The orchid mantis exhibits high ontogenetic colouration variety and intersexual life history differences

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Abstract

Masquerade, the resemblance of animals to inedible or inanimate objects, exists universally throughout the animal kingdom, especially in arthropods. However, masquerade has received little attention from biologists and is often misinterpreted as mimicry by the public and even by scientists, as a consequence of the lack of systematic biological information for any masquerader. Therefore, using the orchid mantis *Hymenopus coronatus* (Insecta: Mantodea), a classic masquerader, as the study species, we first analysed its abundance, life cycle, microhabitats, colour morph diversity and key environmental factors that may affect its life cycle, based on 11 years (2011–2021) of field investigations. The results showed that the orchid mantis a) had an extremely low wild population abundance; b) exhibited four main colour morphs (white, pink, purple and yellow); c) did not coexist with any specific plant or flower; d) had a reproductive period from May to August and a nymph developmental period from September to April; and e) may adapt to local seasonal fluctuations of temperature and precipitation throughout its life cycle. Second, we recorded its life history, colour morph flexibility and intersexual variation under laboratory conditions. The results indicated that 1) its colour morph with high flexibility exists among and within different life stages; and 2) the two sexes can be remarkably differentiated in development, lifespan and body weight. This study is the first systematic investigation of a masquerader; its results should be useful for ecologists and evolutionary biologists to interpret the adaptation and evolution of masquerade.

Introduction

Masquerade is a form of camouflage in which the masqueraders resemble inedible or inanimate objects to render themselves sensorily detectable but cognitively misclassified by predators or/and prey, thereby increasing their survivorship by avoiding predation and gaining success to hunting (Endler 1981, Skelhorn, Rowland et al. 2010, Skelhorn 2015). This strategy evolves when predators and prey perceive the similarity between a masquerader and its model or models, consequently increasing the fitness of the masquerader (Skelhorn, Rowland et al. 2010). The masquerader is often visually comparable to the model in both colouration and morphology. Predator deception and prey deception have been documented as the most common functions of masquerade. Whereas plant-eating species usually favour predator deception, top predators often favour prey deception. These forms of deception are known as protective masquerade (which functions to favour escape from predators) and aggressive masquerade (which functions to increase the probability of access to prey) (Skelhorn, Rowland et al. 2010). However, small carnivores (such as spiders and mantids) are often required to evolve both protective and aggressive masquerade to be successful masqueraders, since they have to manage to survive under evolutionary pressures from both predator avoidance and prey attraction. The bird-dropping-resembling crab spider *Phrynarachne ceylonica*, which conceals itself visually to avoid predators such as birds, but chemically attracts prey items such as flies (Yu, Xu et al. 2021), is a good example. Most masqueraders, such as the ghost mantis and the dead leaf butterfly (Skelhorn 2015), hide themselves against the background. However, a few species are highly contrasted against the background in order to lure prey (Cuthill 2019); we define this type of masquerade as conspicuous

masquerade. Theoretically, conspicuous masquerade would be favoured by small carnivores when both their predators and their prey rely heavily on visual signals. For example, the orb-web spiders have been shown to use their bright body colours to attract and deceive pollinators by their resemblance to the small parts of flowers (Tso, Liao et al. 2006, Bush, Yu et al. 2008). Conspicuous masqueraders often present ontogenetic colouration and morphological polymorphisms among different life stages and between the sexes, which are hypothesised to expand the masqueraders' distribution and hence enhance their adaptation (Higginson and Ruxton 2010, Caro, Sherratt et al. 2016, Yu, Xu et al. 2022). Although conspicuous masquerade has been noted for decades, no species has been systematically studied for its field abundance, colour morph diversity and flexibility, microhabitats and key environmental factors that may affect its life cycle, life history and intersexual variations. The lack of this information restricts our understanding of the evolution and adaptive significance of conspicuous masquerade. Although masquerade is ubiquitous and different from Batesian mimicry, it has received little attention from biologists (Skelhorn, Rowland et al. 2010) and is often misinterpreted as mimicry by public and even scientists. Based on the facts mentioned above, we selected the orchid mantis *Hymenopus coronatus* (Insecta: Mantodea) as the study species to fill this research gap.

H. coronatus is the only masquerader that resembles an entire blooming flower, which makes it as an excellent model of conspicuous masquerade. Its flower-like appearance may functionally integrate pollinator attraction and predator avoidance (O'Hanlon 2016) and is the basis for its vernacular name of orchid mantis for over 200 years. However, all descriptions and interpretations of the orchid mantis were based on individual observations rather than empirical studies until 2013. James O'Hanlon and his colleagues experimentally quantified the colouration and morphology of the orchid mantis (O'Hanlon, Li et al. 2013) and then performed spectral and morphological comparisons with the potential model plant species (O'Hanlon, Holwell et al. 2014). They proposed a contrary opinion to the traditional interpretation, as they showed that the orchid mantis did not mimic orchids or any specific flower. Hence, the orchid mantis was interpreted as a generalist rather than a specialist mimic (O'Hanlon, Holwell et al. 2014). However, this interpretation was not confirmed due to lack of field investigation. Behavioural experiments were then performed to examine the pollinator-deception function of the orchid mantis, and they concluded that the orchid mantis could attract prey (insect pollinators) by its body surface colour, whereas the existence or symmetry of the femoral lobes did not attract pollinators (O'Hanlon 2014). In addition, Takafumi et al. (Mizuno, Yamaguchi et al. 2014) found that the orchid mantis could lure honeybees by emitting the chemical ingredients of honeybee communication pheromones, and hence they concluded that *H. coronatus* employed a chemical aggressive camouflage strategy. Although this evidence supported the hypothesis that the function of the resemblance of *H. coronatus* to a flower was to deceive pollinators, these results were based on only a few individuals or on three-dimensional printed models.

The available scattered information about *H. coronatus* is not enough for ecologists and evolutionary biologists to interpret the adaptive significance and evolutionary mechanism of its conspicuous resemblance to a flower. Hence, a systematic survey of *H. coronatus* will be vital for us to understand how it survives and why its flower-like appearance has evolved (O'Hanlon 2016). We managed to fill these

research gaps by integration of field investigations and laboratory rearing records of the orchid mantis. The specific questions we aimed to answer were the following: 1) What are the population abundance and life-cycle patterns in the field? 2) How is the life cycle affected by key environmental factors (temperature and precipitation)? 3) What are the diversity and flexibility of the colour morphs, and what are the variations of the colour morphs among and within life stages? 4) Is the orchid mantis closely associated with a specific microhabitat? 5) What is the life history of *H. coronatus* and what are the intersexual differences in life history? Answers to these questions would provide the first systematic biological information on a classic conspicuous masquerader, which might help ecologists and evolutionary biologists to interpret the evolution and adaptation of masquerade.

Methods

Field investigation

The records for 11 years (2011–2021) of field observations were collected in and around Xishuangbanna Tropical Botanical Garden (XTBG, 21º 55' N, 101º 16' E, 1125 hm^2 in area), Yunnan, China. XTBG is a tourist destination with dozens of tourist guides and hundreds of staff, who frequently explore the garden and often take photos when they see an orchid mantis. We collected original data mainly by interviews with the guides and staff, and six samples were recorded from the authors of this manuscript. To ensure accurate information, we selected photographic data with necessary information, including recording dates, microhabitats (such as recorded plants) and specific locations. From these photographs, we first recorded the dates of observation, life stages (ootheca, first instar, flower-like juveniles and adults), colour morphs and the plants they remained on for further analysis of their life cycles, colour morph diversity and microhabitats. Second, to analyse the correlations between key environmental factors and the orchid mantis life cycle, we obtained eight-year (2010–2018) average daily temperatures (minimum, mean, maximum) and 10-year (2010–2020) daily rainfall records from Xishuangbanna Station for Tropical Rain Forest Ecosystem Studies, XTBG, Yunnan, China.

Indoor life history

To survey the indoor life history and intersexual variations in development and lifespan of the orchid mantis, we reared 428 orchid mantises (hatched from nine oothecae produced by four females) and recorded the date and body weight of each individual soon after hatching and at each moult until death in the laboratory (located at XTBG) from April 2020 to August 2021. To study colour morph flexibility, we reared another 140 individuals and recorded the colour morphs of each individual for its entire life. The sex of each reared individual was determined when possible according to the females' last slightly upturned-edge sternum and fewer coxosternites (Roeder 1935, Brannoch, Wieland et al. 2017). We did not control the rearing conditions (light cycle, humidity and temperature) for the entire procedure, because our laboratory was located within the natural distribution region of the orchid mantis. The mantises had been kept individually in transparent plastic containers from the hatching stage. Here the newly hatched (first instar) and early life-stage nymphs (the second to the fourth instars) were kept in smaller containers

(length: width: height = 5.7 × 5.7 × 4.2 cm), and later life-stage nymphs (fifth instar and above) were kept in larger containers (upper diameter: bottom diameter: height = 17.5 × 12 × 13.5 cm). Food was supplied according to life stage. For the first and second instars, fruit flies were supplied, and for the third instar onward, house flies were provided as the main diet, mixed with cockroaches, crickets and bees. For adult females, field-collected moths were offered as the main food, especially during the reproductive stage.

Data analysis

The field records of *H. coronatus* were carefully checked to identify the host plants and to define life-cycle stages, including oothecae, newly hatched (first instar), flower-like stage (second instar to the last instar) and adult (male or female) and the corresponding colour morphs in these life-cycle stages. Then all records of each life-cycle stage were pooled monthly to show the monthly distribution. Average daily temperature and total daily rainfall were grouped by month to calculate average monthly temperature and rainfall.

For the indoor life history analysis, 91 reared individuals (38 females and 53 males) were included, as they reached adulthood and had complete data records. First, for each individual, we calculated 1) the duration of development and the growth rate of each instar, 2) the duration of adulthood, 3) the duration of development and the number of moults during the entire nymph period and 4) the whole lifespan. Then, for both sexes, we 1) calculated the average duration of development of each instar and the duration of adulthood and 2) visualised the body weight upon hatching and moulting and the growth rate of each instar for all individuals for the duration of development. Furthermore, to clarify intersexual differences in 1) the duration of development and the growth rate of each instar, 2) the duration of adulthood, 3) the duration of development and the number of moults during the nymph periods and 4) the entire lifespan, we built linear models when model assumptions were fulfilled or performed the Mann-Whitney-Wilcoxon test when the data failed to meet the assumptions of the linear model. Data analysis and visualisation were performed with the use of R 4.1.2 (R Core Team 2021).

For analysis of the flexibility of colour morphs, a pre-experiment and a formal experiment in two generations were performed to verify the accordance of the pattern. We first defined the general colour morph pattern during the first filial generation and perceived that colour morph flexibility existed in the fourth-instar stage. Then we repeated rearing conduction in the second filial generation for life history records, and successfully identified and accessed colour morph data for each life stage of 97 individuals who survived at least to the fourth-instar stage. The proportion of colour morph(s) in each flower-resemblance stage was calculated. To clarify the extent of colour morph shift in a series of life stages, we also counted individuals that shift colour morph from fourth-instar stage and survived to maturity and obtained the rate of colour morph shift. These data were analysed and visualised by Excel Office 16.

Results

Field investigation

Population abundance

Fifty-four orchid mantis records were collected in total (52 were inside XTBG and two were outside but within 3 km from XTBG). The 54 records included one ootheca, two first instars, 39 flower-like juveniles (second instars to the last instar nymphs) and 12 adults (10 females and 2 males), which suggested an extremely low population density.

Colour morph diversity

The first-instar nymphs and adult orchid mantis exhibited stable colour patterns (Fig. 1, **A, B, C, D**), yet individuals in the flower-like stages (second instar to the last instar) presented four main colour morphs (white, pink, purple and yellow) (Fig. 1, **E-H**). Specifically, the first-instar nymphs all exhibited a black-red colour pattern (Fig. 1, **D**), presumably as a mimicry of Reduviidae bugs (Hawkeswood and Sommung 2019). Adults of both sexes presented a brown-white colour pattern (Fig. 1, **A, B**). The 39 flower-like juveniles exhibited four different colour morphs, including 18 white, 8 pink, 9 purple and 4 yellow individuals (Fig. 1, **E-H**), which suggested colour morph diversity of the orchid mantis.

Microhabitats

The recorded 54 orchid mantises were all on plants (except for one that was attracted to the light in a washing room in a yard of a house outside XTBG) and were scattered in various habitats (roadside, managed shrub region, managed tree plantations, secondary forest, etc.) within an area of approximately 22 km^2. All of the recorded individuals were distributed separately in space and time. Specifically, no two individuals were recorded within 100 metres of each other at the same time. Twelve individuals were recorded on plants that could not be identified, and the remaining 42 individuals were recorded on 38 plant species (five monocots, 32 dicots and one fern) belonging to 34 genera and 29 families (**Table S1**). Among the 38 plant species that we identified, 35 species belonging to 27 families were recorded only once with a single orchid mantis, and three species *Litsea glutinosa* (Laraceae), *Heptapleurum heptaphyllum* (Araliaceae) and *Glycosmis pentaphylla* (Rutaceae) were recorded two or three times with a single orchid mantis. These results indicated that the orchid mantis was distributed in various microhabitats and was not highly associated with any specific plant. Only two individuals were recorded on flowers. This suggested that the orchid mantis mainly stayed on the background, such as green plant leaves, which highly contrasted with its body colour.

Life cycle

Seasonal distribution results suggested that the orchid mantis produced one generation per year in the investigated region, without overlap of generations. Oothecae, first-instar nymphs and adults were only recorded in summer (April to September) (Fig. 2, **A, B, C, D**), especially from May to August, which suggested that summer was their reproductive period. The nymph developmental period was from July to the following May, since oothecae and first-instar nymphs were only seen in July and August and larger nymphs were only seen in April and May (Fig. 2, **A-C**). Comparisons between this life-cycle pattern and the local monthly fluctuations of temperature and rainfall suggested that the life-cycle pattern of the orchid

mantis is an evolutionary response to temperature and rainfall, since the reproductive period coincided with the highest average monthly temperature (above 25.9°C) and rainfall (above 219.5 mm) within a year (Fig. 2, **E**). Only two males were seen among the 12 adults, both during the early reproductive period (April and May), which suggested that males may mature earlier and have a shorter lifespan than females.

Indoor life history

Intersexual differences in duration of development, body weight and lifespan

The oothecae hatched after 36.8 ± 3.99 days (N = 10, N_{mother} = 4, SD), and all eggs in the same ootheca hatched synchronously (Supplementary material, **Video 1**) in around two to three hours. The mean body weight of the newly hatched nymphs was 5.51 ± 0.69 mg (N = 91, N_{mother} = 4, SD, no sex difference) (**Table S2**). However, compared with males, females had significantly greater numbers of moults to maturity (female: 7.97 ± 0.28 times; male: 5.72 ± 0.45 times; P < 0.001), body weights after the last moult (female: 1367.00 ± 281.00 mg; male: 241.00 ± 46.00 mg; P < 0.001), duration of pre-adult development (female: 164.0 ± 13.1 days; male: 104.0 ± 18.3 days; P < 0.001) and lifespans (female: 192.00 ± 28.80 days; male: 138.00 ± 37.50 days; P < 0.001) (Fig. 3, **A-E; Table S2, S3**). During the ontogenetic period, the duration of development (12.20 ± 1.52 days) and the growth rate (0.56 ± 0.14 mg/day) of the first instars did not differ significantly between males and females; however, the growth rate and body weight after each moult of females began to be significantly faster and heavier, respectively, than that of males after the second moult, although the duration of development within each instar and the adult lifespan were longer in males than in females after the first moult (Fig. 3F, **G; Table S2, S3**). Furthermore, female body weight remarkably increased from the newly mature to the reproductive stage, whereas male body weight remained relatively stable until death. The heavier body weight in females was due to their longer development time and faster growth rate, especially in the later developmental stages (Fig. 3A, **F, G; Table S2, S3**). Further details of the comparison between males and females are shown in **Table S2, S3.**

Colour morph diversity

Among individuals raised indoors, the orchid mantis exhibited high flexibility of colour morphs during the flower-like stages but stable colour morphs during the first instar and adult stages. The newly hatched first-instar nymphs and the adults had the same colouration patterns as field mantises. After the first moult, they started to show a flower-like appearance and exhibited a stable colour pattern, with a mixture of yellow, pink, purple and white (**Figure S1, A**). This colour pattern was transformed into a stable white-purple pattern after the second moult (**Figure S1, B**). Individual colour patterns showed differences from the third moult to the last moult (**Figure S1, D**) and were dominated by three colours: white, pink and purple (details in **Table S4**). In 94.5% (68/72) of individuals, the main body colour morphs changed from the fourth instar onward. These results suggested that the colour morphs became highly flexible during the flower-like life stages.

Discussion

We investigated the biological features of the orchid mantis, including its field abundance, life cycle, microhabitats, colour morph diversity and the key environmental factors that may affect its life cycle, and then recorded its indoor life history and colour flexibility. The results suggest that the orchid mantis is extremely rare in the field and has highly diverse and flexible colour morphs, which may help it to survive in variable microhabitats. Its intersexual differences in body size and lifespan may be evolutionary adaptations of sex role differences in a conspicuous masquerader for reproductive success.

Only 54 orchid mantis records were collected in 11 years. This suggested an extremely low abundance of the orchid mantis in the field and reflected the adaptive difficulties of conspicuous masquerade under pressures from both predator deception and prey attraction. The diversity and flexibility of its body colour morphs may contribute to its high survival rate in various microhabitats, unlike successful mimics that often closely resemble a specific model and maintain the same spatiotemporal distribution as their models (Rettenmeyer 1970). Masqueraders resemble inedible and generally inanimate objects (O'Hanlon, Holwell et al. 2014, Liu, Blamires et al. 2014, Yu, Xu et al. 2015) and often have highly flexible appearance, which may enhance the masquerader's adaptive success in multiple microhabitats (Skelhorn, Rowland et al. 2010). Both the field and the indoor results showed that the orchid mantis exhibited diversity and flexibility of colour morphs. In addition, the orchid mantis did not coexist with a specific plant or only occur with any flowering plant. These features indicated that the orchid mantis was unlikely to resemble any specific flower (mimicry) but was likely to masquerade as general flowers. This conclusion is consistent with the past presumption (O'Hanlon 2016, Hawkeswood and Sommung 2019) and morphological analysis (O'Hanlon, Holwell et al. 2014). Furthermore, the orchid mantis showed not only diverse colour morphs but also remarkable body size variations among life stages, which also obviously increased its diversity. This diversity and flexibility of appearance may be crucial for conspicuous masqueraders to survive in the tropical rainforest, which has a high diversity of microhabitats (Whitman and Agrawal 2009). In fact, according to the published literature, most recorded conspicuous masqueraders are distributed in tropical rainforest (Liu, Blamires et al. 2014, Yu, Xu et al. 2015, Hawkeswood and Sommung 2019, Yu, Xu et al. 2022). Adaptability to multiple microhabitats may be vital for conspicuous masqueraders, because, unlike herbivores that forage on motionless plants, the well-known conspicuous masqueraders are all tiny carnivores, such as spiders and mantises, which are thereby burdened more from high population density, such as fierce competition for prey, when they are distributed only within a specific habitat (Caro and Allen 2017, Wheatley, Pavlic et al. 2020).

The life-cycle pattern of the orchid mantis is an evolutionary response to key local environmental factors. In our study area, the orchid mantis had a life-cycle pattern of one generation per year, without generational overlap. We concluded that its reproductive period was in the rainy season (May to August),which has high average temperatures and plentiful rainfall. There are three reasons for this conclusion. First, oothecae, newly hatched nymphs and all adults except two were only recorded during this period. Although two adults were observed in April and September (one in each month), we inferred that they were respectively newly matured and aged adults. Second, biological and abiotic factors in this

season could meet the reproductive requirements of the orchid mantis. Female carnivorous insects need not only a large amount of food (Polis 1981) but also multinutrient foods (Krapu 1981) for incubating eggs and appurtenances, such as oothecae (Boggs 1981). Various arthropods that served as food resources were much more abundant during the rainy season than during the rest of the year (Poulin, Lefebvre et al. 1992). Third, favourable temperature and humidity are vital for normal embryonic development in insects (Howe 1967, Singh, Bhat et al. 2009), and both average monthly temperature (above 25.9°C) and average monthly rainfall (above 219.5 mm) in XTBG remained at the maximum level from May to August. Therefore, reproduction during the rainy season is an evolutionary adaptation to fluctuations in local environmental factors, whereas in the subhumid and dry seasons (from September to April) (Chen, Cao et al. 2015), the lower temperature and rainfall may only satisfy the developmental demands of the nymphs.

The orchid mantis exhibited notable intersexual differences in body size (female-biased), duration of development (protandry) and lifespan (female-biased), which were evolutionary responses for reproductive success. First, larger body size in females may be a result of selection for fecundity, which is universally documented in many arthropods, such as spiders (Head 1995) and insects (Honěk 1993, Berger, Walters et al. 2008). Their larger body size enables females to produce greater numbers of offspring or larger offspring in a limited reproductive period (Pincheira-Donoso and Hunt 2017), which obviously benefits the orchid mantis by shortening its reproductive period while prolonging its embryo-hatching time for more oviposition trials. Second, we suggest that larger body size benefits adult females because they are motionless and hence are seldom noticed by predators. In contrast, the smaller body size of adult males may help them to escape from predators and search for mates, as being small may enhance their agility (Husak and Fox 2008). Intersexual variation in nymph developmental time (sexual bimaturism) may only be a by-product of the larger body size of female orchid mantises, as has been documented frequently in many taxa, especially in insects (Tammaru, Esperk et al. 2010, Morbey 2013). Protandry confers remarkable advantages by avoiding the drawbacks of inbreeding, guaranteeing the existence of intersexual reproductive synchrony, reducing virgin females' waiting costs, and increasing the number of male copulatory trials for reproductive success (Wiklund and Fagerström 1977, Morbey and Ydenberg 2001). The shorter duration of development and lifespan of males may explain why fewer adult males were recorded than females (2 males and 10 females) and why they were only recorded in the early reproductive stage (May) in the field.

In conclusion, this is the first study to systematically investigate basic biological characteristics in a classic conspicuous masquerader, and it may provide crucial information for ecologists and evolutionary biologists to interpret how conspicuous masqueraders adapt and evolve. However, some essential questions are waiting to be addressed for further understanding of the masquerade phenomenon and the orchid mantis, including 1) Do intraspecific recognition and evaluation exist in conspicuous masquerader species, and if they do, how do they work? 2) What mechanism and factors cause the change and variety of colouration in the orchid mantis? 3) How do males and females achieve reproductive synchrony with the huge dimorphism in development time and lifespan in the orchid mantis? Answers to these questions

would contribute to further clarification of the evolutionary process and adaptive strategies of conspicuous masqueraders.

Declarations

Author contributions

J.X.L, X.Z. and Z.C. designed the experiments. X.Z. and J.X.L collected data. X.Z. and Z.C. wrote the original manuscript. J.X.L, X.Z. and Z.C. revised the manuscript and figures.

Competing interests

We declare no competing interests.

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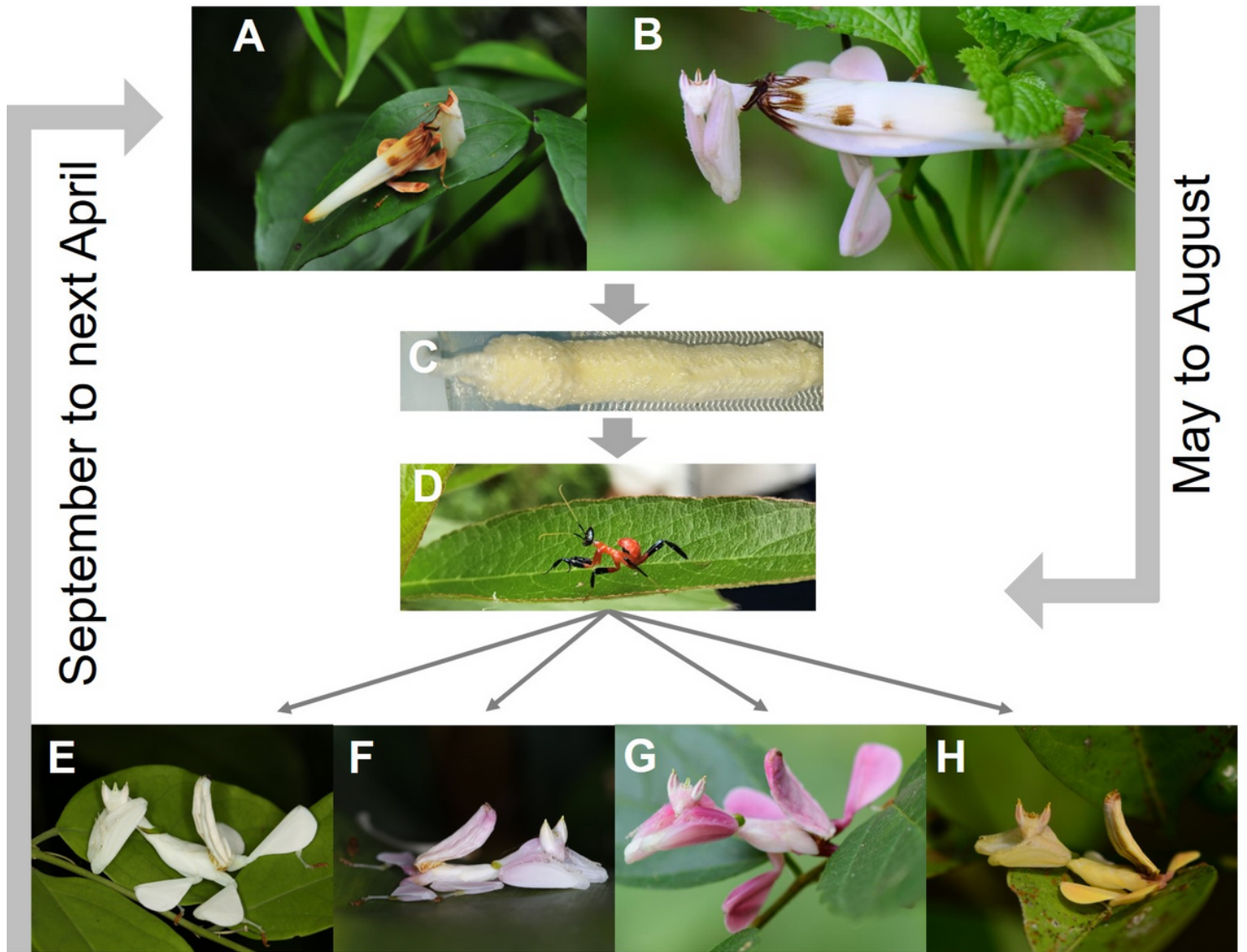
Supplementary Material

Supplementary material, Video 1 is not available with this version

Figures

Figure 1

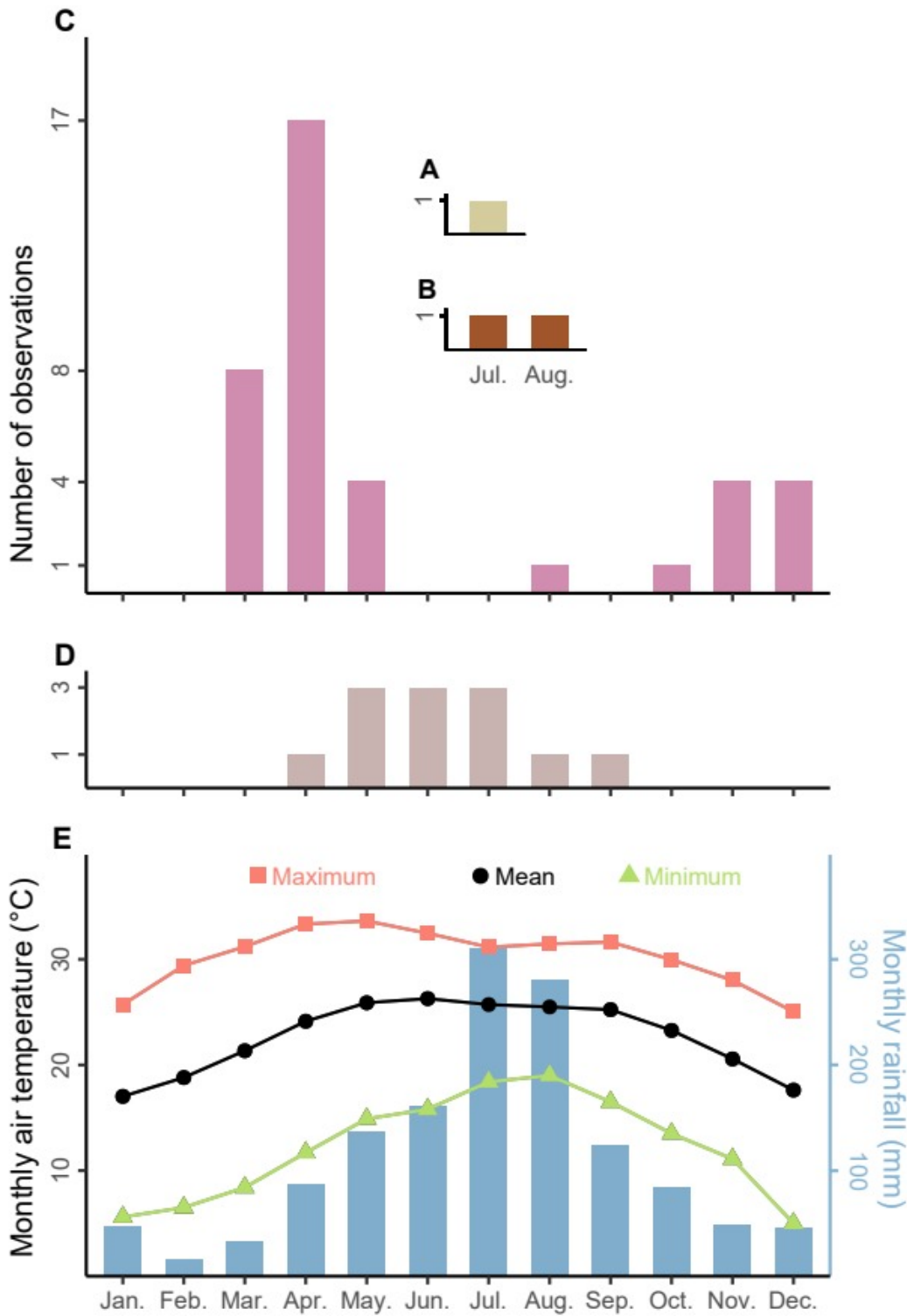Legend not included with this version.

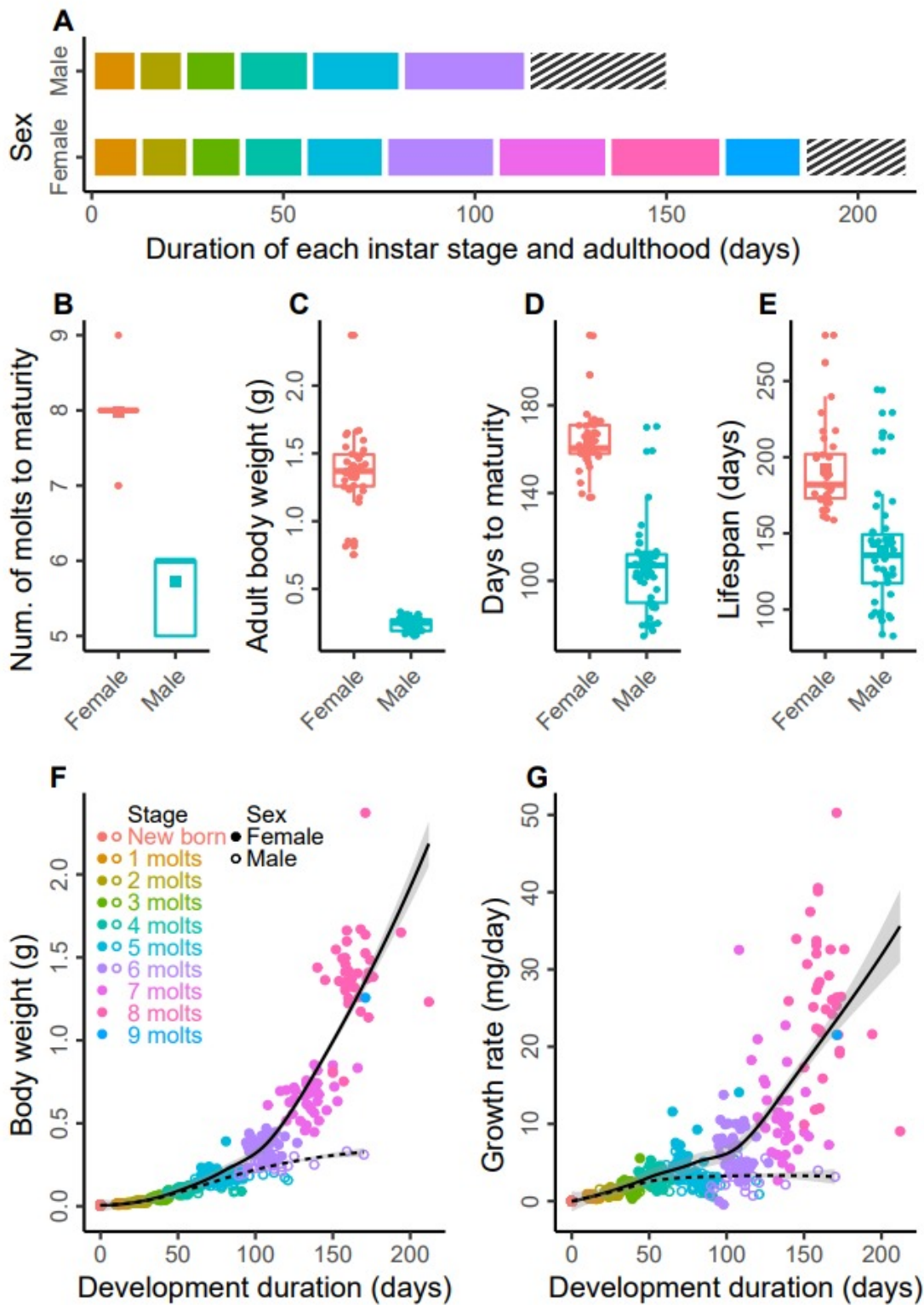**Figure 2**

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Figure 3

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