Notes on the lifecycle and distribution of *Sphodromantis gastrica* (Stål, 1858) (Mantodea: Mantidae) in South Africa

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Limited information is available regarding the distribution of the African mantis, *Sphodromantis gastrica* (Stål) (Mantodea: Mantidae) and no information is available on its biology. The aim of this study was to determine the distribution of *S. gastrica* in South Africa based on historic insect collection records and citizen science platforms occurrence data, and to study its basic biology and developmental parameters under captive breeding conditions. A total of 153 South African museum records of *Sphodromantis* spp. were recorded during this study, while 39 Research Grade observations from iNaturalist were also included. These records indicated that *S. gastrica* occurred in all provinces of South Africa. The incubation time of the *S. gastrica* ootheca were approximately 10 weeks and each ootheca contained an average of 84 egg chambers. The mean fertility rate was 54.6% while the survival rate until adulthood was 41.8%. The mean lifespan of *S. gastrica* individuals were approximately 332 days and females lived longer than males. This study will provide a baseline as it is the first published data on the distribution and biology of this common and charismatic insect in South Africa.

**INTRODUCTION**

*Sphodromantis gastrica* (Stål) (Mantodea: Mantidae), also known as the African/Common green mantis, is one of 38 species in the genus (Roy 2010). *Sphodromantis gastrica* is suggested to occur throughout sub-Saharan Africa and is one of the largest and most common mantid species in the region (Picker et al. 2019; Erhmann 2002; Kaltenbach 1996). Scientific literature regarding the distribution and biology of this and other *Sphodromantis* species is scarce and the few studies that were done on species in this genus focussed on behavioural aspects and species interactions.

Ene (1964) described a study that investigated parthenogenesis in Mantodea. In the latter study, the eggs of a *Sphodromantis* sp. were also artificially inseminated with spermatozoa of *Mantis religiosa* L. (Mantodea: Mantidae), unfortunately the outcome was not reported or discussed further. Abasa and Matheg (1971) investigated the use of *S. gastrica* as a potential biological control agent for the Giant Looper (*Ascothis selenaria*) (Denis & Schiffermüller) (Lepidoptera: Geometridae) in coffee plantations in Kenya. In the latter study, *S. gastrica* consumed 44% of the *A. selenaria* larvae provided to it under laboratory conditions, and was shown to potentially reduce pest infestations by 50% per tree. However, since *S. gastrica* and mantids in general are not specialist predators various other potentially beneficial insects could also be consumed (Abasa and Mathenge 1971).

A closely related subspecies, the giant African mantis, *Sphodromantis viridis* Forsskål (subspecies undetermined but is thought to be *S. viridis vischeri*) which occurs in North, Central and East Africa has recently been listed as an alien species after it expanded its distribution to various European and Mediterranean countries (Battiston et al. 2020; Oliveira and Ferreira 2019; van der Heyden 2018; Battiston et al. 2017). The seasonality and oviposition site preference of *S. viridis* was investigated by Younes and Gabre (2003) who reported that it prefers to lay oothecae on stems of *Acacia* trees instead of on the branches and leaves.

While *S. gastrica* is listed in various Mantodea checklists which include some notes on their distribution (Patel and Singh 2016; Kaltenbach 1996) information gaps exist regarding the distribution and biology of all *Sphodromantis* spp. (Roy 2010). In this study we investigated the distribution of *S. gastrica* in South Africa, based on historic insect collection records in museums and occurrence data from citizen science platforms, as well as the biology and developmental parameters of *S. gastrica* under captive breeding.

**MATERIALS AND METHODS**

*Species distribution data base*

Distribution records of *S. gastrica* and *Sphodromantis* spp. were collected during visits to the following institutions that host curated insect collections in South Africa: Ditsong Museum of Natural History (Pretoria) (DNMNH), Agricultural Research Council (Bioysystematics Division, Pretoria) (ARC), National Museum (Bloemfontein) (NMB), Albany Museum (Makhanda) (AMG), Rhodes University (Makhanda) (RU), Durban Natural Science Museum (DNSM), Iziko South African Museum (Cape Town) (Iziko) and KwaZulu-Natal Museum (Pietermaritzburg) (NMSA). Most specimens in these collections were previously identified by visiting taxonomists while many were sent for identification to the Vienna Museum in Germany, the University of Drexel in Philadelphia, USA, the Muséum National d’Histoire Naturelle (MNHN) in Paris, France and the research collection of Nicolas Moulin in Montérolier, France.
Sphodromantis specimens and distribution labels where photographed and digitised, after which the data was used to compile a distribution database. This database contains the following information for each specimen record: genus and species name (to the available level of identification), collector’s details and collection date where available, and the georeferenced locality. Scientific literature (Roy 2010; Ehrmann 2002) was used to determine the current nomenclature within the Sphodromantis genus, while the latest updates and changes applied to the classification system of the Order of Mantodea, as described by Schwarz and Roy (2019), were also incorporated in this paper. All locality data was georeferenced using the principles suggested by Wieczorek et al. (2004). Furthermore, the citizen science platform iNaturalist (iNaturalist 2022), in cooperation with the Global Biodiversity Information Facility (Gbif 2022) were used to increase the occurrence data of S. gastrica in South Africa. Only “Research grade” occurrences from the citizen science platforms were included since these records are the most reliable with regards to species identification. Ootheca records from the citizen science platforms were disregarded since it is unreliable in terms of species identification (Brannoch et al. 2017). Decimal degrees were used for developing the distribution maps for S. gastrica and Sphodromantis spp. in South Africa by means of GIS software (ESRI [ArcMaps], Version 10.6.1).

Rearing and biology of Sphodromantis gastrica

Specimens were collected in the Grassland biome in the North West province (Collection Permit number: HQ 08/05/17-152NW) of South Africa during the summer of 2016/2017. Adults of these field-collected individuals were mated and nymphs that emerged from oothecae were reared to adulthood after which males and females were identified. This was done based on the number of abdominal segments and the appearance of the wings (McMonigle 2013; Fatimah et al. 2016; Brannoch et al. 2017).

For breeding purposes, pairs of males and females were placed in glass containers. Large glass containers (30 cm × 20 cm × 20 cm) were used to ensure that ample space was available for the male to avoid sexual cannibalism before, during or after mating. To further limit the likelihood that females would cannibalise the males, ample food was provided before males were introduced into the breeding containers. After copulation concluded, males were removed from the breeding containers. The terrariums (15 cm × 10 cm × 20 cm) in which females were kept after mating was checked daily for the presence of oothecae. Oothecae were removed and put into small containers (5 cm diameter and 5 cm high) inside a desiccator. A humidity level of 68 ± 5% was maintained inside the closed desiccator, following the method described by Solomon (1951). Desiccators were kept in an insect rearing room at a temperature of 27 ± 1 °C with a 14L: 10D photoperiod until nymphs emerged from oothecae.

Rearing of nymphs was done under the above-mentioned conditions. Each nymph was placed into a terrarium (7 cm diameter and 15 cm high) with three holes (each 2 cm in diameter) covered with gauze to allow air flow. Thin twigs (5 mm × 10 cm) were placed inside each jar for climbing and hanging purposes, especially during moults. Food was provided every second day when fine water mist was also sprayed into each container. Live crickets (Acheta sp., Orthoptera: Gryllidae) of different sizes (nymphal instars, i.e. pinheads) were provided as food. After molting to the second-instar, nymphs were removed from the communal terrariums and placed in separate terrariums to prevent cannibalism. Nymphs (Figure 1A) were reared until adulthood after which males and females were identified. This was done based on the number of abdominal segments and the appearance of the wings (McMonigle 2013; Fatimah et al. 2016; Brannoch et al. 2017).

The following life history parameters were recorded during this study: size of oothecae, number of egg chambers inside fertilised and unfertilised oothecae, numbers of days between moults and survival rate (based on nymphs reaching the adult phase). The mean number of days between moults and days to adulthood were calculated separately for males and females. The data were recorded for 63 individuals (22 males and 41 females) that completed their life cycles. Despite 157 nymphs hatching successfully, only 63 reached adulthood. The mean hatch and survival rates as well as duration of male and female life cycles was calculated.

A distinction was also made between different types of oothecae, i.e., fertilised (produced by field collected and laboratory-mated females) and unfertilised (produced by laboratory-reared unmated females). The length, width and height of each ootheca were recorded, based on descriptions by Brannoch et al. (2017). The ootheca length was measured along the area of emergence, excluding the residual process (Greyvenstein et al. 2021; Brannoch et al. 2017). To determine the number of eggs per ootheca, oothecae were dorsally dissected along the length and inspected under a microscope according to the methods described by Greyvenstein et al. (2021; 2020; 2021). Measurements of ootheca parameters were done according to the method proposed by Brannoch et al. (2017) (Figure 1C).

Data analysis

The descriptive statistics (means and standard error) and the statistical analyses of the developmental parameters were done using Statistica Version 13.3 (TIBCO Software Inc. 2017) and SPSS Version 27 (IBM Corp. 2020). Shapiro–Wilk normality test was used to determine if the data was normally distributed. Subsequently, the parametric Student’s t-test was used to determine if differences existed between the mean numbers of days between moults, adult longevity and mean number of days required by nymphs to reach adulthood between the males and females of S. gastrica. No statistical tests were done between the unfertilised and fertilised oothecae with regards to length, width, height and number of eggs as a low number (only four) of each oothecae type was collected/produced by female S. gastrica females during the study.

RESULTS

Distribution of Sphodromantis gastrica

Historic distribution records were compiled from records that are available in the seven South African institutions mentioned above, and iNaturalist observations. The results presented in this paper should be viewed in this context since no museum
records were included beyond those residing in South Africa. A total of 192 records of *Sphodromantis* spp. specimens were recorded in museum collections and iNaturalist records. Six of the museum records were not identified to species level but were included as distribution records (Figure 2). The majority of the historic distribution records were from the northern parts of the country in the Mpumalanga and Limpopo provinces, with a few records from the Pretoria area in Gauteng. Only 16 records of specimens collected in KwaZulu-Natal province were found while in the Northern and Western Cape provinces only four and two distribution records of *S. gastrica* were recorded, respectively (Figure 2).

**Biology of Sphodromantis gastrica**

The oothecae of *S. gastrica* is somewhat rectangular in shape, with the base being longer than it is wide or high (Figure 1C). The dorsal side of the oothecae is attached to the substrate and in some instances somewhat encircled the substrate, for example in the case of thin branches. The oothecae usually have a light brown colour and a very short residual process and are thus not as elaborate as many other mantid species. The oothecae contained egg chambers arranged in rows following the shape of the oothecae with approximately six egg chambers per row.

Eight oothecae were used during this study, four of which were produced by four laboratory-mated females and four by unmated laboratory-reared females. Although 41 of the latter females were reared, only four produced oothecae before they died.

The overall morphology, i.e., height, length, width and number of eggs per fertilised and unfertilised oothecae were similar (Table 1). Each ootheca contained approximately 84 eggs. Due to the low number of oothecae collected, morphological parameters could not be statistically compared. Fertilised oothecae were 17.0 mm (± 5.7) long and 12.0 mm (± 3.56) high.

**Developmental parameters**

A total of 157 nymphs hatched from the four fertilised oothecae. These nymphs were reared to adulthood and provided with food until natural death occurred. Only 63 (22 males and 41 females) completed their life cycle under laboratory conditions.

The mean incubation period of *S. gastrica* oothecae was 75 days (Table 2). However, one ootheca only required 44 days while another only hatched after 109 days, thus indicating great variation in the incubation period despite all oothecae being exposed to similar laboratory conditions. Although the size of the different oothecae were within narrow margins of each other (Table 1), the number of eggs per fertilised oothecae varied between 54 and 104 (Table 2).

The shortest incubation period (44 days) was recorded for the ootheca that contained the largest number of eggs (104 eggs). The mean hatch rate was 54.63% while the mean survival rate to the adult phase was 41.81% (Table 2). More females emerged per ootheca than males and only one ootheca was male dominated (64.2% males and 35.7% females). The overall sex ratio for *S. gastrica* was female skewed and estimated to be 1:1.86 (Table 2).

Most of the nymphs required seven instars to become adults (37 individuals), with only nine individuals that required more than seven instars (Table 3). Two nymphs required only five instars to become adult females, while one female required nine instars. Significant differences in the duration of only two of the developmental phases between male and female *S. gastrica* were recorded, i.e. duration of incubation period (p = 0.008) and **Table 1.** Size parameters and mean number of egg chambers of *Sphodromantis gastrica* oothecae reared under captive breeding conditions

| Ootheca | Length (mm ± SD) | Width (mm) ± SD | Height (mm) ± SD | No. of eggs (mean ± SD) |
|---------|-----------------|----------------|-----------------|-----------------------|
| Overall (8) | 17.23 ± 4.12 | 11.68 ± 3.31 | 9.38 ± 1.30 | 84.38 ± 50.27 |
| Unfertilised (4) | 17.25 ± 2.63 | 11.75 ± 3.59 | 9.50 ± 1.73 | 89.50 ± 72.15 |
| Ootheca 1 | 12.00 | 17.00 | 10.00 | 62.00 |
| Ootheca 2 | 17.00 | 9.00 | 8.00 | 97.00 |
| Ootheca 3 | 25.00 | 12.00 | 9.00 | 104.00 |
| Ootheca 4 | 14.00 | 10.00 | 10.00 | 54.00 |
| Fertilised (4) | 17.00 ± 5.72 | 12.00 ± 3.56 | 9.25 ± 0.96 | 79.25 ± 24.92 |
| Ootheca 1 | 16.00 | 10.00 | 9.00 | 86.00 |
| Ootheca 2 | 21.00 | 9.00 | 8.00 | 190.00 |
| Ootheca 3 | 15.00 | 17.00 | 12.00 | 21.00 |
| Ootheca 4 | 17.00 | 11.00 | 9.00 | 61.00 |

**Figure 2.** Historic distribution records of *Sphodromantis* species in South Africa
duration of the 5th instar ($p = 0.003$) (Table 3). The incubation period of female eggs was significantly longer than that of males and male nymphs took significantly longer than females to complete the 5th instar. Overall, individual $S. gastrica$ nymphs required approximately 251 days ($±$ 9 months) to become adults and their entire lifecycle was completed in approximately 332 days ($±$ 11 months) (Table 3). Although no statistically significant difference was recorded, female adult longevity (mean: 77 days) was longer than that of males (mean: 51 days) (Table 3).

**DISCUSSION**

**Distribution of Sphodromantis gastrica**

Distribution records in South African museums together with observation data collected from the citizen science platform (iNaturalist) and previous publications (Picker et al. 2019; Erhmann 2002; Kaltenbach 1996) indicate the distribution of both subspecies of $S. rudolfae$. This is however in contradiction to the distribution of both subspecies of $S. rudolfae$ as recorded in South Africa was $Sphodromantis rudolfae$ Rehn. The two specimens of $S. rudolfae$ that were collected in the “Transvaal” (a province of South Africa prior to 1994) are currently in the Swedish Museum of Natural History (NRM) and the Transvaal Museum (South Africa).

**Biology of Sphodromantis gastrica**

Although some publications exist on the biology of other mantid species there is no specific information about the biology of $S. gastrica$. Observations on $Sphodromantis$ spp. in South
Africa date as far back as 1898 but are limited to brief reports on feeding and oviposition behaviour. Marshall (1902) reported that *Sphodromantis* spp. females could survive at least a month of starvation. Unfortunately, the only literature found on the biology of the *Sphodromantis* genus was from studies done on *S. viridis* viridis. Zohdy & Younes (2003) studied the biology of *S. viridis* and reported that females only took approximately 86 minutes to lay an ootheca as opposed to the four hours recorded by Williams & Buxton (1916). Although the study by Williams & Buxton (1916) contained a detailed schematic of the oothecae and protective layers that are present in *S. viridis* oothecae, no measurements were made and thus cannot be used to compare to results of this study. The oothecae of *S. viridis* which was studied by Zohdy & Younes (2003) are also visually similar to that of *S. gastrica* in this study. Unfortunately, no measurements or dissections of oothecae were made by the latter authors, making comparisons impossible. Studies on *S. viridis* indicated that their oothecae contain approximately 200 eggs (Biernacka 2020), which was also the case for *S. lineola* (Ène 1964). The latter two species therefore produce much higher number of eggs per oothecae than *S. gastrica* in this study (84.38 eggs). Zohdy & Younes (2003) recorded an average of ten oothecae per *S. viridis* female while *S. gastrica* females in this study only produced one ootheca each.

**Developmental parameters**

Due to the lack of information on the biology and developmental parameters of *Sphodromantis*, the biology and nymphal development of *S. viridis* (Zohdy and Younes) will be used for comparison purposes with the results obtained in this study of *S. gastrica*.

The mean incubation period for oothecae was 75 ± 28.45 days, which is shorter than that recorded for *S. viridis* (93 days) by Zohdy and Younes (2003) but longer than the average of 57 days recorded for *Sphodromantis bioculata* (Burmeister) (Adair 1914). Although egg incubation period could be a species-specific trait, it may also be influenced by environmental conditions. The study conducted by Zohdy and Younes (2003) was done at a lower temperature (25°C ± 2°C) than that used in this study and at a higher relative humidity (70 ± 5%). *Sphodromantis gastrica* in this study was kept at a relative humidity of 68 ± 5% for the duration of this study, since this more accurately represents the average conditions in the grassland biome of South Africa, where the specimens of this study were collected. The photoperiod also differed between these two studies with that used by Zohdy and Younes (2003) being a 13L:11D compared to the 14L:10D cycle in this study. These differences in environmental conditions could have influenced several of the biological activities and developmental parameters recorded in the current study and that of Zohdy and Younes (2003) on *S. viridis*.

The number of moults of *Sphodromantis* spp. seems highly variable. The maximum number of moults recorded for *S. gastrica* in this study was nine, but most individuals required only seven, which is lower than that of *S. viridis* which become adults after 12 instars (Zohdy and Younes 2003). Higher temperatures do not always result in fewer instars during the nymphal stage. Uvarov (1931) reported that temperature influenced the number of moults of *S. viridis* and that eight to nine moults were recorded at 25°C, compared to nine to ten moults at 37°C. In this study, a longer nymphal developmental period was recorded for *S. gastrica* males (163 days) and females (149 days) compared to *S. viridis* males (163 days) and females (149 days). Injury or loss of appendages have also been reported to influence the numbers of moults required by a *S. bioculata* nymph to reach adulthood, probably because an extended development period allows time for the injured or lost appendage to be regenerated (Przibram and Megusar 1912).

Abahussain and Younes (2006) reported that high prey availability, especially during the first three instars of *S. viridis*, was positively related to development rate of nymphs but that development rate decreased when more than a certain number of prey individuals were consumed by mantid nymphs. Despite providing mantid nymphs with the same number of prey individuals, Abahussain and Younes (2006) reported that different developmental rates still occurred, which suggests a natural variation in consumption rates between individuals. Marshall (1902) reported differing behaviour among *S. lineola* individuals which were offered various butterfly species as prey. Some individuals would eat a certain butterfly with vigour while another would take a bite and drop the prey and start 'wiping its mouth' as if the butterfly was 'disgusting'. Such differences in consumption rates and preference could therefore also influence nymphal developmental rates.

Male *S. gastrica* took longer to develop into adults than females which is in contrast to the males of *S. viridis* which developed faster than the females (Zohdy and Younes 2003). Although *S. viridis* had overall shorter nymphal developmental periods than *S. gastrica*, the adult longevity of both males and females were almost double that of male and female *S. gastrica* individuals. The longer adult longevity of *S. viridis* could also explain the relatively high number of oothecae laid compared to *S. gastrica*.

Despite these differences between both studies and species (*S. gastrica* and *S. viridis*), longevity of female adults was longer than that of males. This is also the case for various other mantid species including *Galepsus lenticularis* (Saussure) (Greyvenstein et al. 2020), *Tanachodes azelfii* (Stål) (Ène 1964), *Ephesiaustula pictipes* Giglio-Tos (Vanitha et al. 2016), *Harpagomantis tricolor* L. (Greyvenstein et al. 2021) and *Popa spara* Stål (Greyvenstein et al. 2021). Various reasons for this phenomenon have been suggested, from changing sex ratios from male-dominant to becoming female-dominant and vice versa between seasons and years (Vanitha et al. 2016, Christensen and Brown 2018), to more time for females to mate and oviposit. Extended oviposition may also result in reduced sibling competition if resources are limited (Greyvenstein et al. 2020).

Seasonal changes in environmental conditions were not considered in this study since *S. gastrica* was reared in captivity and at constant temperature and photoperiod. Mesnier (1984) reported that photoperiod influenced ootheca production in *S. lineola* and that no egg laying occurred when rearing was done under conditions of continuous light. However, when a subsample of these females were exposed to a light:dark photoperiod of 12 hours, females immediately laid normal oothecae (Mesnier 1984). Although photoperiod could influence the incubation period of oothecae, other factors such as temperature may also influence the survival strategies of mantids during unfavourable periods. Overwintering strategies of the Mantodea differ between species but little information is available for this group of insects. Some species, for example *Miomantiscaffra* Saussure (Mantidae), go into a facultative diapause phase during the ootheca stage (Ramsay 1984), Shcherbakov and Govorov (2021) reported that *Severinaturuncamiae* (Saussure) (Toxodoridae) overwintered as late-instar nymphs.

Further research should be conducted to determine the effect of different temperatures on *S. gastrica* development rates as well as the strategies of this species to survive the wide-ranging environmental conditions throughout its distribution area in South Africa. The occurrence of fire, which is common in the grassland where this species occurs, may also have a significant effect on the ecology of a predatory species such as *S. gastrica* that has a very long life cycle.
CONCLUSION

This study indicated that S. gastrica occurs throughout South Africa. Museum and iNaturalist records indicate that S. gastrica is the only species of this genus that occurs in South Africa. Although it is likely that other Sphodromantis species also occur in the country, research into this field is hampered by a lack of taxonomic expertise in the region and low numbers of Mantoea in South African museum collections compared to other insect groups. Due to the longevity of S. gastrica and long incubation period of its oothecae, S. gastrica could potentially expand its distribution range throughout Africa, similar to what was recorded for S. viridis in recent years. However, field studies under natural conditions should be conducted in future, as there is no artificial substitute for a species biology as it occurs in nature.

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