

The natural history of *Argiope anasuja* (Araneae: Araneidae) with special reference to their mating behavior

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Abstract. *Argiope anasuja* Thorell, 1887 is a species of orb-weaving spider found in tropical and subtropical regions of the world. Despite its widespread distribution, little is known about its natural history and mating behavior. In this study, I describe some aspects of the natural history and mating behaviors of *A. anasuja* in captivity and in natural habitats. The spiders were found to occupy less shady areas close to water bodies, building their webs between 50 to 200 cm above the ground level. Web decorations were common in female webs, primarily in the central area, and consisted of dense zigzag bands of silk. A significant difference in copulation duration was observed between cannibalized and non-cannibalized individuals. Furthermore, a significant difference in copulation duration was found between individuals in natural environments and laboratory conditions. However, no significant difference was observed in courtship duration between individuals in natural environment and laboratory conditions. Understanding the mating behaviors of *A. anasuja* is important because they play a key role in determining the success of mating. This study highlights the natural history and mating behavior of *A. anasuja*, contributing to our understanding of this species in Sri Lanka.

Keywords: South Asia, cannibalism, copulation, habitat utilization
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The complexity of biodiversity and ecological processes is best understood through the documentation of natural history. The Global South is often underrepresented in natural history descriptions, although there are notable exceptions such as the work of the Robinsons (Robinson & Robinson 1974, 1976; Robinson 1982), who have extensively documented spider behavior and natural history in the tropics. Their work has yielded numerous papers that focus on the behaviors of *Argiope* spiders from the global south.

Sri Lanka is a country rich in biodiversity, ranked among the highest in Asia in terms of ‘biodiversity per unit area’ (MOE 2012). Among the invertebrates, spiders are one of the major taxonomic groups in Sri Lanka, and they serve an important role as predators in urban and rural as well as natural ecosystems. There are currently 563 spider species recognized for Sri Lanka, spanning 49 families. Sri Lankan spiders show high endemism with a total of 275 endemic species, almost 50% of the spiders of Sri Lanka (Platnick 2011; MOMD & E 2019). Sri Lankan spiders have not been thoroughly examined despite the fact that they are one of the most visible features of the Sri Lankan forest (Benjamin & Bambaradeniya 2006). More than 75% of the Sri Lankan spider species reviewed for the red listing process were classified as Data Deficient (DD), indicating a significant gap in the information base about Sri Lankan spiders (Benjamin et al. 2012).

Spider species in the genus *Argiope* Audouin, 1826 are popular models for investigating sexual selection for a variety of reasons, including availability and ease of laboratory maintenance, as well as special features such as considerable sexual size dimorphism, sperm limitations, genital damage, and sexual cannibalism (Fromhage et al. 2003; Wignall & Herberstein 2013; Schneider et al. 2015; Kuntner & Coddington 2020; Weiss et al. 2020; Golobinek et al. 2021). Web building (Chmiel et al. 2000; Blackledge & Gillespie 2002; Blackledge & Hayashi 2006; Rao et al. 2007; Blamires et al. 2009; Yazawa & Sasaki 2021) and the function of silk decorations (Herberstein et al. 2000; Wang et al. 2021) are common research topics and evolutionary genomics is a more recent area of research (Sheffer et al. 2021). The genus *Argiope* contains over 88 species (World Spider Catalog 2023) on all continents except Antarctica, and while they can vary dramatically in size, all *Argiope* share some

common features, including bright coloration with black and yellow stripes. Six *Argiope* species have been described in Sri Lanka: five regional species—*Argiope aemula* (Walckenaer, 1841), *Argiope aetherea* (Walckenaer, 1841), *Argiope anasuja* Thorell, 1887, *Argiope catenulata* (Doleschall, 1859), *Argiope pulchella* Thorell, 1881—and one endemic species, *Argiope taprobanica* Thorell, 1887. Most of these species are considered Data Deficient (DD) in the latest IUCN red list (Benjamin et al. 2012; MOMD & E 2019). Comparative behavioral studies have uncovered significant species-specific differences in this genus (Schneider et al. 2015), indicating the need for further exploration of species that have not yet been studied.

The goal of this research is to record the natural history of *A. anasuja* in Sri Lanka. There is only one published record on this species describing sexual size dimorphism (SSD) and overall morphometrics (Jalajakshi & Vinutha 2014). Therefore, here I describe microhabitat utilization, dispersion, and web features. Furthermore, I describe the mating behavior of *A. anasuja*, including courtship, copulation, and post-copulatory behaviors.

METHODS

Study species.—*Argiope anasuja* is known as the Signature Spider (English) or Liyana Dal Viyanna (in Sinhalese) (See Supplemental Figs. S1, S2, online at <https://doi.org/10.1636/JoA-S-23-029.s1>). Owing to the zig-zag patterns on their webs (Supplemental Fig. S1B), these spiders are also known as *writer spiders*. *Argiope anasuja* can be found on the Seychelles, Cocos Islands and Maldives, in Iran, Pakistan, India, Sri Lanka, and Australia (GBIF.org 2021). The web of this spider has up to four zigzag silk bands (web decorations).

Study site.—Study sites were in the Western province situated in the wet zone of Sri Lanka. A natural population of *A. anasuja* was surveyed in the vicinity of the Runakanda area and urban gardens (Fig. 1) in the wet zone from 6th June 2021 to 30th December 2021 and 3rd January 2023 to 22nd January 2023.

Runakanda (6.457°N 80.324°E) is a low-elevation tropical rainforest situated in the Western province of Sri Lanka that receives 2,500–1,800 mm of annual rainfall. Throughout the year, the temperature stays between 27 and 30°C. Relative humidity ranges

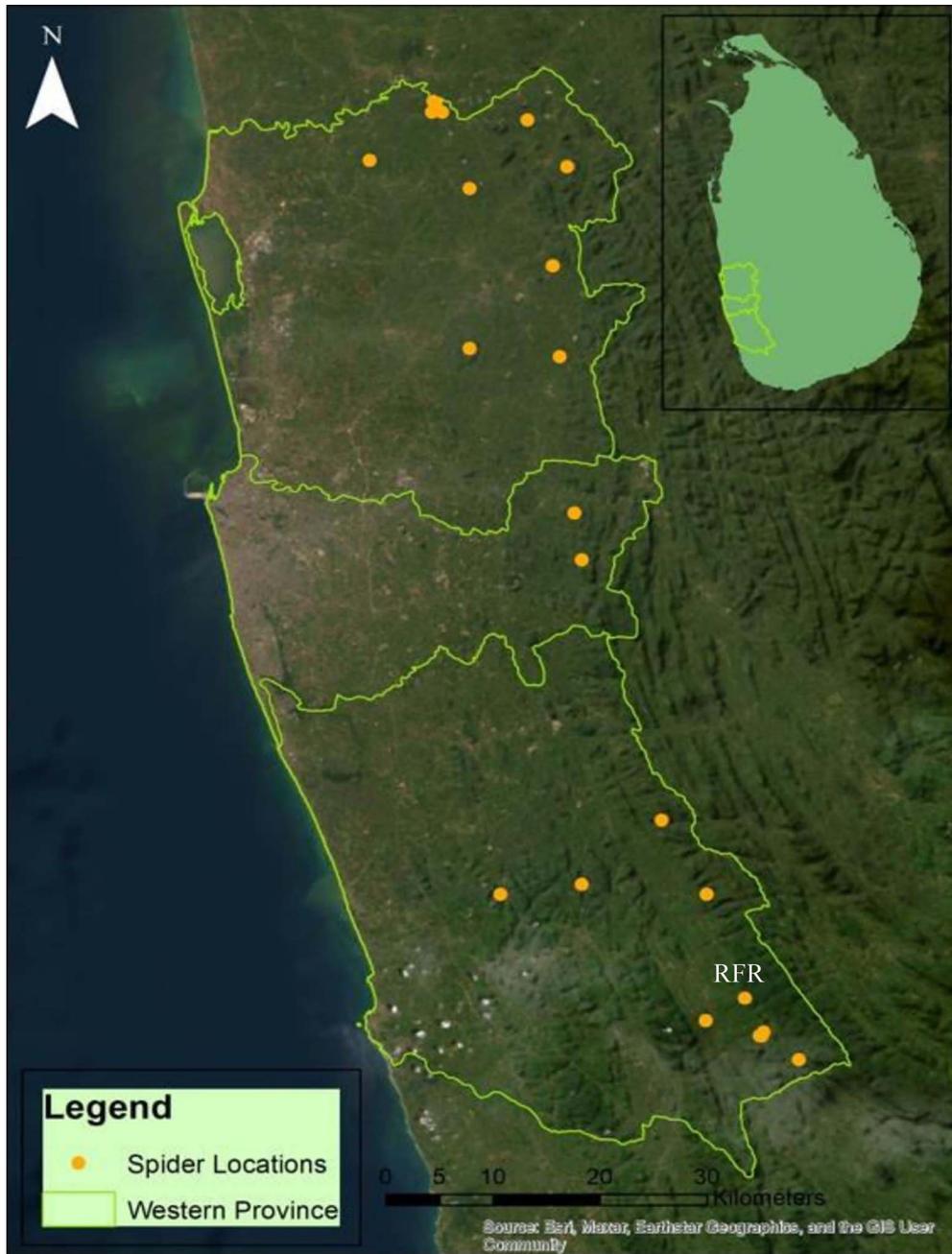


Figure 1.—Map of study sites and sampling locations in Sri Lanka (Dulan Jayasekara).

between 75%–85% (Green 1990). Multi-story vegetation characterizes this tropical rainforest, with the crowns of dominating trees forming a closed canopy. The undergrowth is minimal in these woodlands, but epiphytes and lianas abound.

Natural history.—Linear transect surveys ($1 \times 500 \text{ m} \times 2 \text{ m}$) were conducted in each prominent habitat type of Runakanda: Primary Forest (PF), Riverine Forest (RF), and Shrub Lands (SL) (Fig. 2) from 8 am to 12 noon over two days in each habitat. A direct count method was used following the ‘looking up and looking down’ methods proposed by Coddington et al. (1991). Once I located individuals of *A. anasuja*, the sex of adults was determined, and juveniles were classified as such.

As adult males do not construct webs, I focused on measuring the webs of adult females and sub-adult or juvenile males and quantified the following web parameters (see Supplemental Fig. S3, online at <https://doi.org/10.1636/JoA-S-23-029.s1>): web vertical and horizontal diameter (cm), hub vertical and horizontal diameter (cm), distance between the first and last sticky spiral at the lower half of the web, the number of spirals in the lower half of the web, number of anchor lines, presence or absence of web decorations, length of decorations if present (measured to the nearest mm) and height of hub above ground (measured to the nearest cm). The webs of adult females are often occupied by males and kleptoparasites such as spiders of the genus *Argyrodes* Simon, 1864

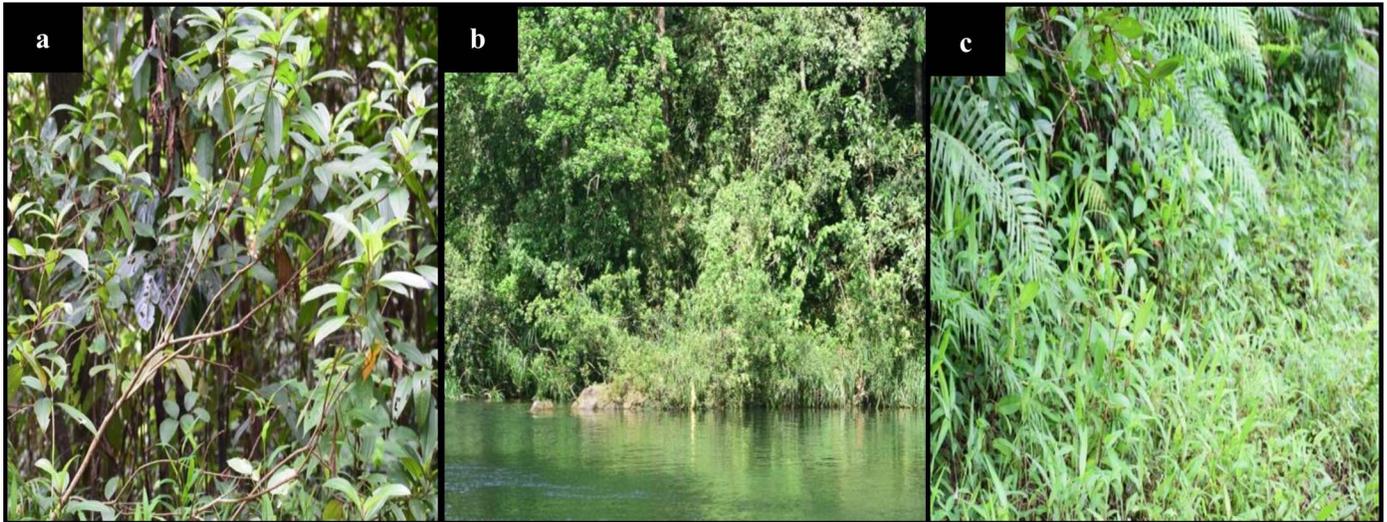


Figure 2.—Habitats of *A. anasuja*, (a) Primary Forest, (b) Riverine Forest, and (c) Shrub lands, Runakanda, Western Province, Sri Lanka, 2021. Photos: Chathuranga Dharmarathne.

(Theridiidae) and I noted if and how many males or kleptoparasites were present in the web.

I also noted whether the web occurred in an aggregation or was solitary. An aggregation was defined as a group of three or more spiders that share anchor lines or link their webs together (see Rao et al. 2009). According to Rao et al. (2009), solitary spiders are separated by a distance of a few metres. Web area was determined using the ellipse formula (Herberstein & Tso 2000):

$$\text{Web area} = \frac{1}{2} \times \text{vertical diameter} \times \text{horizontal diameter} \times \pi$$

$$\text{Mesh height} = \frac{\text{Distance between the first and the last sticky spirals in the lower half of the web}}{\text{The number of spirals in the lower web half} - 1}$$

The following habitat and micro-habitat characteristics were recorded: GPS location of each individual, compass orientation of the dorsum of each individual (i.e., east, west, north, south, north-east, north-west, south-east and south-west), attachment substrate of the web (i.e., a bush or a tree). Host plants were identified using standard plant identification guides (Ashton et al. 1997).

Mating observations.—Juvenile males and females of *A. anasuja* were collected from home gardens in Kotadeniyawa, Waradala, Divulapitiya, Badalgama, Kaduwela, Hedigalla, and Thiniyawala areas, Western Province, Sri Lanka, from July to December 2021 and in January 2023. The spiders were housed individually in glass boxes (50 × 50 × 5 cm) or upturned plastic cups (10 × 7.3 cm). Spiders were sprayed with water daily and fed house flies and crickets twice a week.

When the spiders reached sexual maturity, total body length (mm), carapace length (mm) and tibia-patella length (mm) of the right first leg were measured using the VINCA™ scale built-in digital callipers (0.001 mm) and body mass was measured using the AMIR™ digital scale (0.001 g). An individual adult male was placed into the web of a virgin adult female and the duration of courtship (from the time the male entered the web until the onset of copulation) and copulation (when the male inserted his pedipalp until he dismounted from the female or was captured and wrapped

by the female) were documented. For each copulation, I kept track of the occurrence of cannibalism and leg loss. To see if there are any differences in the mating behavior in the field compared to the laboratory, I also conducted mating trials in the field by introducing a single adult male into the web of an adult female. Male and female individuals used in laboratory experiments were virgins. The mating status (mated or unmated) of both the male and the female individuals used for the field observations was unknown.

Data analysis.—Minitab 20 (Minitab inc., 2021) statistical software was used for the statistical analyses and to generate descriptive statistics. Mann-Whitney U test was conducted to compare the differences in courtship and copulation durations of mating pairs in the laboratory and in the natural environment and to compare copulation durations of cannibalized and non-cannibalized individuals. I tested for statistical significance with alpha = 0.05. All values are reported as mean ± SD.

RESULTS AND DISCUSSION

Natural history.—Seventy spiders (58 females and 12 males) were observed in December 2021 in the three main habitat types (see Supplemental Fig. S4, online at <https://doi.org/10.1636/JoA-S-23-029.s1>). Most of them were found with their webs attached to small herbaceous plants ($n = 17$) such as *Flacourtia indica*, and grass species ($n = 49$) such as *Cymbopogon natus*, *Cymbopogon flexuosus*, *Cymnopogon citratus*, *Garnotia exaristata* and *Garnotia fuscata*. Four individuals were found in the understory on plants including small *Vernonia cinerea*, small palms like *Calamus* spp. and small trees of *Macaranga peltata*. Most spiders were found at a height under 2 m ($n = 39$) (Supplemental Fig. S4).

The distribution of habitat characteristics of *A. anasuja* was as follows: The average distance of webs to the nearest source of water (rivers, small streams, lakes, or natural pools) was 10.43 ± 11.13 m. Most webs were oriented facing East ($n = 42$) (60%), followed by West ($n = 13$) (18.6%), North-East ($n = 7$) (10%) and South-East ($n = 1$) (1.4%). The function of the predominately east orientation is unknown (Bishop & Connolly 1992).

Webs of *A. anasuja* occupy less shady areas in open or dense forests, close to water bodies, between 50–200 cm above the

Table 1.—Morphometric measurements and web characteristics of *A. anasuja* in Runakanda, Sri Lanka. Morphometric measurements were obtained from adult males ($n = 32$) and adult females ($n = 32$). Web characteristics were analysed from Sub adult males ($n = 12$) inhabiting their own webs in close proximity to adult females and adult females ($n = 58$) (mean \pm SD).

| Characteristics | Subadult male | Adult female |
|---------------------------------|-------------------|---------------------|
| Mass (g) | 0.012 \pm 0.001 | 0.488 \pm 0.126 |
| Total body length (mm) | 2.447 \pm 0.015 | 9.326 \pm 0.452 |
| Tibia-patella length (mm) | 0.186 \pm 0.011 | 6.686 \pm 0.390 |
| Carapace length (mm) | 0.112 \pm 0.009 | 3.842 \pm 0.578 |
| Web height from the ground (cm) | 55.72 \pm 20.53 | 115.86 \pm 70.36 |
| Web vertical diameter (cm) | 6.75 \pm 1.06 | 31.98 \pm 11.94 |
| Web horizontal diameter (cm) | 5.45 \pm 1.04 | 22.03 \pm 3.74 |
| Hub horizontal diameter (mm) | 6.48 \pm 0.75 | 38.49 \pm 2.09 |
| Hub vertical diameter (mm) | 5.87 \pm 0.64 | 35.98 \pm 2.61 |
| Number of anchor lines | 3–7 | 4–8 |
| Web area (cm ²) | 59.16 \pm 18.09 | 1517.90 \pm 509.5 |
| Mesh height (cm) | 0.256 \pm 0.09 | 0.382 \pm 0.08 |
| Web decorations present in webs | None | Yes (60.51%) |
| Kleptoparasites | None | Yes (10.29%) |

ground. When compared to other *Argiope* species, *A. anasuja* seems to occupy more open habitats compared to the more closed habitats occupied by *A. keyserlingi* Karsch, 1878 (Blamires et al. 2007) or the more densely vegetated habitats occupied by *A. aurantia* Lucas, 1833 (Enders 1973). There are no recorded natural history observations of other *Argiope* species in Sri Lanka with which to compare my results.

This species is sexually dimorphic (Jalajakshi & Vinutha 2014). The female has a grey cephalothorax with yellow horizontal stripes on the dorsal abdomen, and ventrally, two yellow vertical stripes on either side of the epigynum (Supplemental Fig. S1). The males are brown (Supplemental Fig. S2). For detailed species description see Levi (1983). *A. anasuja* is somewhat larger than *A. aemula* and *A. aetherea* recorded in Sri Lanka (Tharanga et al. 2017). Females of *A. anasuja* are 2.8 times larger than males (mean total female body length/mean total male body length) (Ranta et al. 1994, Table 1). In comparison to the sexual size dimorphism ratio (3.52) (mean total female body length/mean total male body length) documented within this genus (22 species) (Hormiga et al. 2000), *A. anasuja* demonstrates a moderate degree of sexual dimorphism. However, females are approximately 40 times heavier than males (Table 1).

All individuals surveyed in this study were solitary, never sharing anchor lines with other webs, and they were generally spaced a few meters apart. Web decorations were common (of 35 webs) in female webs (Table 1). The web decorations consisted of between one and four dense zigzag bands of silk. The bands frequently cross through the hub, forming a cross or part thereof. The most common arrangement of the web decoration was three arms ($n = 16$), followed by two arms ($n = 8$), four arms ($n = 6$), one arm ($n = 4$), and no arm ($n = 1$). The web decorations in *A. anasuja* were similar to the ones in *A. keyserlingi*, described by Rao et al. (2007). I did not observe any decorations in male webs. The function of these decorations is still a subject of debate, but they are believed to have several, non-mutually exclusive functions (e.g., Herberstein et al. 2000; Walter & Elgar 2012) such as prey attraction, predator deterrence or preventing damage to the web by birds (Hauber 1998; Herberstein 2000; Bruce et al. 2005; Cheng & Tso 2007).

Kleptoparasites (*Argyrodes flavescens* O. Pickard-Cambridge, 1880 (Theridiidae) Tanikawa et al. 1996; Agnarsson 2003) were observed in 10.3% of the webs of adult females ($n = 58$) (Supplemental Fig. S5, online at <https://doi.org/10.1636/JoA-S-23-029.s1>). *Argyrodes flavescens* are known to pilfer prey caught in the webs of larger orb-web spiders (Koh & Li 2002). They opportunistically steal captured prey or feed on leftover food items (Koh & Li 2003; Silveira & Japyassu 2012). The presence of *A. flavescens* as kleptoparasites within the webs of *A. anasuja* raises interesting questions about the ecological interactions between these two spider species. This behavior is thought to be a form of commensalism, where one species benefits while the other is neither significantly harmed nor benefited (Iyengar 2008), but direct tests of the costs of kleptoparasites are rare.

Mating behavior.—A total of 32 mating experiments were conducted, under laboratory conditions ($n = 22$) and in the field ($n = 10$) in January 2023. In nature, adult males waited near subadult females, either in their own web or on the outer part of the female's web ($n = 10$). Once I introduced an adult male into the web of an adult female, the male spent some time on the outer edge of the web moving slowly towards the central hub where the female was positioned. Eventually the male started touching and tapping the female with his legs for several minutes. The male also tugged the female web from time to time during courtship. Next, the male cut a small hole in the orb web just below and to one side of the hub. The male then constructed a horizontal mating thread across the created opening and hung upside down on the mating thread while plucking and bouncing on the thread. In response, the female moved onto the mating thread and assumed the distinctive “copulatory position” or “acceptance posture,” revealing her external genital structure, the epigynum.

This courtship behavior can be considered type B courtship, as described in Robinson et al. (1980). Courtship in this species is similar to other *Argiope* species such as *A. keyserlingi* (Herberstein et al. 2002). The length of a courtship in *A. anasuja* lasted anywhere from 5 to 26 minutes, while copulations lasted from 22 seconds to longer than 60 mins. About 60% of males ($n = 20$) managed to escape without being cannibalized, although some survivors lost a leg in the process.

Courtship duration of mating individuals in the natural environment (13.81 ± 4.69 min, $n = 10$) and laboratory (10.66 ± 5.11 min, $n = 22$) did not differ ($U = 116$, $z = -1.28461$, $P = 0.1002$). However, copulation duration was shorter in the natural environment (326.14 ± 48.54 s, $n = 10$) than in the laboratory (466.8 ± 10.36 s, $n = 22$) ($U = 62$, $z = -1.93115$, $P = 0.0268$). However, the mating status of those individuals used in natural environment was unknown. Copulation duration of cannibalized individuals ($n = 12$) and non-cannibalized ($n = 20$) significantly difference ($U = 77$, $z = -3.98981$, $P = 0.0001$) (Fig. 3). Cannibalized males copulated longer.

The shorter copulations in the natural environment may be attributed to the unknown mating status of the males, some of which may have been already mated. Due to genital damage, common in *Argiope*, and the inability to reuse a used pedipalp, mated individuals tend not to escape from the female and engage in longer copulation durations (Foellmer & Fairbairn 2003; Gaskett et al. 2004; Welke & Schneider 2010; Schwartz et al. 2016).

An examination of the mating behavior of *Argiope anasuja* in comparison to studies conducted on various other *Argiope* species (Robinson et al. 1980) reveals conspicuous parallels in courtship

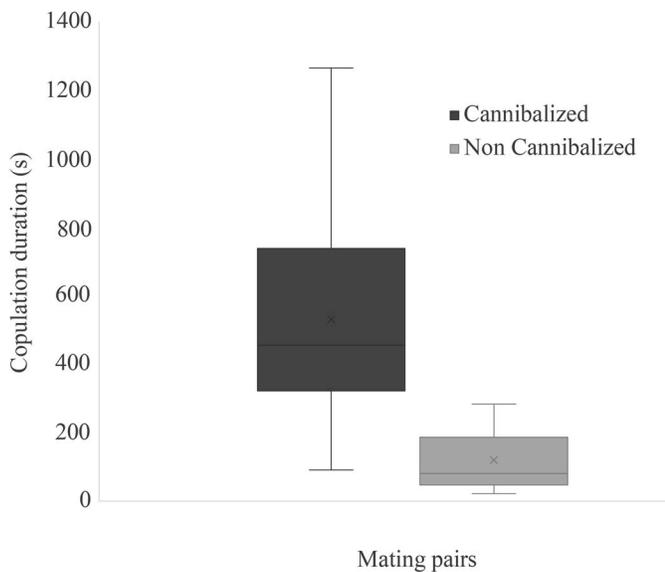


Figure 3.—Comparison of copulation durations among males cannibalized after mating ($n = 12$) and non-cannibalized individuals ($n = 22$).

rituals and copulation durations within this genus. Notably, species like *A. aemula* and *A. aurantia* manifest a comparable copulation duration to that observed in *A. anasuja*, typically lasting less than one hour. Conversely, species such as *A. ocyalooides* L. Koch, 1871 demonstrate considerably shorter copulation events, with durations averaging around 30 seconds. These findings emphasize the variation in copulatory behavior among different species within the genus *Argiope*.

Despite variations in courtship behaviors among the observed *Argiope* species in this study, all studied species of *Argiope* exhibit post-copulation attacks that result in either sexual cannibalism or genital damage (Schneider et al. 2015). Here, I describe the natural history of *A. anasuja* for the first time. Comprehensive comparative studies across multiple *Argiope* species in Asia would be necessary to understand the ecological and evolutionary relationships among them. The data underlying the work are available in Supplemental Materials.

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SUPPLEMENTAL MATERIALS

Supplemental Figures available online at <https://doi.org/10.1636/JoA-S-23-029.s1>

Figure S1.—*Argiope anasuja* female in the Western province of Sri Lanka, September 2021.

Figure S2.—*Argiope anasuja* male identification features.

Figure S3.—Characteristics of *A. anasuja* webs measured for this study.

Figure S4.—Relative abundance of *A. anasuja* in three different habitats, and web heights.

Figure S5.—Kleptoparasites *Argyrodes flavescens* (Theridiidae) observed in webs of adult female *Argiope anasuja*, *Argyrodes flavescens* kleptoparasites on the webs of female *A. anasuja*, Waradala, Sri Lanka 2021.

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