Defaecation behaviour of *Argiope aurantia* (Araneae: Araneidae)

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Summary

We examined the defaecation behaviour of *Argiope aurantia* both in natural situations and in a greenhouse. The spiders defaecated more frequently at night than during the day. The nightly pattern of defaecation was not related to time of feeding. *A. aurantia* displayed at least two distinct behaviours related to defaecation, one of which involved leaving the web. These results are discussed in relation to endogenous biological rhythms, daily patterns of activity, and predator avoidance.

Introduction

The roles of form and behaviour in predator avoidance are reasonably well established in spiders and many other animals. Examples of cryptic and aposematic coloration, in conjunction with behavioural repertoires that enhance the effectiveness of such coloration, are commonplace (e.g. Edmunds, 1974; Holl, 1987). Often, an effective method of avoiding visually oriented predators is simply for the subject to remain motionless (Robinson, 1969).

Daily periods of inactivity have been documented in both hunting spiders (Seyfarth, 1980) and web spiders (Horn, 1969). These periods of inactivity are usually associated with the photoperiod (Cloudsley-Thompson, 1987), but their occurrence can be affected by both abiotic factors (e.g. temperature, humidity, etc.) and biotic factors (Humphreys, 1976) such as availability of prey, age of the spider, and the activity of predators. Major predators of spiders are insectivorous mammals (Dryden, 1977), birds (Marples, 1969), lizards (Schoener & Toft, 1983), predatory wasps (Landes *et al.*, 1987), and other spiders (Jackson, 1992), including conspecifics (Enders, 1974). With the possible exception of some araneophagous spiders, most predators of spiders, especially those of web-building spiders, are diurnally active and visually oriented. Hence, mechanisms that reduce movement by spiders during daytime should be highly adaptive.

Among the orb-weaving spiders that remain on the web throughout the day, many decorate the web in some fashion using silk or debris. Although there is debate as to the adaptive functions of such decorations (Schoener & Spiller, 1992), one suggestion is that they may aid in concealing the spider (e.g. *Cyclosa*, Levi *et al.*, 1968; Rovner, 1977). Remaining motionless would greatly enhance the effectiveness of the decorations. *Argiope aurantia* Lucas is a large orb-weaving spider that remains at the hub of its decorated web throughout the day (Gertsch, 1949). Except when engaged in prey capture, *A. aurantia* remains relatively motionless during the day. Web construction, grooming and oviposition occur mostly at night, although these activities may extend into the twilight periods at dawn or dusk.

Like most other orb-weavers, *A. aurantia* hangs at the centre of its web in a head-down position (Gertsch, 1949). Presumably this posture confers some selective benefit. However, this position may complicate certain behaviours. In particular, defaecation from this position without fouling either the spider's body or the web is likely to be difficult since the anus is pointing upward. The spider must at least re-orient itself. During preliminary observations, we found that *A. aurantia* sometimes leaves the web entirely at night to defaecate. These observations also revealed that defaecation occurred more frequently during the night than during daylight hours.

In this paper we describe the defaecation behaviour of free-living *A. aurantia*. In addition, we test whether the temporal pattern of defaecation is simply the result of transit time through the gut, or if it follows a daily rhythm.

Methods

This study was conducted from late August through late September in Boone Co., Missouri. To discern patterns of faecal production, paper was placed under the webs (*in situ*) of four free-living, adult female *A. aurantia*. Individual defaecation events (droppings) could be identified as small (*c.* 4 mm) circles of faecal material on the paper. Observation confirmed that individual droppings typically fell on slightly different spots on the paper and thus could be identified as discrete events. The papers were checked each morning and evening (0700–0800h and 1800–1900h, respectively) for 3 days and the number of droppings produced by each animal during the preceding time period was noted. The mean number of droppings from the three diurnal or nocturnal periods for each spider was defined as the dropping production for that animal for that period.

In addition, 24 adult female *A. aurantia* were collected, transported to a greenhouse at the University of Missouri-Columbia, and housed individually in screen cages (76 cm cube). All spiders were allowed to produce webs and acclimate for ≥ 1 week before manipulation of feeding regimens. During the acclimation period all spiders were fed two mealworms daily in late morning or late afternoon. Water was provided by misting the cages on alternate days. Light-dark cycles followed the natural photoperiod and temperature was not closely controlled but was monitored using a max-min thermometer.

After the acclimation period, all spiders were fed two mealworms at 0700–0800h daily for six days. Spiders typically wrapped mealworms, consumed them, and then cut the remains out of the web within two hours. During the last three days, paper was placed on the bottom of each cage to catch droppings. The papers were checked twice daily (0700–0800h and 1800–1900h) and the number of droppings was recorded. These data were used to compare with similar data collected from free-living spiders and they served as a baseline against which comparisons with spiders with altered feeding

regimens could be made (see below). Spiders occasionally were observed off their webs. Data from time periods when the spider was not on the web at both the beginning and the end of the time period were excluded from the analyses. Spiders with more than one missing data point were also excluded from the analyses. The presence of a new egg-sac in the morning was taken as an indication that the spider had spent some time off her web during the night, and these periods were likewise excluded from the analyses.

After baseline data were collected, the spiders were randomly assigned to one of two groups. Spiders in Group A (n=6) continued to receive two mealworms each morning (0700–0800h). The feeding time for the remaining spiders (n=7, Group B) was switched to evening (1800–1900h). These feeding regimens were maintained for six days, during the last three of which the number of droppings produced during the day and night periods was monitored as outlined above.

Wherever possible, mean values for dropping production are presented. However, because temperature, ageing, and diet might have influenced spiders over the course of the study, when comparisons are made of data collected at different times from the same spiders, the data are expressed as a percentage of the total number of droppings that were produced at night. Two-way ANOVA was used for comparison of the data from the wild spiders with those from spiders in the greenhouse. Two-way repeated measures ANOVA was used for comparison of the data from captive spiders on the different feeding regimes.

Results

A. aurantia displayed two types of behaviour concerned with defaecation. The first behaviour involved minimal movement on the part of the spider, with the spider reorienting itself on the web so that the anus was pointed downward. From this position the spider could defaecate without fouling itself or the web. This rotation did not always result in the anus pointing directly toward the ground, but often ended with the anus below the level of the prosoma. The second defaecation behaviour involved the spider leaving the web completely. In this case, the spider attached a dropline to the hub of the web and released its hold on the hub. Descent on the dropline appeared to be controlled by contact between one leg IV and the dropline. The spiders halted their descent at about the level of the lowest extent of the web and rotated both legs I back under their ventral surface to grasp the dropline. After grasping the dropline with legs I, the spider inverted itself so that the anus was pointing straight down. At this point a dropping was released and the spider rapidly climbed back to the hub using the dropline. The entire process was completed quickly, within 10–15 seconds.

Wild spiders (n=4) produced 83 ± 7% (mean ± SE) of their droppings at night, whereas those in captivity (n=18) produced a mean of 87 ± 4% of droppings at night. In both groups the number of droppings produced during the night and during the day differed
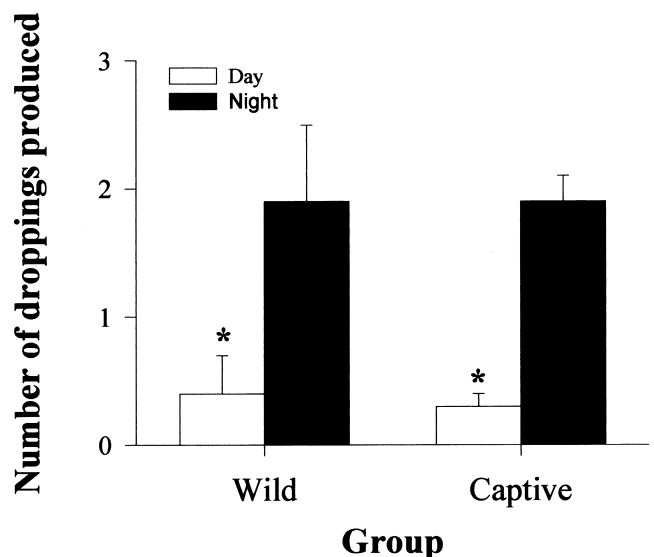

Fig. 1: Number of droppings (mean ± SE) produced per day and per night by free-living and captive *A. aurantia*. *Significantly different (p<0.05) from the number of droppings produced at night within a group.

significantly (Fig. 1). Individual animals occasionally produced more droppings during the day than they did during the preceding or following night (12 out of 171 possible day-night combinations, 7.1%). Wild spiders produced an average of 2.3 ± 0.9 droppings per 24 h period, with 1.9 ± 0.6 of these produced during the night. Captive spiders produced an average of 2.2 ± 0.6 droppings per 24 h period, with 1.9 ± 0.2 produced at night.

In tests of the effects of feeding time on the temporal pattern of defaecation, the pattern of dropping production did not differ between groups A and B when both groups were fed during the morning, both groups producing >90% of their droppings at night. This pattern of night-time defaecation did not change significantly when Group B was switched to an evening feeding schedule (Fig. 2). Hence, there was no difference in defaecation pattern between the spiders fed in the evening and those fed in the morning. In both groups, the absolute numbers of droppings declined slightly with time, but were not significantly different from those during the control period.

The mean greenhouse temperature was somewhat higher during the period when all spiders were being fed in the morning (17–31°C, mean=23°C) than during the subsequent period when the two groups were on different schedules (15–25°C, mean=20°C). Data from the feeding schedule manipulation were collected one week later in the year that were the baseline data, thus the photoperiod was slightly shorter.

Discussion

To our knowledge, this is the first study of defaecation behaviour of a spider. The nocturnal pattern of defaecation by *A. aurantia* under natural conditions was maintained by spiders held in captivity. Thus, moving the spiders into the greenhouse and placing them on a
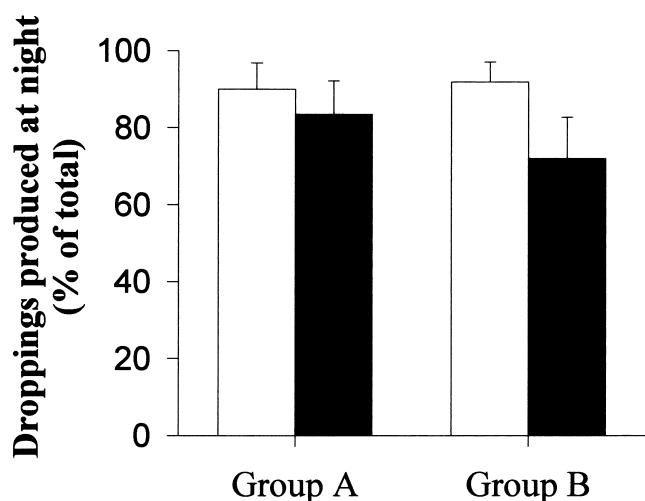
Fig. 2: Percentage of total droppings (mean ± SE) produced at night by *A. aurantia*. Open bars=baseline period, both groups fed in the morning. Solid bars=experimental period, Group A maintained on morning feeding, Group B switched to evening feeding.

fixed diet did not alter their behaviour. Apart from the fixed diet, the spiders in the greenhouse were subjected to many of the same environmental cues as spiders in natural conditions. No artificial lighting was used, so the spiders kept in the greenhouse were exposed to the same photoperiod as wild spiders and temperature was allowed to fluctuate in the greenhouse. Whether spiders were examined in natural situations or in captivity, a greater percentage of defaecation occurred during the night. The nocturnal pattern of defaecation was maintained even when the timing of food consumption was changed from morning to evening. Thus, the daily pattern of defaecation appears to be a circadian rhythm.

There are several possible explanations for the nocturnal pattern of defaecation seen in *A. aurantia*. Circadian rhythmicity has been found in a number of systems in arachnids (Legendre, 1985; Fleissner & Fleissner, 1985; Cloudsley-Thompson, 1987). Daily periods of increased activity have been documented in a variety of spiders (Cloudsley-Thompson, 1987) and are usually associated with the photoperiod. In addition to behavioural changes, physiological cycles have also been observed. Daily changes in the sensitivity and structure of the visual system (Fleissner & Fleissner, 1985; Cloudsley-Thompson, 1987; Blest, 1978), metabolism (Moulder & Reichle, 1972), and respiration (Anderson, 1970) are documented in a variety of species. Arachnids are known to possess central neurosecretory organs that exhibit cyclic activity (Legendre, 1985). In addition, peripheral neurosecretory organs are present which receive efferent signals from the brain (Legendre, 1985). Among these peripheral organs are two small intestinal ganglia which are innervated by branches of the same nerves that serve the musculature of the foregut (Legendre, 1985). In more advanced species the retrocerebral glands apparently serve the same function as the intestinal ganglia, and nerve ramifications arising from these glands innervate the musculature of the midgut (Legendre, 1985). The presence of neuro-

secretory and central connections to the digestive tract provides a possible route for cyclic hormonal or neural influence on transit time through the digestive tract on which selective pressures may act.

It is also known that the heartbeat and the pattern of contractions of the digestive tract in spiders can be tightly correlated (Dunlop *et al.*, 1992) and that heart rate increases with activity (Carrel, 1987). Although *A. aurantia* is considered to be diurnally active since it remains on the web and captures prey during the day, web renewal, grooming and egg-sac production occur at night. It is possible that increased heart rate during nocturnal activity results in a concurrent increase in the contraction rate of the digestive tract. This could result in more waste being voided at night.

Alternatively, the nocturnal pattern of defaecation exhibited by *A. aurantia* may be an adaptation that allows the spider to avoid detection by predators. *A. aurantia* possesses a variety of behaviours that may deter predators (Tolbert, 1975); however, from an energetic standpoint, it is probably more efficient simply to avoid attracting the attention of a predator. In Missouri, the animals that are most likely to prey on *A. aurantia* are predominantly diurnally active. Many of these predators are likely to be visually oriented and may cue on movement. The major predators of web-spiders are probably birds and parasitic wasps, with other taxa (excluding araneophagic spiders) taking a smaller proportion of spiders. Among birds, the hummingbirds (Bent, 1940) and tyrannid flycatchers (Marples, 1969) are most likely to attack spiders since their flight capabilities best allow them to remove spiders from their webs. Spiders have also been found in the diets of other passerine birds, most frequently during the breeding season. It has been shown that some birds avoid spiders on a web with a stabilimentum (Horton, 1980). For this to be effective the spider must remain at the hub of the web. Thus, waiting until dark to defaecate may be a way of avoiding predation by birds. Predatory wasps also appear to be visually oriented and to cue on movement. Eberhard (1970) reported that a predatory wasp passed within 2 cm of a stationary spider without noticing the spider but could detect a moving spider from a distance of 1 m. Rau (1928) reported a wasp losing a spider it was pursuing when the spider moved behind a rock. By reducing movement during the day when these wasps are active, the spider may reduce the probability of attracting the attention of predatory wasps.

The present study suggests that the temporal pattern of defaecation does not result simply from a fixed amount of time necessary for material to pass through the digestive tract. Spiders possess a stercoral pocket which serves as a storage reservoir for excreta (Seitz, 1987). This structure may allow *A. aurantia* to maintain control over the timing of defaecation. It is interesting to note that the defaecation behaviour involving leaving the web is very similar to one of the predator avoidance behaviours described by Tolbert (1975). A link between stress and defaecation is well established in many species. Seitz (1987) suggested that the stercoral pocket may store faecal material for sudden release in stress

situations. Perhaps the escape behaviour described by Tolbert arose as a modification of an existing behavioural sequence involved in defaecation.

A. aurantia typically assumes a head-down posture on the underside of the web. Although the exact reason for this head-down position is unknown, this posture complicates defaecation. The observation that these spiders may drop from the web to defaecate may in part explain (or be a result of) the tendency of *A. aurantia* to remain on the underside of the web. However, the costs incurred in leaving the web to defaecate include being out of contact with a large part of the sensory system, the possibility of increased exposure to predation, and the expenditure of silk to produce the dropline. Thus, defaecation behaviour should be taken into account in any studies assessing the costs and benefits of the head-down posture exhibited by many orb-weavers.

Acknowledgements

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