadult male showing the enlarged developing palps; (d) ventral adult male showing the transformed palps.

The male continues to strum until the female makes contact, at which point they rapidly touch legs. At this stage, the female is hanging with her ventral side facing upwards, and either splays her front four legs out and down to expose her epigyne to the male, or she turns and walks towards the web hub again. If she turns, the male strums to entice her to return, but if she splays, he carefully adjusts his position before he attempts copulation. Females may turn away from the male up to 101 times (mean = 72, median = 35, $n = 116$ mating pairs).

After orienting towards the female, a male attempts copulation by lunging towards the female. During the lunge, he attempts to both interlock one palp with the epigyne and clasp the front four legs of the female with his own front four legs. Clasp is facilitated by the thickened spines on the tibiae of his second pair of legs. Most lunge attempts failed (max = 57 attempts, mean = 9, median = 6, $n = 116$), in which case the female turns from the male, who then strums again. However, when the male succeeds, he successfully restrains the female and copulation begins (Fig. 6). This interlocked position, which continues for the duration of copulation, lasts 80–120 seconds on average, ranging between 5 seconds and 775 seconds under laboratory conditions ($n = 116$). Copulation ends either by the male releasing and pulling away, or by the female struggling free. The latter case is usually followed by an attempt by the female to cannibalize the male. Overall, females attempted to cannibalize the male in 40% of laboratory mating trials.

Several morphological traits that play key roles in mating were correlated: males with larger body masses at maturation had longer legs ($r = 0.95$, $P < 0.0001$), longer tibia spines ($r = 0.84$, $P < 0.0001$), and more tibia spines ($r = 0.60$, $P < 0.0001$). However, I found no significant correlations between morphological traits and copulation duration or risk of cannibalism attempts (see Supplemental Table S1, online at <https://doi.org/10.1636/JoA-S-22-061.s1>),

with one exception: risk of cannibalism attempts increased with increasing female-biased sexual size dimorphism in body mass (estimate: 1.18 ± 0.49 , $z = 2.44$, $P = 0.01$).

Diet and foraging behavior in the field.—The following is based on a literature review. These spiders rest off the web during the day on a nearby substrate such as tree branches or bark, and at night they sit at the hub of the orb web. Small insects such as flies (Diptera) are important prey for early juveniles, and they will also consume pollen on their web. The adult diet consists of larger insects including Coleoptera, Diptera (e.g., the robber fly *Colepia abludo* Daniels, 1983), Hemiptera (e.g., cicadas and the shield bug *Scutiphora pedicellate* Kirby, 1826), and Odonata, and adults can capture prey much larger than themselves (Brunet 1994; Dennis et al. 2012). In particular, moths (Lepidoptera) form a major component of their diet. For example, *H. transmarina* is an important predator of the light brown apple moth (*Epiphyas postvittana* (Walker, 1863)), which is a major pest of Australian crops (Dondale 1966). The diets of *Hortophora* include Lepidoptera (primarily moths), Diptera (largely mosquitoes and gnats), Hymenoptera (mostly ant alates), Coleoptera, and rarely Isoptera (termite alates) (Herberstein & Elgar 1994; Willmott et al. 2019). Predation on other spiders has been observed in both species, including *H. transmarina* eating the triangular spider, *Arkys lancearius* Walckenaer, 1837 (Arkyidae) (Brunet 1994), *H. biapicata* eating a social huntsman *Delena cancerides* Walckenaer, 1837 (Sparassidae) (Allan 2023), and both *H. transmarina* and *H. biapicata* consuming both male and female conspecifics (pers. obs.). Webs of *H. transmarina* have been observed catching birds and bats (McKeown 1952; Kaston 1965), and *H. biapicata* have been observed feeding on the New Holland honeyeater (*Phylidonyris novaehollandiae* (Latham, 1790)) (Brooks 2012). There was a single recorded event of an adult female *H. transmarina* catching an adult feathertail glider (*Acrobates*

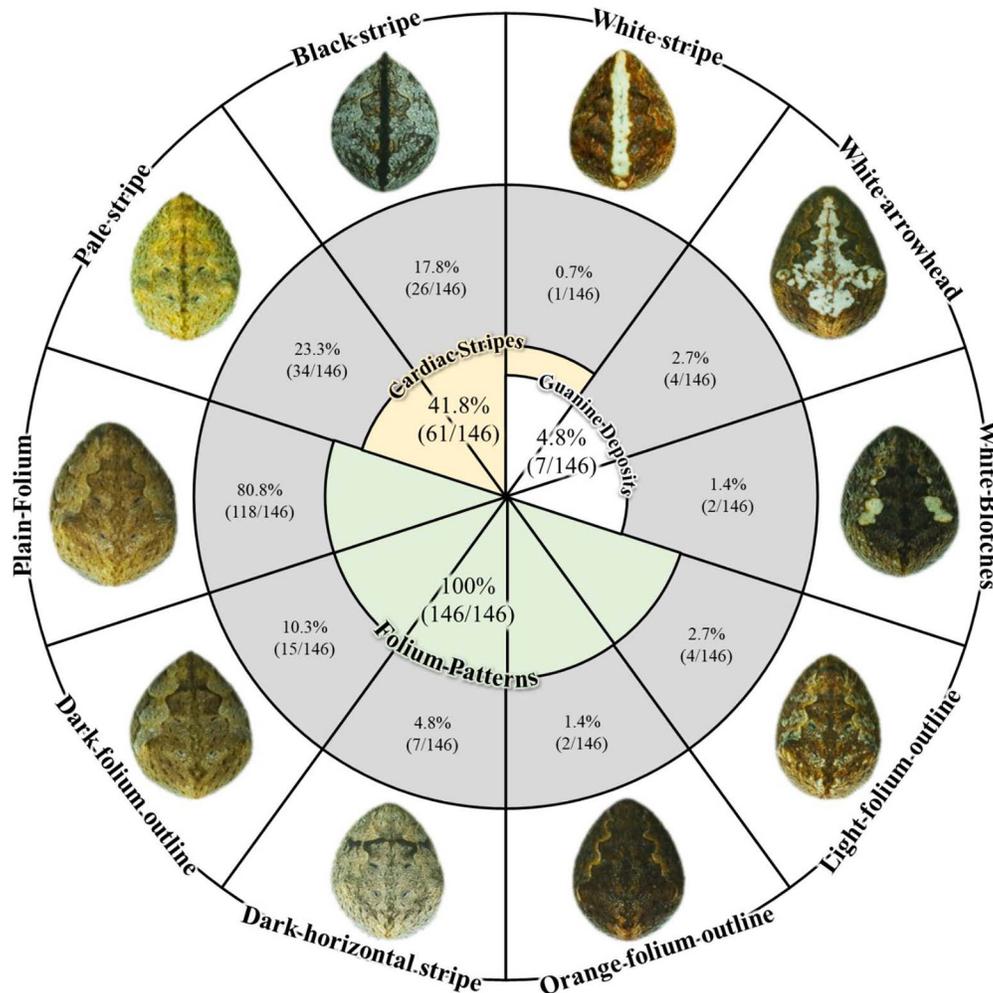


Figure 4.—Frequency of abdominal patterns in adult *Hortophora biapicata* collected from Melbourne, Australia in 2019. Different patterns are not mutually exclusive across the three groupings (Cardiac Stripes, Guanine Deposits, Folium Patterns), but they are mutually exclusive within groupings. The majority of individuals lacked distinct Cardiac Stripes and Guanine Deposits.

pygmaeus (Shaw, 1793)) in its web and feeding on the glider over a two-day period (R. Soanes, K. Soanes pers. comm.; Fig. 7).

Diet and foraging behavior in the lab.—The following is based on my observations during laboratory rearing experiments. Web construction takes approximately 15 minutes in early instars, and up to 60 minutes in adult females. Under laboratory conditions, I observed *H. biapicata* feeding on house fly (*Musca domestica*) pupae both in the web and on the ground, suggesting that *H. biapicata* is capable of foraging when not in the web, although the prevalence of this unusual phenomenon in the wild is unknown. I was not able to replicate this behavior in other native orb-weavers such as the araneids *Argiope keyserlingi* Karsch, 1878, *Trichonephila plumipes* (Latreille, 1804), *Araneus psittacinus* (Keyserling, 1887), or *Austracantha minax* (Thorell, 1859). When *Hortophora* attempt to subdue small prey, they generally begin by biting, but for larger prey such as dragonflies or other spiders, they begin by wrapping the prey in copious swathes of fine silk before getting closer to bite, to avoid injury. For example, *H. transmarina* has been observed subduing a large tree cricket caught in its web – the cricket has powerful jaws and spined legs that could easily puncture the abdomen and kill the spider. The spider covered the cricket in copious

swathes of silk, then bit the cricket for longer than usual, suggesting it injected a larger amount of venom than for smaller prey (McKeown 1936).

Predators and parasitoids.—A literature review reveals that Australian garden orb-weavers have a wide range of predators, including birds, reptiles, spiders, wasps, and other insects. Overall, wasps—particularly the families Ichneumonidae, Pompilidae, and Sphecidae—are likely their greatest natural enemies (Brunet 1994; Mason et al. 2018). Wasps may specialize on certain spider species, or they may be generalists that exhibit variation in preferences within a wasp population (Powell & Taylor 2017). Pompilid wasps are important predators of *Eriophora ravilla* (Kurczewski 1981; Scharff et al. 2020), which are ecologically and morphologically similar to *Hortophora*; the nests of mud-dauber wasps (family Sphecidae) are often found containing juvenile *Hortophora*, which are consumed by the wasp larvae (E Lowe unpublished data). The dynamics and timing of these attacks on *Hortophora* are poorly studied, although *Pison spinolae* Shuckard, 1837 wasps capture *Hortophora transmarina* in early to mid-summer (Evans et al. 1980). Orb-weavers are also common targets for ichneumonid wasps, which lay their eggs under the cuticle of the spider, after which the



Figure 5.—Photo series depicting changes in colouration of two individual *H. biapicata* over their final three instars. The first column shows the colouration of the spider as collected in the field, the second column shows colouration after the first moult in the lab, and the third column shows their adult colouration. The individual depicted in the top row (a) was provided a black substrate in its enclosure, while the spider shown in the bottom row (b) was provided a light brown substrate.

larvae hatch and slowly consume the spider (Brunet 1994). Additionally, the ichneumon wasp *Paraphylax sp.* Förster, 1869 lays its eggs within the eggsacs of *H. transmarina* (Chadwick & Nikitin 1975; Austin 1985).

Hortophora are prey for a range of other animals. This includes other spiders; if captured in another spider's web, they may be consumed by other *Hortophora* (i.e., cannibalism) (pers. obs., $n = 4$) and by the redback spider, *Latrodectus hasselti* Thorell, 1870 (Theridiidae) (Caitlin Henderson, pers. comm., $n = 1$). The araneophagic assassin bug *Stenolemus bituberus* has been observed occupying the webs of *H. biapicata*, although a direct predation event has not been observed (Wignall & Taylor 2008). Spiders in general are important components of the diets of vertebrates, including mammals, reptiles, and birds. There are no records of *Hortophora* in the diets of mammals and reptiles, likely a result of a lack of taxonomic specificity in diet analysis studies which often only identify prey to the order level, but they have been found in the diets of birds. Gizzard analysis of the southern boobook (*Ninox boobook*) found one record of predation on *H. biapicata* and two records for unidentified species of *Hortophora* (Penck & Queale 2002). Compared to other invertebrates, spiders made up a small component of the boobook diet (8.5%), and orb-weavers constituted a small percentage of spiders eaten (3%), so boobooks are unlikely to be major predators. If these spiders remain on their web during the day, they may be susceptible to attacks by honeyeaters (Meliphagidae), which swoop through the web and catch the spiders in their beaks (Brunet 1994).

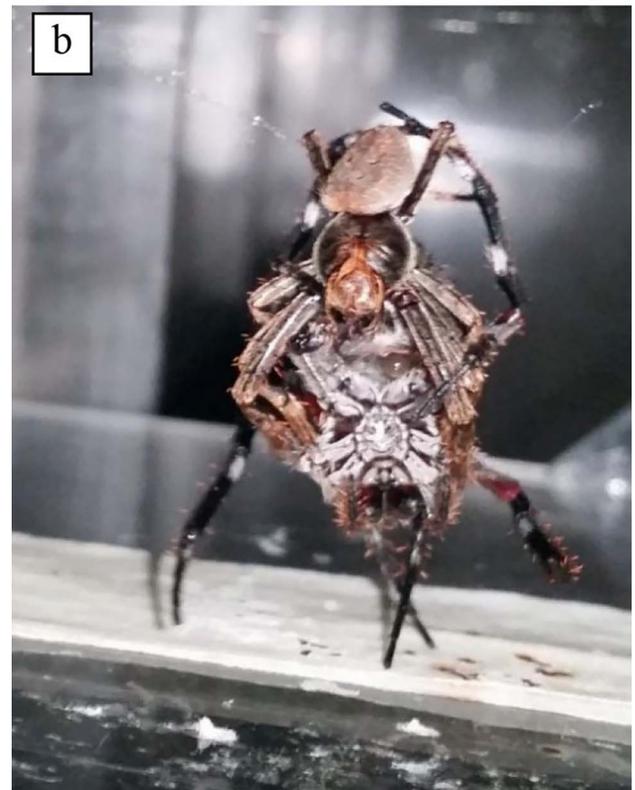
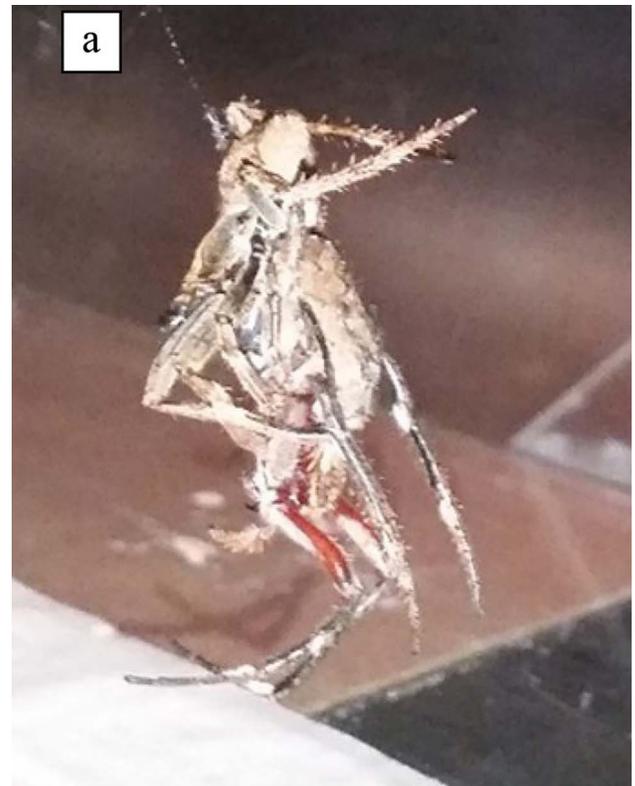


Figure 6.—Copulation position in two mating pairs of *Hortophora biapicata*: (a) male left/top, female right/bottom – the male did not clasp female's front legs, but still successfully copulated; (b) male top, female bottom – the male successfully clasped all four of the female's front legs. Copulation occurs on a mating strand constructed by the male between the edge of the orb of the female web and nearby scaffolding.



Figure 7.—An adult female *Hortophora transmarina* feeding on an adult feathertail glider (*Acrobates pygmaeus*). Photo credit: Rebekah Soanes.

In addition to the color change abilities described above, these spiders also show behavioral anti-predator traits. When disturbed, *Hortophora* often drop from their web or resting position and fall to the ground in a thanatosis display, bringing their legs close to their bodies as they fall. Leaf litter and ground cover plants provide camouflage, so this is likely to afford escape from predators. Some individuals drop immediately from their webs when touched with a paintbrush, whereas others remain steadfast, and some individuals even attack the paintbrush.

DISCUSSION

The Australian garden orb-weaving spiders are widespread across a diverse range of habitat types, and show a range of biological traits that distinguish them from better-studied species. They exhibit some of the greatest color variation amongst spiders, and display interesting predator-prey dynamics, including various anti-predator defences and consumption of vertebrate prey in their webs. Their mating dynamics differ from *Argiope* and *Trichonephila*, which have been the focus of orb-weaver mating research in Australia. Further, *Hortophora* are synanthropic spiders that are easily reared under laboratory conditions, and so provide an excellent model for answering a number of biological questions.

Development and morphological variation.—Much of the biology of *Hortophora* is tightly linked to their morphological variation, both in terms of their morphometrics and their coloration. I found considerable variation in traits such as body size and tibia spine counts. Variation in body mass is linked to fitness outcomes like reproductive output, as in other spiders (Heiling & Herberstein 1999; Lowe et al. 2014; Willmott et al. 2018). The Australian garden orb-weaving spiders exhibit considerable variation in their coloration and

patterning. Their dorsal coloration shows the greatest variation between individuals and provides camouflage against their substrate when they are resting during the day. I found that *Hortophora* is capable of changing the coloration over successive molts to match the substrate, similar to some other spiders (Graf & Nentwig 2001; Anderson & Dodson 2015). This may provide protection against predators that visually locate their prey, such as birds, lizards, and wasps. The high proportion of spiders that remained unchanged was partially due to the spiders that already matched their background at the start remaining that matching color, and the fact that some spiders didn't sit on the provided tape substrate during the day. This raises questions about their choice of resting place during the day; the relevance of this choice to their relative success in different habitats could be further elucidated through habitat choice trials. This ability to change color may partially facilitate their success in urban habitats, allowing them to color-match the surfaces of introduced plant species and artificial structures such as roof gutters. In contrast to their dorsal coloration, their ventral coloration is relatively stable between individuals, and may play a role in prey attraction (Chuang et al. 2007; Peng et al. 2020). Because ventral coloration is not visible while resting during the day, it may not show a trade-off between prey attraction and camouflage, explaining the lack of variation between individuals. Intriguingly, a small proportion of *Hortophora* individuals possess vibrant white stripes, blotches, or crucifixes on the dorsal opisthosoma. These patterns are UV-reflective, and so may aid in attracting insects to their webs or advertising their webs to ward off unwanted flying animals (Walter & Elgar 2012). However, this white coloration is likely to compromise their camouflage during the day, which may explain its rarity. Hence, these spiders provide a useful model for studying signalling trade-offs for predators and prey. It will be important to investigate the effects of these patterns

quantitatively, in particular using models of the visual capabilities of their predators.

Mating dynamics.—Morphometric shifts potentially interact with their mating dynamics, and *Hortophora* females with larger body masses produced more offspring (Willmott et al. 2018). Similarly, as seen in *Trichonephila*, it is likely that larger males will generally have more success in fending off other males (Elgar & Jones 2008). Hence, these morphological shifts could drive evolutionary responses in urban environments (Hopkins et al. 2018). Mating dynamics in *Hortophora* differ from the better-studied Australian orb-weavers in the genera *Argiope* and *Trichonephila*. Thus, they can provide insights into the evolution of mating systems in spiders. Unlike *Argiope* and *Trichonephila*, which exhibit extreme sexual size-dimorphism (females are considerably larger and heavier than males), males and females are similar in body length in *Hortophora*, although females are much heavier. The strong sexual size dimorphism in *Argiope* and *Trichonephila* allows smaller males to sneak towards the female (Elgar et al. 2000; Elgar & Jones 2008), whereas in *Hortophora*, the courtship dynamics prevent this sneaking strategy, and the male must be large and strong enough to restrain the female during copulation. Thus, unlike in extremely sexually dimorphic species where there is selection for variable male sizes (smaller males benefit by sneaking and more energy-efficient climbing, larger males benefit by excluding other males) (Elgar & Jones 2008), in *Hortophora* there is likely directional selection for larger males, limited by the longer development time and greater foraging success required to reach larger sizes. Given the difficulty of finding a common explanation for sexual size dimorphism in araneids, due to multiple evolutionary events independently resulting in dimorphism, it is important to investigate these processes in more taxa (Hormiga et al. 2000). *Hortophora* provides an excellent avenue for this because it is distinct taxonomically, morphologically, and behaviorally from other Australian araneids that have been studied, and because it is distantly related to northern hemisphere species that exhibit comparable courtship behaviors and a similar lack of sexual dimorphism (Scharff et al. 2020). Male *Hortophora* possess large, robust spines on the tibia of the second pair of legs and males that have larger and more spines likely have a stronger grip on females during copulation. Further, a recent taxonomic revision of *Hortophora* has identified female genital mutilation by males in some species in the genus, but this does not include *H. biapicata* or *H. transmarina*, and the occurrence of this mutilation has no apparent relationship with variation in genital morphology between species (Framenau et al. 2021). Hence, these spiders and their close relatives provide an excellent model for studying multiple aspects of sexual conflict and the evolution of spider mating systems.

Diet and foraging behavior.—*Hortophora* exhibit a broad potential diet, including primarily insects, other spiders, and rarely birds and mammals, as well as flexibility in their foraging behavior. This flexibility is supported by the copious amounts of fine silk they produce to wrap up their prey, allowing them to subdue large and dangerous prey, such as large tree crickets, while minimising the risk of injury. Consumption of animals other than insects is likely rare and opportunistic, but their ability to exploit such food sources may facilitate success in novel habitats, such as cities (Willmott et al. 2018, 2019), and makes them a good model species for lab studies (Willmott et al. 2018, 2019). Their diet is also tightly linked to their body size – the quality of a habitat and the prey available determine the adult body size, which in turn determines their ability to catch larger prey such as tree crickets or birds. Anthropogenic

stressors can then influence this, such as artificial light at night (ALAN) reducing body size (Willmott et al. 2018) but also increasing prey attraction and changing the types of prey found in webs (Willmott et al. 2019). This increased prey capture rate supports their persistence in disturbed habitats.

However, when studying foraging dynamics in orb-weavers, it is important to consider the effects of laboratory rearing. For example, although moths form a major component of the diet of *Hortophora*, webs constructed in the lab by spiders reared on crickets (*Acheta domesticus*) and house flies (*Musca domestica*) failed to catch moths when placed in the field (Willmott et al. 2019). Their laboratory diet may have shifted the allomone profile or architecture of the webs, thereby reducing their ability to attract and retain moths. The need for careful consideration of laboratory results is also highlighted by my unusual finding of *Hortophora* feeding on house fly pupae in the lab, which has not been observed in the field. While the artificial conditions of laboratory rearing may induce novel behaviors, such studies nevertheless provide useful insight into suitable areas for field-based investigations.

Predators and parasitoids.—Detailed descriptions of the natural enemies of spiders are rare. My literature search exemplifies the difficulty of capturing the diversity and relative threats of natural enemies, as these events are relatively rare, and there is a lack of taxonomic-specificity in studies conducted by non-arachnologists. Despite this, these results demonstrate the utility of broad literature searches that encompass studies such as dietary analyses of birds (Brunet 1994; Penck & Queale 2002) or prey surveys for wasps (Brunet 1994; Powell & Taylor 2017). These preliminary descriptions indicate that in addition to being important predators, orb-weavers such as *Hortophora* are a valuable food source for a range of predators, including birds, mammals, reptiles, amphibians, other spiders, and primarily wasps. In addition, wasps have likely shaped the evolution of eggsac structure in *Hortophora* (Chadwick & Nikitin 1975; Austin 1985). While wasps may pose the biggest threat to these spiders and their eggsacs, other predators such as reptiles, birds, and other spiders (e.g., redbacks *Latrodectus hasselti*), may also pose threats to dispersing *Hortophora*. More extensive dietary analyses with greater taxonomic specificity will improve our understanding of the roles of spiders as not only predators, but as prey. Furthermore, new metabarcoding techniques will allow the detection of prey DNA in the guts of predators (Paula et al. 2015). This knowledge will also facilitate meaningful studies of the anti-predator defences of these and other spiders, which are tightly linked to their morphology and behavior. Much is still unknown about these predator-prey interactions, so they offer fertile ground for future research.

CONCLUSIONS

The Australian garden orb-weaving spiders, *H. biapicata* and *H. transmarina*, are unique and charismatic members of the Australian fauna. Although they are common across a wide range of both natural and anthropogenically disturbed habitats, very few studies have investigated their basic biology or ecology. The morphological and behavioral traits that I have described here demonstrate their potential utility for investigating the evolution of mating systems, anti-predator defences, and the impacts of anthropogenic change on their biology. Further, these spiders are relatively easy to rear under laboratory conditions, and so are a highly tractable species for experimental studies. While the majority of the limited ecological research on the ‘backbourniines’ clade (*sensu* Scharff et al. 2020) has been restricted to *H. biapicata* and

H. transmarina (Herberstein & Elgar 1994; Willmott et al. 2018, 2019; Framenau et al. 2021), there are a number of closely related species in Australia. Despite their morphological and ecological similarities, these species exhibit variation in important traits such as coloration, body size, habitat use, and morphological characteristics that are important for mating dynamics. Thus, they provide an excellent system for testing ecological and evolutionary hypotheses, particularly as a contrast with better studied diurnal genera. Currently, much of our knowledge of these spiders comes from field observations, particularly regarding their diet and natural enemies. Hence, increased research, especially with controlled experiments, into these common but poorly studied Australian spiders would not only improve our understanding of spiders, but also provide key insights into more fundamental questions in biology.

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SUPPLEMENTAL FILES

Supplemental Table S1.— Relationships between key morphological traits and mating outcomes (copulation duration and risk of cannibalism); available online at

Supplemental Figure S1.— Inverted plastic cup enclosures used to house juvenile *Hortophora biapicata*.

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