

Research articleSubmitted: December 21st, 2018 - Accepted: April 20th, 2019 - Published: May 31st, 2019**Rhythmic abdominal pumping movements in praying Mantises
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Greg M. PRETE¹, Bart van ALPHEN³, Gavin J. SVENSON⁴¹ Department of Biology, Northeastern Illinois University - 5500 N. St. Louis Ave, Chicago, IL 60625, USA - fprete@neiu.edu² Department of Biology, Northeastern Illinois University - 5500 N. St. Louis Ave, Chicago, IL 60625, USA - a-schirmer@neiu.edu³ Department of Neurobiology, Northwestern University - Hogan 2-160, 2205 Tech Drive Evanston, IL 60208, USA - bart.alphen@northwestern.edu⁴ Cleveland Museum of Natural History - 1 Wade Oval Drive, Cleveland OH 44106, USA - gsvenson@cmnh.org

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Abstract

We analyzed the rhythmic, cyclical dorsal-ventral abdominal pumping movements of nymphal and adult *Hierodula patellifera* (Audinet-Serville 1839), and adult *Stagmomantis carolina* (Johansson 1763), *Tenodera sinensis* (de Saussure 1871), *Miomantis paykullii* (Stål 1871), and *Sphodromantis lineola* (Burmeister 1838) using a combination of customized video analysis software and frame-by-frame video analyses. Despite the phylogenetic and ecological diversity of these species, we found fundamental similarities in the overall, intermittent patterns of their abdominal pumping movements. In adults of all species, intermittent bouts of abdominal pumping had median durations of 64-89 sec, and were separated by intervals with median durations of 10-25 sec. Bouts began with rhythmic upward abdominal deflections of progressively increasing amplitude and frequency which were superimposed on an overall, progressive abdominal elevation. Bouts ended with 1-4 very high amplitude, low frequency upward deflections after which the abdomen returned to its horizontal (resting) position. In *H. patellifera*, the overall adult pattern emerged gradually during larval development. Given the diversity of the species tested, our data suggest that intermittent abdominal pumping (which has been associated with respiratory behavior in insects) may be independent of ecological niche or acute environmental stressors in mantises. Instead, our data support the hypothesis that these apparently respiratory related, intermittent abdominal pumping movements are an emergent property of the mantis central nervous system organization.

Key words: Mantodea, praying mantis, insect breathing, respiration.**Introduction**

Rhythmic physiological activity patterns underpin the systematic regulation of behaviors in animals across levels of analysis from individual cells to whole organisms. These patterns can be windows into the ways in which the underlying control mechanisms operate. Rhythmic respiratory-related behaviors are particularly intriguing, especially in insects wherein they are both more complicated and more temporally varied than in vertebrates. For instance, in insects, respiratory-related behaviors (and resultant gas exchange rates) may be continuous, discontinuous, or episodic, and may be inconsistently so both within and across individuals and species.

Respiration in insects includes both passive gas diffusion and active convective ventilation (Jögar et al. 2011; Käfer 2013; Lighton 1996; Terblanche et al. 2008). The sites of gas exchange are the walls of the smallest branches of a dense, labyrinthine network of tracheal tubes that ram-

ify body wide. Gases enter and leave this network through the distal ends of the main tracheal trunks via valve openings (*i.e.*, spiracles) on the sides of the insect's thorax and abdomen. Under varying circumstances, these muscular valves may be held open, closed, or rapidly flutter thereby modulating the potential rate of gas exchange. In addition to varying the pattern of spiracle valve activity, insects can indirectly affect gas exchange rates by active thoracic or abdominal pumping movements. These movements change hemolymph pressure (Harrison 1997; Miller 1971), and compress trachea, which forces bulk gas flow (Socha 2008). However, the precise relationship between spiracle valve position, abdominal pumping movements, and gas exchange, *sensu stricto*, remains unclear.

Understandably, both spiracle valve activity and abdominal pumping were originally thought to function exclusively as gas exchange mechanisms (*e.g.*, Heller 1930; Punt et al. 1957; Wilkins 1960). This led to the intriguing hypothesis that irregular spiracle opening and closing, and

the periodic cessation of abdominal pumping create discontinuous gas exchange cycles (DGC's) which evolved to reduce respiratory water loss (e.g., Chown 2002; Kestler 1985; Lighton 1994; Schneiderman & Schechter 1966). More recently, several other hypotheses have been suggested to explain DGC's. These include optimizing gas exchange in hypoxic and hypercapnic environments, minimizing oxidative damage, responding to O₂ and CO₂ set points, and protection from parasites (reviewed in Chown et al. 2006). However, Matthews & White (2011) have pointed out that DGC's are not ubiquitous among insects, and have apparently evolved independently five times among diverse insect groups (Marais et al. 2005). More importantly, they argue that the range of niches in which insects live, the irregularity of short-term intra-niche variability, and the diversity of insect life histories suggest that a single adaptive explanation for the existence of DGC's may be unidentifiable (Chown 2002). Instead, Matthews & White (2011) argue that the variability in insect respiratory related behaviors (across species and within individuals) is actually neuronal in origin, and independent of gas exchange mechanisms, *per se*. Specifically, they suggest that DGC's are an emergent property of a circadian, developmental, or experimentally induced diminution of brain activity which leads to the withdrawal of an overriding, continuous cephalic pattern generator. This withdrawal relinquishes control over abdominal pumping to a discontinuous, lower-level (thoracic/abdominal) pattern generator. Interestingly, there is some correlational evidence that the plasticity of cephalic control over abdominal pumping is a capacity of complex insect brains with large mushroom bodies and a large central complex such as exist in the Blattodea (sister group to the Mantodea), and some Mantodea, respectively (F.R. Prete, unpublished data; Rosner et al. 2017; Matthews & White 2011).

The failure of any one model to emerge as a satisfactory explanation for the irregularity of insect respiration across all groups in which it has been documented may also be due (at least in part) to the fact that abdominal pumping has functions beyond those of respiration. For instance, Sláma (1994, 1999, 2000) and Tartes (2002) have argued, respectively, that the function of abdominal pumping –the so-called coelopulse– is to increase hemolymph pressure (enhancing circulation), to initiate heart activity, or to control circulation during histolysis. However, as Tartes (2002) points out, the mechanisms by which respiration, circulation and abdominal pumping movements are coordinated, or the precise functional relationships between them remain largely unclear.

As part of a larger ongoing research program examining the control of behavior patterns in mantises (e.g., Prete et al. 2011, 2012, 2013a,b; Schirmer et al. 2014), we sought to describe the patterns of rhythmic abdominal

pumping movements in several species of praying mantis (Insecta: Mantodea). Only a limited number of studies have undertaken a thorough analysis of the topology or kinematics of abdominal movements in insects (e.g., Coquillaud 1990; Harrison et al. 2015; Heinrich 2013; Käfer 2013; Sláma 1986, 1991, 2010; Socha 2008; Tartes et al. 2002). In addition, of those that have, many have focused on the pupae of holometabolous insects; there is little information on hemimetabolous species. In the current study we utilized a custom MatLab® video analysis program and frame-by-frame video analyses to describe the rhythmic abdominal pumping movements of nymphal and adult *Hierodula patellifera* (Audinet-Serville 1839), and adult *Stagmomantis carolina* (Johansson, 1763)¹, *Tenodera sinensis* (de Saussure 1871), *Miomantis paykullii* (Stål, 1871), and *Sphodromantis lineola* (Burmeister, 1838).

Methods

Mantises

Five species of praying mantis were treated in this study, as representatives of Neotropical, Afrotropical, and Indomalayan lineages (Svenson & Whiting 2009). Three of these species, *Hierodula patellifera*, *Tenodera sinensis*, and *Sphodromantis lineola*, are included in the morphologically heterogeneous family, Mantidae (Ehrmann 2002). Most species within this family have a generalist mantid appearance, which is true for the three we have studied (Wieland & Svenson 2018). However, they do differ in their ecological characteristics. Species of *Tenodera* range throughout Africa, Asia, and Australia and reside in a broad array of climate and vegetative conditions. *Tenodera sinensis* originates from temperate to semi-tropical regions of Eastern Asia and was introduced into North America in 1896 (Blatchley 1920). *Tenodera sinensis* appears to prefer open meadows and forest margins with either dense grass or mixed vegetation. *Hierodula patellifera* ranges across Southern Asia into the Southeast Asian islands (Ehrmann 2002). Species within the genus are found often in moist forest and marginal habitats with mixed vegetation. *Sphodromantis lineola* ranges across most of sub-Saharan Africa in moist to dry forest types in mixed vegetation. Both *H. patellifera* and *S. lineola* perch on or within dense vegetation on low, marginal plants, but they are often found high in trees among leafy branches. All three of these species are thought to be ambush predators that take advantage of a wide array of suitable prey that includes insects and sometimes vertebrates (Nyffeler et al. 2017; Prete & Wolfe 1992). The three species have also been observed in different color morphs that range from green to brown and can include a dull yellow. Females are much larger by weight and slightly larger in length than conspecific males.

¹ Johansson, B., 1763. Centuria Insectorum Rariorum, doi: <https://doi.org/10.5962/bhl.title.10429>

Like most mantises, females appear to live a more sedentary lifestyle while males move through the environment searching for female mates (Svenson et al. 2016).

Stagmomantis carolina is a Neotropical Mantidae, but allied within a lineage that diverged from Old World Mantidae around 53 million years ago (Svenson & Whiting 2009). *Stagmomantis carolina* ranges from Central America north into the United States (Ehrmann 2002). The species appears to be cold limited in its northerly range, but the species is commonly found in Pennsylvania and Ohio. Females are stouter in build, and have reduced wings that limit flight capabilities. Like the other three Mantidae species in this study, *S. carolina* has different color morphs that range from green to brown, but yellow is typically not observed. The species lives in mixed vegetation in meadows and forest margins and appears to be an ambush predator.

Miomantis paykullii is the most distantly related species included in the study. It is included within the subfamily Miomantinae, which has historically been included within Mantidae (Ehrmann 2002). However, the subfamily is an ancient lineage with Cretaceous origins at around 80 million years ago and is not allied with other Mantidae or any other family (Svenson & Whiting 2009). *Miomantis paykullii* ranges across Africa and is found in arid to semi-arid habitats. The species can be found in a diversity of vegetation and habitat types that include mixed vegetation open habitat, grasslands, and forest margins. Males and females are sexually dimorphic with females being stouter with slightly reduced wings. Like other Miomantinae species, *M. paykullii* is most likely an ambush or semi-active predator.

Species size measurements are as follows:

- *Tenodera sinensis* female 76-85 mm, male 83 mm;
- *Hierodula patellifera* female 53-70 mm, male 56 mm;
- *Sphodromantis lineola* female 60-79 mm, male 60-65 mm;
- *Miomantis paykullii* female 36-39 mm, male 37 mm;
- *Stagmomantis carolina* female 60 mm, male 53 mm (Giglio-Tos 1927).

All mantises were lab reared with the exception of *Tenodera*, which were wild caught near Northeastern Illinois University (N 41° 58' 48.76", W 87° 43' 7.67"). Lab reared nymphs were group housed through the third instar in a humidified chamber as described in (Prete & Mahaffey 1993). Thereafter, mantises were maintained in individual plastic containers within an enclosure under a 12:12 light/dark cycle at temperatures between 20 (dark phase) and 35° C (light phase) as described previously (e.g., Prete et al. 2013a, b). Mantises were fed *Drosophila melanogaster* or size appropriate *Acheta domesticus*.

Video Analysis of Abdominal Movement

Mantises were anesthetized by brief exposure to CO₂ after which the wings were removed. The appendages were

gently folded against the prothorax and wrapped loosely with plastic film such that abdominal movements were not hindered. The wrapped mantises were affixed to an armature with a band of tape around the prothorax such that their entire abdomen overhung the end of the armature, which allowed free movement of the abdomen in all directions. The armature was placed within a light tight chamber (41x41x38 cm) under constant light conditions (45 lux), 7.5-10 cm in front of a Sabrent USB 2.0 web-camera (Sabrent Inc. Los Angeles, USA). The mantis was positioned such that longitudinal axis of its abdomen was parallel to the plane of the camera lens. Recordings of abdominal movements lasted 2-72 hours after a two-hour habituation period.

Abdominal movements were recorded using a custom-made image analysis program, written in MatLab (The MathWorks, MA USA). The software program used a luminance threshold function to invert the image of the mantis' abdomen such that it appeared as a white image against a black background. Pixels representing the abdomen were replaced by a minimum ellipse using the "region props" function, which is part of MatLab's Image Processing module. This process created and stored size, location, and angular change values, which were both graphed and stored for further analysis in real time. Both MatLab® and subsequent off-line computer-generated graphs were visually verified against the original recordings.

From these data, we derived the following dependent measures: (i, ii) bout and phase durations, (iii, iv) interbout and inter-deflection intervals (IBI, IDI), (v, vi) overall change in abdominal elevation during each phase and bout. Bouts were defined as a series of abdominal movements that began with an initial deflection of greater than 1 degree and ended with a period of quiescence lasting at least four seconds.

Across species, bouts of repetitive dorsal deflections, or abdominal pumping (AP) movements fell into three distinct phases. During Phase 1, the abdomen began to display a series of low amplitude, irregularly spaced deflections that were variable in both amplitude and temporal spacing. The transition to Phase 2 was marked by a dramatic increase in deflection amplitude and frequency, which were superimposed on a gradual overall abdomen elevation. Phase 3 was characterized by a few very high amplitude/low frequency deflections immediately followed by abdomen relaxation, return to horizontal, and immobility. In quiescent animals this three-phased pattern of abdominal pumping persisted. Interbout intervals were the times between the end of phase 3 and the beginning of the subsequent phase 1. Inter-deflection intervals are defined as the time between the end of the falling phase of one deflection and the beginning of the rising peak of the subsequent deflection. Changes in elevation were calculated by the difference between the initial and the final angle of the major axis of the abdominal ellipse. The same procedures were used to collect and analyze the abdominal movements of

H. patellifera instars 3, 5, 7, and 9. The only exception was that the armature holding the mantis was placed 5-7.5 cm from the camera lens, and recording periods ranged from 4-24 hrs.

All statistical analyses were done using Data Desk® (Data Description, Ithaca, NY, USA).

Results

Hierodula patellifera Adults

We divided the overall pattern of abdominal movements into four periods, one quiescent, and three distinct phases of repetitive, upward abdominal deflections, which we termed “abdominal pumping” (AP). We defined the three AP phases as constituting one “bout” of AP behavior, and the intervening periods of quiescence (during which the abdomen remained stationary and horizontal) as interbout intervals (IBI).

Graphs depicting upward angular deflections of the abdomen (from horizontal) during representative AP bouts in an adult male and female *H. patellifera* are shown in Figure 1. In general, during Phase 1, the abdomen began to display a series of relatively low amplitude irregularly spaced upward deflections that were quite variable in both degree and temporal spacing, and ended with the abdomen returning to its original position (arrow a-b). As Phase 1 transitioned into Phase 2, abdominal deflections increased in amplitude and frequency, and became more regular. In addition, during Phase 2, the individual upward deflections were superimposed on a gradual overall elevation of the abdomen (arrow c). Phase 3 (after arrow d) consisted of several very high amplitude low frequency deflections (up to 18.5 deg from trough to peak), after which the abdomen relaxed back to its original horizontal position (quiescence). In the absence of any other spontaneous activity, this overall pattern remained consistent during recording periods lasting up to 72 hours.

We did a detailed analysis of 88 randomly selected bouts recorded in nine *H. patellifera* (five females and four males; 7-12 bouts per individual). Although the overall AP patterns were similar across mantises, bout durations varied significantly between individuals within sex (as documented in a variety of other insects, Marais et al. 2005) ($F_{(3-4)} \geq 11.53$, $p \leq 0.0001$). Overall, male bouts tended to be longer than females’ but not significantly so; Median male bout lengths ranged from 86.7-207.7 secs; female bouts ranged from 40.2-104.6 secs (see Table 1 for all species). Likewise, IBIs varied significantly within sex ($F_{(3-4)} \geq 5.18$, $p \leq 0.0016$), and tended to be longer in males; median IBIs ranged from 31.1-94.2 secs in males, and 24.4-33.6 secs in females.

Of the three AP phases, Phase 1 was the most variable both within and between individuals. Phase 1 included a series of 2-16 irregularly spaced, low amplitude (<10 deg, median = 1 deg), deflections some of which were separated by intervals lasting as long as 70 secs. With the exception of two (out of 88) bouts, the median Phase 1 duration ranged from 12-63secs in males, and 16-40 secs in females. The number of deflections and durations of Phase 1 differed significantly both between ($F_{(1)} \geq 5.88$, $p \leq 0.0174$), and within sexes ($F_{(3-4)} \geq 2.80$, $p \leq 0.0376$). Subjectively, Phase 1 deflections appeared to be artificial and functionally distinct from the more consistent series of abdominal deflections seen in Phases 2 and 3.

As noted, Phase 2 consisted of regularly spaced AP movements superimposed on an overall progressive abdominal elevation. The median Phase 2 duration ranged from 4-11 secs, and 3-15 secs in males and females, respectively. Again, there were significant differences in total phase durations between sexes ($F_{(1)} \geq 75.45$, $p \leq 0.0001$), and within females ($F_{(3)} \geq 15.36$, $p \leq 0.0001$), but not within males.

The median number of deflections ranged from 8-22, and 7-10 in males and females, respectively, and differed significantly between ($F_{(1)} \geq 27.86$, $p \leq 0.0001$) and within

Table 1 – Characteristics of abdominal pumping in *H. patellifera* nymphs.

	Instar 3 (n=4)	Instar 5 (n=2)	Instar 7 (n=5)	Instar 9 (n=2)	Adults
Parameters Measured (n = 25 bouts)	Median (min-max)	Median (min-max)	Median (min-max)	Median (min-max)	Median (min-max)
Number of abdominal deflections	18 (9-36)	21 (11-33)	24 (11-40)	24 (11-43)	13 (8-46)
Overall elevation change (deg)	6.5 (3.8-20.9)	6.5 (2.5-10.2)	10.1 (0.2-47.9)	21.3 (14.1-34.7)	17.2 (1.8-30.1)
Bout duration (sec)	92.2 (19.2-150.2)	108.9 (52.4-201.5)	104.8 (55.1-221.4)	105.6 (41.2-278.4)	111.0 (15.5-252.7)
Inter-bout interval (sec)	133.3 (15.8-253.2)	55 (23.4-98.4)	79.3 (17.3-210.0)	99.3 (10.5-253.3)	37.1 (6.1-132.0)

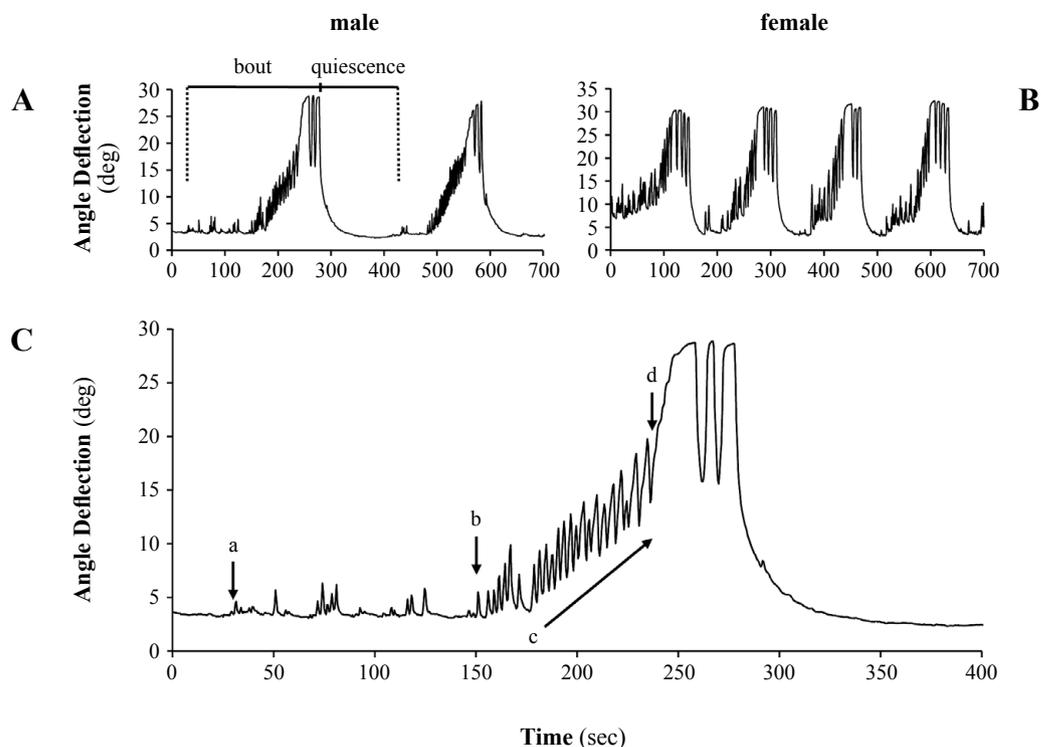


Fig. 1 – Representative angular deflections of the longitudinal abdominal axis during bouts of abdominal pumping (AP) in male (**A**) and female (**B**) *H. patellifera*. **C**, an expanded view of a single AP bout in a male *H. patellifera*. Bouts began with a series of very low amplitude irregularly spaced upward deflections indicated by arrow a. These were followed by a series of deflections higher in amplitude and frequency (arrow b) that were superimposed on a progressive overall abdominal elevation (arrow c). The final phase of each bout consisted of 1-5 very high amplitude, low frequency upward deflections (arrow d). These were followed by relaxation of the abdomen to its original horizontal position (labeled quiescence in A).

sexes ($F_{(3-4)} \geq 2.98$, $p \leq 0.0289$). The median overall abdominal elevation during Phase 2 ranged from 6-11 degs in males, and 3-15 degs in females. There were no between sex differences in this measure; however, there were differences between individuals within sexes ($F_{(3-4)} \geq 34.59$, $p \leq 0.0001$). Phase 2 deflections occurred in rapid succession, so much so that measurable inter-deflection intervals occurred only 13 times in 939 deflections, and these were confined to just 9 out of the 88 bouts analyzed (e.g., asterisk in Fig. 1C).

Phase 3 was characterized by several relatively dramatic, regularly spaced, high amplitude deflections. The median Phase 3 durations ranged from 32.3-94.9 secs in males and 7.6-46.0 secs in females. Durations were significantly different between ($F_{(1)} \geq 23.03$, $p \leq 0.0001$), and within sexes ($F_{(3-4)} \geq 16.33$, $p \leq 0.0001$). The median number of deflections ranged from 3-9 and 1-4 in males and females, respectively. Again, there were significant differences in the number of deflections between sexes ($F_{(1)} \geq 13.17$, $p \leq 0.0005$), and within males ($F_{(3)} \geq 18.39$, $p \leq 0.0001$), but not within females. There were also significant differences in deflection amplitude between individuals within sex ($F_{(3-4)} \geq 25.36$, $p \leq 0.0001$), but not between sexes. As in Phase 2, Phase 3 inter-deflections intervals were rare occurring in only 3 out of 369 Phase 3 deflections and these

occurred in only two of the 88 bouts analyzed. These intervals lasted 2 secs or less.

Hierodula patellifera Nymphs: Stadia 3, 5, 7, 9

We analyzed the pattern of AP in 13 nymphs (2-5 in each of stadia 3, 5, 7, and 9). Each mantis was recorded for a period of 4-24 hrs. As with adults, abdominal deflections were clustered into discrete bouts separated by periods of relative inactivity. Twenty-five randomly selected bouts were analyzed in detail for each of the stadia. Typical bouts are depicted in Figure 2 (also see Table 2). Overall, the median number of abdominal deflections per bout remained consistent across instars (median range = 18-24), as did bout durations (median range = 92.2-105.6 secs). Interbout intervals were variable but not significantly different between instars (median range = 55-133.3 secs), however were significantly longer in nymphs than in adults ($U = 23$, $n_1 = 9$, $n_2 = 13$, $p = 0.017$).

Interestingly, in the youngest (third instar) nymphs, AP was not superimposed on abdominal elevation, and there was no clear distinction between Phases 2 and 3 (Fig. 2; Table 1). Adult-like abdominal elevations emerged gradually beginning with the fifth instar mantises (median = 7 deg). These increased over time to a median of 21 deg in

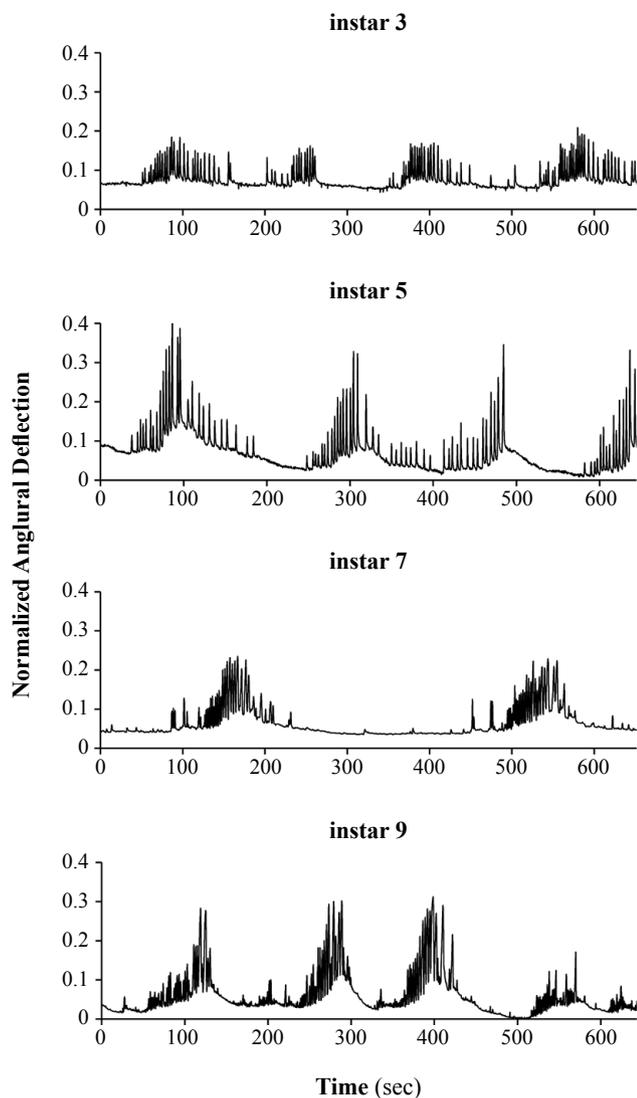


Fig. 2 – Representative angular deflections of the longitudinal abdominal axis during AP bouts in *H. patellifera* instars 3, 5, 7, and 9. In instar 3, AP bouts were more irregular than in adults. The adult-like pattern of deflections superimposed on an overall, gradual abdominal elevation emerged in instar 5. The adult-like pattern is clear in instar 9.

the ninth instar. Intermittent, high amplitude, low frequency deflections at the end of AP bouts (similar to those seen in adults) began to appear in the seventh and ninth instar mantises. However, these were neither as consistent nor as closely spaced as in adults.

Other species

We analyzed a total of 10-12 AP bouts in one adult female of each of three additional species, *Stagmomantis carolina*, *Tenodera sinensis*, and *Miomantis paykullii*. In general, the overall patterns of AP deflections were similar in these species and consistent with that seen in *H. patellifera* (Fig. 3; Table 1). That is, a period of sporadic, low amplitude deflections (Phase 1) was followed by a series of

higher amplitude and higher frequency deflections superimposed on a progressive abdominal elevation (*i.e.*, Phase 2). As in *H. patellifera*, this was followed by a smaller number of high amplitude, low frequency deflections (*i.e.*, Phase 3).

The only notable difference between these species was the relative infrequency and/or brevity of interbout intervals in *M. paykullii*, the smallest of the three mantises. In this species, IBI occurred between only 48 of the 100 recorded AP bouts (Fig. 3C).

Minimum AP bout durations were similar across all three species (overall range = 43.7-53 secs), but maximum bout durations varied widely (79.2-136.4 secs). Mean bout durations were significantly longer in *T. sinensis* than the smaller *S. carolina* and *M. paykullii* ($t > 3.71$, $p < 0.002$). It is noteworthy that the median numbers of deflections per bout were similar across all four species tested.

Finally, we did an empirical frame-by-frame video analysis of the AP deflections of five female *Sphodromantis lineola*. Four mantises were recorded for one hour and one for 30 min. In the analyses, we recorded the times at which each upward abdominal deflection began and ended. The end time of the upward deflection marked the beginning time of the subsequent downward abdomen movement.

Representative results from two animals are depicted in Figure 4. The filled circles indicate the duration of the contraction phase (upward abdominal movement; right axis) of each deflection. The open circles indicate the duration of each subsequent abdominal relaxation plus the interval between periods of muscular contraction (*i.e.*, the inter-contraction interval; left axis). As in the other species, *S. lineola*'s AP behavior occurred in episodic bouts, which ranged from 55.9 to 564.9 secs, and were followed by IBI's lasting 2.3 to 97.8 secs.

As with the other species examined, the repetitive cycles of AP movements occurred in discrete bouts. The first three quartiles of each bout consisted of a series of contraction/relaxation cycles during which the contraction phases (filled circles Fig. 4) were relatively shorter and more consistent than the subsequent relaxation phases (open circles). During this period, contraction durations ranged from 0.14-1.79 secs. The subsequent inter-contraction intervals ranged from 0.41-6.3 secs. In some bouts, the inter-contraction intervals appeared to be greatest at bout mid-point, giving those data the appearance of curvilinearity. However, this was not consistent within or across animals and we believe it to be artifactual in these data.

During the final quartile of each bout, abdominal contraction durations progressively increased as indicated by the inflexion point in the linear models (filled squares in Fig. 4B; range = 11.5-106.3 secs). As durations increased, the intervening relaxation intervals decreased, again, as indicated by the intersection of the linear models in Figure 4D (filled squares; overall $F_{(1, 413)} = 14.3$, $p = 0.0002$). As in all other mantises tested, each bout ended with 1-4 very long contractions that lasted 1.3-38.7 secs.

Table 2 – Characteristics of abdominal pumping in four species of mantis (females).

		<i>Hierodula</i>	<i>Stagmomantis</i>	<i>Tenodera</i>	<i>Miomantis</i>
Parameters Measured		Median (min-max)	Median (min-max)	Median (min-max)	Median (min-max)
Entire Bout	Bout duration (sec)	67.2 (15.5-252.7)	63.9 (43.7-79.2)	88.4 (53.0-136.4)	64.9 (50.4-80.8)
	Number of deflections	18.0 (8.0-28.0)	19.0 (16.0-22.0)	17.0 (13.0-25.0)	12.0 (8.0-16.0)
	Inter-bout interval	24.7 (6.1-72.9)	36.3 (11.6-54.9)	27.6 (10.6-92.7)	9.7 (5.3-79.5)
Phase 1	Phase duration (sec)	25.3 (3.8-146.4)	26.2 (14.0-45.8)	41.9 (16.3-71.5)	NA
	Number of deflections	6.0 (2.0-16.0)	9.0 (5.0-13.0)	6.0 (3.0-11.0)	NA
Phase 2	Phase duration (sec)	20.6 (5.5-43.6)	20.2 (14.0-25.2)	24.9 (17.2-40.8)	38.2 (17.2-52.6)
	Number of deflections	8.0 (5.0-14.0)	7.0 (6.0-11.0)	8.5 (6.0-13.0)	8.0 (4.0-13.0)
Phase 3	Phase duration (sec)	20.4 (4.4-75.4)	17.7 (4.1-24.3)	23.7 (11.0-37.1)	29.4 (20.8-40.2)
	Number of deflections	3.0 (1.0-9.0)	3.0 (2.0-4.0)	3.0 (2.0-4.0)	3.5 (2.0-5.0)

Discussion

Our data on the abdominal pumping (AP) behavior of five species of mantises are consistent with those collected on a wide variety of other insects including one study that examined partial gas pressure fluctuations during respiration in the mantis *Sphodromantis gastrica* (Marais et al. 2005). In addition, our data indicate that simple discontinuous AP movements are evident in the early nymphal stages of the species, *H. patellifera* but that the more complex, adult-like AP movement pattern emerges gradually during early development. We also found that although the overall AP movement pattern is similar across all mantises tested, the details and timing of the pattern varies within and across both species and sexes. This, too, is consistent with data collected on a variety of other insects (e.g., Marais et al. 2005).

As noted, a number of plausible hypotheses for the evolution of discontinuous respiration in insects have been suggested. These include some that are related to ecological niche (e.g., gas exchange optimization in stressful environments, prevention of water loss in arid environments, or parasite avoidance), and others that are strictly physiological (e.g., responding to differing partial gas pressure set points, modulating hemolymph pressure or heart rate). In individual cases and for specific species, one or more of these functional outcomes of discontinuous respiration

may occur. However, we wish to distinguish between a functional outcome of, and the putative reason for a behavior's existence. That is, a behavior may arise as an emergent property of the serendipitous (but genetically orchestrated) organization of a central nervous system. Should that behavior (e.g., discontinuous breathing) confer a selective advantage to a particular species in a particular ecological niche (e.g., prevention of water loss, or optimizing gas exchange under hypoxic conditions), it will be selected for within the population. Similarly, if the behavior interfaces with other existing physiological systems (e.g., is consistent with the cellular mechanisms that give rise to 'set-points'), it may confer a selective advantage and increase in prevalence within the breeding group. Hence, there may be no specific reason for the behavior's emergence but there may be a number of distinct (and advantageous) functional outcomes of the behavior once it does emerge. In this case, the outcomes may affect both respiratory and non-respiratory behaviors as suggested by Sláma (1994, 1999, 2000) and Tartes (2002). This line of reasoning is also consistent with that of Matthews & White (2011) and Marais et al. (2005).

Further, given the degree of phylogenetic separation and differences in ecological niches of the species examined, in conjunction with the overall similarities in their respiratory-related AP patterns, we agree with Chown (2002) that inter- and intra-niche variability argues against

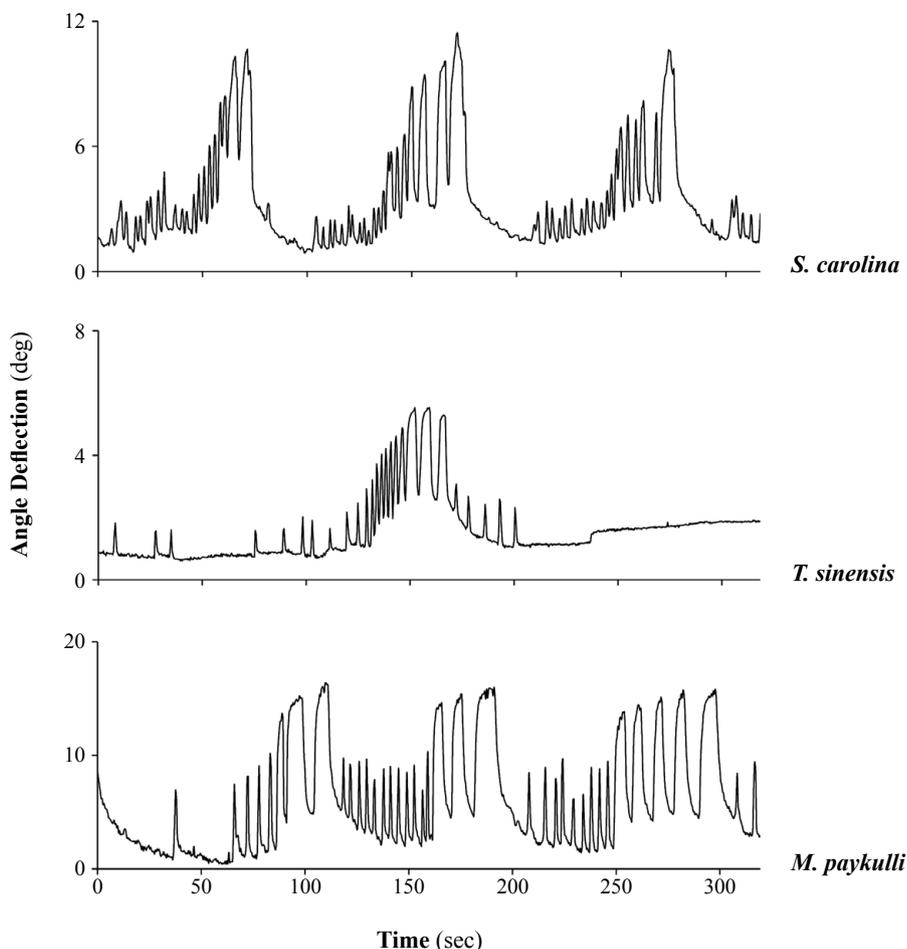


Fig. 3 – Representative angular deflections during AP bouts in three ecologically and morphologically diverse species of mantis. In all three species, AP bouts showed similar kinematic characteristics. Each bout began with a period of irregular, variable deflections. These were followed by a series of larger, higher frequency deflections that were associated with an overall abdominal elevation in *S. carolina* and *T. sinensis*. An overall abdominal elevation was less evident in the smallest mantis, *M. paykullii*. In all three species, bouts ended with 1-5 very high amplitude, low frequency upward deflections after which the abdomen returning to its horizontal resting position. The most noteworthy difference between the species was the comparatively short duration of the interbout intervals in *M. paykullii* (i.e. a median of 10 sec vs. 28-36 sec in the other two species).

a single adaptive explanation for discontinuous breathing even with the group Mantodea. Considering the deep phylogenetic separation between *M. paykullii*, *S. carolina*, and the three Old World Mantidae species (Svenson & Whiting 2009), the respiratory-related AP patterns must have been established early in mantodean evolution and have been maintained, at a minimum, for 80 million years. Although the five species tested are not extreme versions of the diversity Mantodea has to offer, they do differ in sexual dimorphism, overall body size, geographic range, and niche specialization. Therefore, recent ecological and morphological specialization appears to be independent of respiratory-related AP patterns. This level of functional constraint across different lineages suggests the respiratory-related AP patterns are symplesiomorphic for Mantidae plus Miomantinae. This pushes the origin of this characteristic to the Late Cretaceous (apx. 80 million years ago) and could possibly extend deeper into the ancestry of Man-

todea, which would indicate that other, more distantly related groups might also exhibit similar patterns.

Four of the species tested are tropical in distribution while *T. sinensis* is one of the most northerly distributed species in the world, consistently dealing with cool temperatures typical of temperate environments. Of the four tropical species, each is capable of occupying a broad array of habitats, but *M. paykullii* and *S. lineola* range into drier habitats than do *S. carolina* and *H. patellifera*. Testing species that range from temperate to tropical dry to tropical moist habitats should capture AP patterns that differ if they were adapted to specific environmental conditions. Perhaps expanding this study to include extremely specialized species (in habitat and/or morphological specialization) would be the ultimate test for the origins of these patterns, whether they are ancestrally derived or adapted more recently in association with niche specialization. It may be the case that the species we tested were

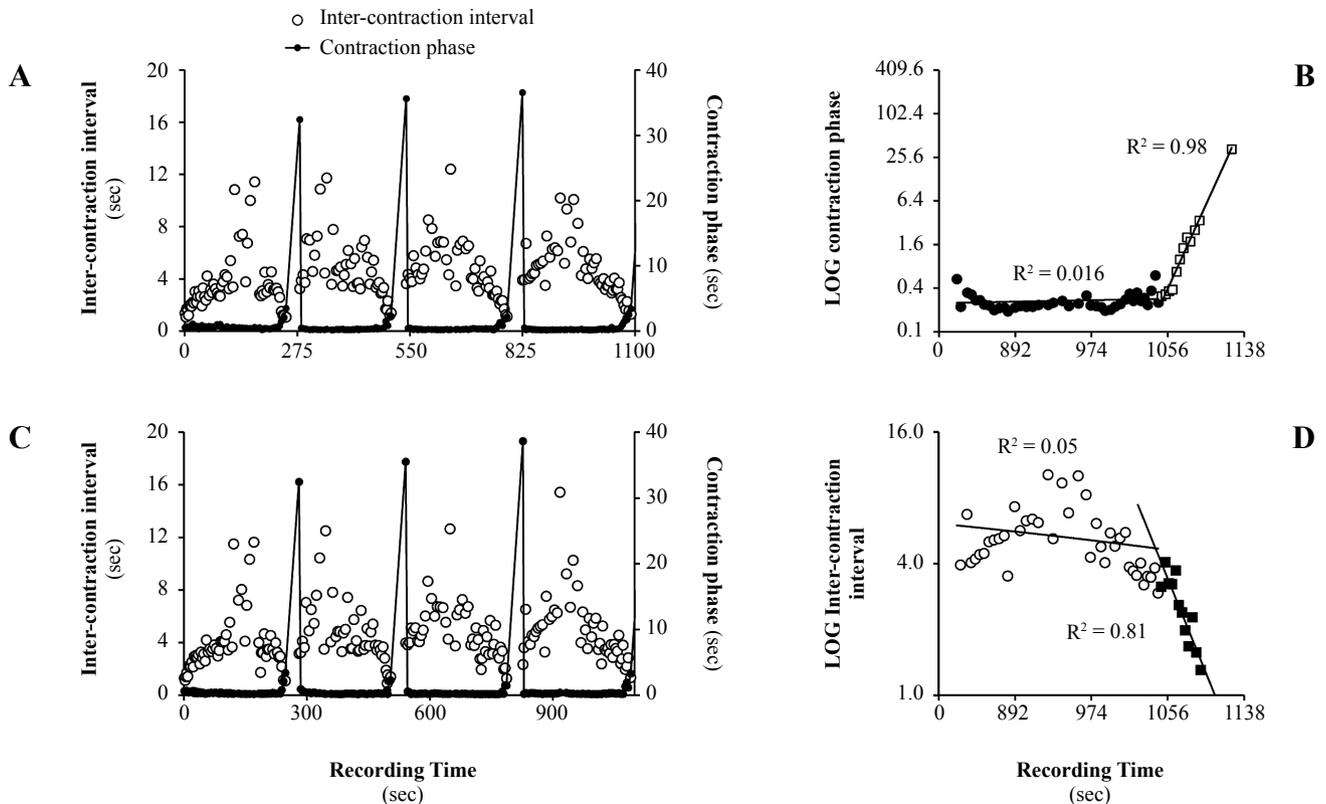


Fig. 4 – A, C, filled circles indicate durations of the contraction phases (upward abdominal deflections; right axis), and open circles indicate the inter-contraction intervals during typical AP bouts in adult, female *S. lineola*. Inter-contraction intervals include the abdominal relaxation phase (lowering of the abdomen) plus the intervening time until the next upward deflection began. During the final quartile of each bout, the contraction duration progressively increased, and ended in a sustained contraction that could last up to 39 sec. **B**, The log of the durations of contraction phases from a single AP cycle. Note the sharp change in contraction durations as the cycle progresses. In contrast, note the opposite trend in the log of the inter-contraction intervals (**C**) which decreased sharply as the former increased.

too versatile in their ability to occupy a relatively broader range of habitats and environmental conditions. More answers could come from testing a species from a narrow niche specialization.

Our findings that *H. patellifera* nymphs display discontinuous AP and that the adult pattern emerges over development is consistent with Matthews & White's (2011) hypothesis that insect respiratory related behaviors are neuronal in origin and an emergent property of central nervous system organization. We most strongly agree with this explanatory model for discontinuous breathing. In addition, the fact that the within bout complexity of AP patterns increases during development suggests that it is independent of ecology. However, it may also be the case that nymphs do not need to generate the complex adult AP pattern because of differences in their metabolic requirements compared to adults. Analogous size related metabolic differences may also account for the shorter interbout intervals seen in *M. paykullii* compared to the larger species examined. Similarly, metabolic factors or morphological differences may also account for the sex differences in AP patterns. However, our data do not specifically address any of these issues. On the other hand, the fact that AP patterns

were stable in tethered mantises over 72 hour recording periods suggests that they are not modulated in a circadian manner as are some physiological process and behaviors in mantises (Schirmer et al. 2014). This long-term stability also suggests that AP patterns are not a product of, for instance, high activity level or acute stress. Further, if AP behavior was linked to energy expenditure rates, one might expect AP bout length or patterning to change over a 72 hour period.

It is well documented that insect behavior is hierarchically organized as suggested by Matthews & White (2011) for respiratory behaviors. Even so-called 'innate' behaviors can be modulated neuronally in response to environmental cues, metabolic demands, or physiological states (e.g., Bidaye et al. 2018; Kim et al. 2017; Prete et al. 2013a, b; Ritzmann & Zill 2017). Such hierarchical organization and cephalic modulation of downstream control circuits have been demonstrated to exist in mantises (e.g., Liske 1999), although the interpretation of the mechanisms has sometimes been erroneous (Prete 1995). Further, the correlational evidence that the plasticity of cephalic control over AP circuitry is a product of more complex brains such as those in mantises (Matthews & White

2011) is consistent with the data presented here. Hence, our data open the door to a number of potential research questions using the mantis as a model system. For instance, anecdotal data from our lab suggests that AP behavior changes when mantises recognize a potential prey item, or when they are engaged in (so-called) ‘courting’ or mating behavior. In addition, although our data do not directly address any of the interesting hypotheses suggested by Sláma (1994, 1999, 2000) and Tartes (2002), the relatively large size, and complex, variegated behavioral repertoire of mantises make them a particularly intriguing model system in which to pursue these and many of the other unanswered questions regarding insect respiration.

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