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Biodiversity, ecology, and behavior of the recently discovered insect order Mantophasmatodea

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Abstract

The spectacular discovery of the new insect order Mantophasmatodea in 2002 was immediately followed by detailed studies on morphology and scattered information on different aspects of its behavior and general biology. A distinct feature of these predatory insects is the development of large arolia, which are typically held upright; hence, their common name is heelwalkers. The first mantophasmatodean species were described based on two museum specimens originally collected in Tanzania and Namibia. To date, these insects have been observed at surprising levels of diversity and abundance in Namibia and South Africa. For our studies on the phylogenetic relationships within Mantophasmatodea, we collected and analyzed numerous populations that belong to all known mantophasmatodean lineages, including East African populations. These collections not only provided a comprehensive biogeographical overview but also facilitated a comparative analysis of behavior, which was mainly analyzed under laboratory conditions. Here, we review and discuss the published data, as well as provide additional information on Mantophasmatodea distribution, evolutionary lineages, morphology, and biology, with a specific focus on reproductive biology.

Keywords: Behavior, Biodiversity, Evolutionary lineages, Life history, Mantophasmatodea, Polyneoptera

Introduction

The insect order Mantophasmatodea [1,2] was the first new order described since 1914 [3], and several taxa were immediately characterized (e.g. [4-6]). These descriptions were accompanied by a comprehensive description of the morphological features, such as genitalia of both sexes [4], the structure of sperm [7], eggs [8,9], head [10,11], circulatory organs [12], arolium and tarsus [13-16], and antennae [4,17,18], as well as studies on reproductive biology [19], communication [20-22], peptide hormones [23,24], physiology [25], and development [17,26,27]. In addition to molecular studies [4,28-31], these studies provided the initial information for reconstructing the Mantophasmatodea phylogeny. Although the interordinal relationship has been disputed with Mantophasmatodea either to Phasmatodea [28] or Grylloblattodea [13,29,31,32], more convincing morphological and also molecular data support Mantophasmatodea as the closest relatives of Grylloblattodea. Considering the short period since Mantophasmatodea was first described, an extensive body of literature has been generated, which includes behavior and morphology as well as systematic and phylogenetic studies. However, certain general aspects of their biology and ecology are less well-known. Scattered reports have been published as short notes either in diverse scientific (see references above) or more popular publications (e.g. [33-36]). In this manuscript, we summarize the available information on Mantophasmatodea distribution, ecology, life history, reproduction, and feeding behaviors. Most data are based on our field studies and laboratory observations (see Additional file 1 for methods), for which we sampled specimens from all mantophasmatodean lineages (see [31]) in Southern Africa (Figure 1) and East Africa. In addition to presenting our data, we review the previously available information on ecology and behavior from the scientific literature and other public resources.

Review

General remarks and intraordinal relationships

Mantophasmatodeans superficially resemble mantises and stick insects. Different common names are used in the literature, including gladiator [37,38], rock crawler

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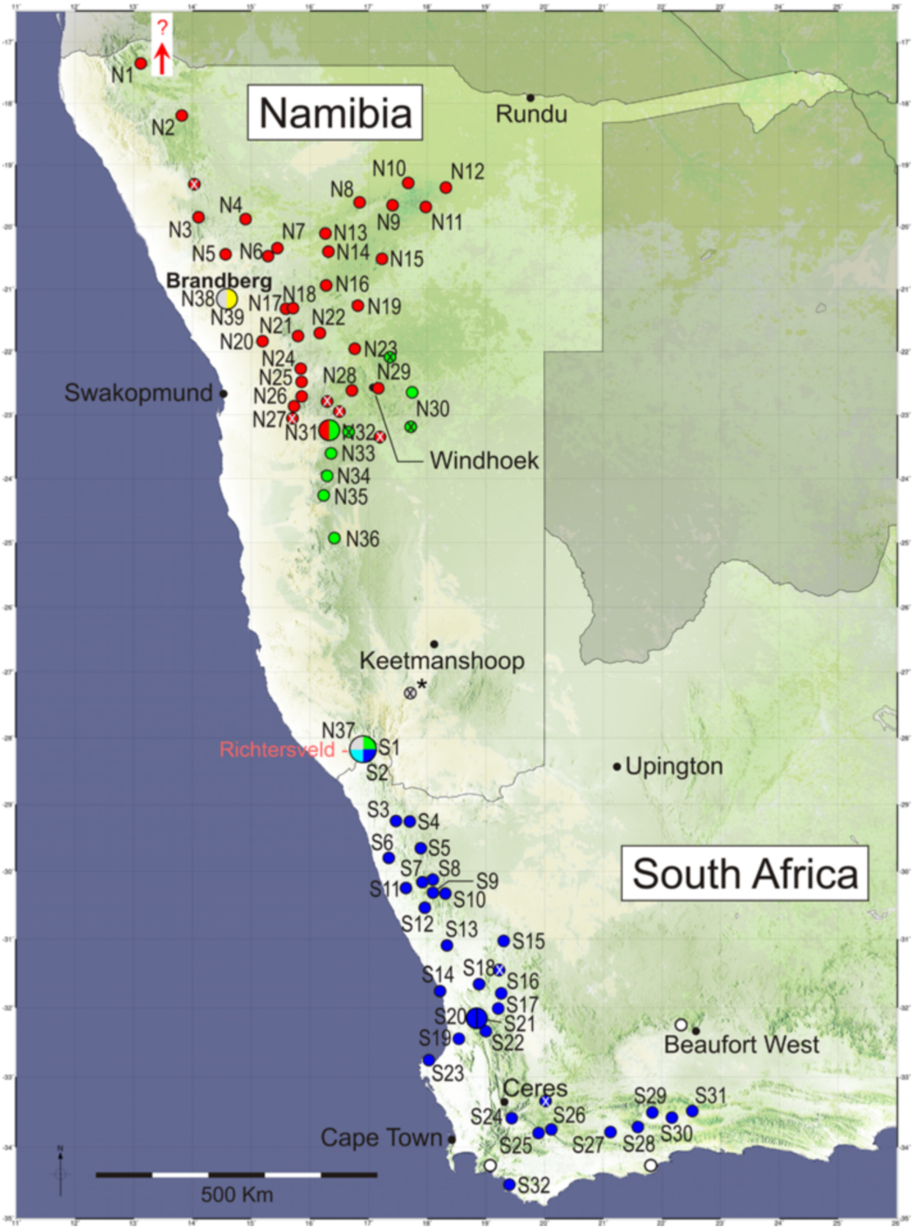

Figure 1 Distribution for Mantophasmatodea in Southern Africa (modified from [31]). The numbered sample spots refer to populations that were analyzed using peptidomics [33]. South African Austrophasmatidae taxa for which the mtDNA sequences were analyzed by [30]) have been collected within the same distributional range in the Western and Northern Cape provinces, except for the populations of Austrophasmatidae marked with white circles (see [30]). The circles marked with an X refer to populations that were recently collected and are not yet included in the phylogenetic studies. The large circles represent areas where several taxa co-occur (genus level). Whereas the respective taxa from Brandberg (N 39, greenish *Pachyphasma*; N38 grey brownish *Tyrannophasma*), and Clanwilliam (S21, greenish *Viridiphasma*; S20, grey brownish *Karoophasma*) inhabit different microhabitats, different taxa in the Gamsberg area (N31, greenish *Mantophasma*; N32, greenish *Striatophasma*) were occasionally identified in the same bushes. The Richtersveld (arrowhead), which is part of the most northern extension of the winter rainfall region in South Africa, is inhabited by at least four distantly related taxa (*Praedatophasma*, *Namaquaphasma*, and two additional undescribed taxa) and, thus, shows exceptionally high diversity at the genus level. A presumptive *Praedatophasma* population has been reported from the Fish River catchment area (asterisk), which is approximately 100 km north of the established range (H. Vollbrecht, EduVentures Windhoek; pers. comm.). Red circles, *Mantophasma*; green circles, *Striatophasma*; blue circles, Austrophasmatidae sensu [4]); grey circles, *Tyrannophasma/Praedatophasma*; yellow, *Pachyphasma*; light blue/light green, undescribed taxa from Richtersveld.

[39], and heelwalker (e.g., [25,30,40,41]). Because 'heel-walker' reflects the typical Mantophasmatodea phenotype, we prefer this designation. Both sexes of all known species, including fossil species [38,39,42] are apterous, which yields a nymph-like appearance. This appearance might be one reason that the Mantophasmatodea specimens were

not recognized as members of a new insect order for a long time. Mantophasmatodean fossils were discovered in Baltic amber [38,39,43] which indicates a wide distribution in the past. Jurassic fossil findings (165 mya) in China confirm this hypothesis [42]. Currently, Mantophasmatodea have a relict global distribution; most of the 18 described species are concentrated in western Southern Africa areas, except for *Tanzaniophasma subsolanum* (Tanzaniophasmatidae) in East Africa [1,4,5,30,44,45].

The extant Mantophasmatodea species have been provisionally grouped into three families: Tanzaniophasmatidae (which comprise only the described Tanzanian species of Tanzaniophasma), Austrophasmatidae (9 described species from African genera *Namaquaphasma*, *Karoophasma*, *Hemilobophasma*, *Lobatophasma*, *Austrophasma*, *Viridiphasma*), and the Namibian genus *Striatophasma*, Mantophasmatidae (8 described species from Namibian genera *Tyrannophasma, Praedatophasma, Mantophasma, Sclerophasma, Pachyphasma*). Another family-level group has been proposed for accommodating Praedatophasma and Tyrannophasma [30]. In particular, the species identity within the Mantophasmatidae and the placement of *Striatophasma* in Mantophasmatidae or Austrophasmatidae must be clarified in future studies. A recent phylogenetic analysis of peptide hormone sequences suggests at least eight distinct lineages in Mantophasmatodea, including *Tyrannophasma*, *Praedatophasma*, *Pachyphasma*, *Mantophasma* (incl. *Sclerophasma*), *Tanzaniophasma*, *Striatophasma*, Austrophasmatidae sensu [4], and an undescribed taxon from the Richtersveld (see [31]). A second undescribed taxon from the Richtersveld (Wipfler & Predel; in prep.) may link *Striatophasma* from Namibia and the South African Austrophasmatidae. The monotypic *Tyrannophasma*, *Praedatophasma*, and *Pachyphasma*, as well as the two undescribed taxa from the Richtersveld, are relict taxa with a limited distribution range. In contrast, *Mantophasma*, *Striatophasma*, the South African Austrophasmatidae sensu [4], and most likely the poorly known *Tanzaniophasma* clade are currently successful and widespread taxa. Although a number of *Mantophasma* species have been described [1,4,46], recent analyses of numerous populations of the genus *Mantophasma* did not reveal conclusive lineage sorting within this taxon [31]. Even the relationship between the *Mantophasma* lineage and *Sclerophasma paresisense* is poorly resolved [16] and requires further analyses to resolve the taxonomical status of this clade. The relationships within the family Austrophasmatidae, which was originally proposed to encompass taxa from the Western and Northern South African Cape Provinces, are well-supported at the genus and species levels. Ambiguities exist on an intrafamilial level for analyses of mitochondrial DNA sequences [30] and peptide hormone sequences [31]. However, these analyses clearly indicate that the family Austrophasmatidae derived from Namibian Mantophasmatodea species. Species from this family may have evolved in a rapidly speciating lineage, which produced a monophyletic group of mostly allopatric species [31].

Distribution patterns and habitats

All records of extant Mantophasmatodea are from Africa, south of the equator. In East Africa, in the mountainous regions of Malawi (Dedza Mountains, Nyika Plateau), we identified slightly distinguishable populations based on their general appearance and habitus, which most likely belong to the *Tanzaniophasma* clade (Figure 2). These localities are near the South Tanzanian region, where the only scientifically described (museum) *Tanzaniophasma* specimen was collected in 1950 (see [1]). In Malawi, the specimens were located in areas characterized by a mixture of grasses and dense bushes (open shrubland and savanna); no specimens were observed in forest biomes. The Mantophasmatodea distribution in East Africa, at least in Malawi, may be negatively affected by extensive vegetation burn off, which is common and widespread in Malawi [47,48]. We observed heelwalkers that were

Figure 2 ***Tanzaniophasma*** **spec. female from the Dedza Mts. (Malawi) with an adult fleshfly as her prey (photo taken in laboratory).**

restricted to dense bushes of different size on rocky hills that were not recently burned (Figures 3 and 4). Hockman et al., [17] noted putative *Tanzaniophasma* specimens from Cape Maclear, which is on the southern bank of Lake Malawi. In this area we observed nymphs in bush edging an open patch of unused dense shrubland along a creek. The data on Mantophasmatodea distribution in Namibia and South Africa have been discussed in detail by [31]. In short, the southern African distribution appears largely confined to the westernmost Great Escarpment upfoldings; the range of the genus *Mantophasma* likely extends into southwest Angola (see Figure 1 with multiple new localities). In the Western Cape (South Africa), a few species also inhabit the coastal region, including Sand Fynbos vegetation in the Strandveld, and the Dune Thicket (Fynbos); no specimens have been observed on the Cape Peninsula. The distribution map (Figure 1) suggests that a contemporary dispersal barrier (between 25 and 27 degrees south latitude) exists between the species in the winter rainfall area of Southern Africa and species living in the summer rainfall region of Namibia. A similar distributional discontinuity between Namibia and Namaqualand has been reported for several faunal elements, including other insects, birds, frogs, and mammals [49] (and references therein), and for plant species [50]. Our phylogenetic analyses and their recent distribution suggest that *Striatophasma*-like species have crossed this region in the past and established a founder population that yielded the present Austrophasmatidae sensu [4] (see [31]).

The spatial patterns of Mantophasmatodea in Southern Africa have been influenced by range fragmentation on a large scale (Namibian versus South African species) and range-edge speciation on a smaller scale. The latter form of speciation was likely driven by geological uplift during the Miocene to Pliocene [51], serial climatic oscillations during the Pleistocene [52], and alternating dry and wet climatic fluctuations. Thus, Mantophasmatodea speciation in Southern Africa was most likely allopatric through vicariance, which has been assumed for other insects [53] and arthropods (Diplopoda; [54]) in the region. Remarkably, the core regions of their recent distribution, such as the Brandberg in Namibia and Succulent Karoo-Fynbos biomes [55-57] typically show exceptional levels of biodiversity and endemism. In these regions, Mantophasmatodea are part of a very unique insect fauna [58,59]. Notably in the context of Mantophasmatodea distribution, no additional mantophasmatodean taxa have been identified within the large *Mantophasma* distributional range, whereas two distinct monotypic genera are sympatric in different ecological niches on the Brandberg Massif immediately outside the *Mantophasma* range. Both the genera *Tyrannophasma* and *Pachyphasma* appear restricted to the Brandberg Massif and have not been observed in other areas. The Brandberg Massif (the highest mountain in Namibia) has volcanic origins and is isolated from the longitudinal Namibian escarpment (*Mantophasma* habitat); this isolation has generally ensured that it is a significant relict habitat for numerous endemic organisms (see [53,55]). On the Brandberg Massif plateau, *Pachyphasma brandbergense* was found in the same biotope as *Tyrannophasma gladiator*. The large and impressive-looking grey-brown *T. gladiator* is mainly found in grass tussocks (see also [33]); however, under dry conditions, nymphs have also been found in dense bushes (altitude 1400-2400 m). The much smaller and greenish *P. brandbergense* is the only mantophasmatodean taxon primarily collected from flowering composite bushes; the ecological relevance of this finding is unknown. The Brandberg Plateau vegetation is characterized by plant species confined to the upper regions of mountains (higher than 1500 m); Asteraceae is the most speciose family [60]. The different *Mantophasma* populations (including *Sclerophasma paresisense*) inhabit well-

Figure 3 Characteristic habitat for *Tanzaniophasma* in Malawi (Nyika Plateau).

Figure 4 Preferred type of vegetation for *Tanzaniophasma* at Nyika Plateau (Malawi).

vegetated mountains in central Namibia up to the Otavi Mountains in the northeast; they also live in mountainous mopane savanna (Kaokoveld) in the northwest. Throughout most of their range, these insects are common in grasses, shrubs, and even trees given sufficient rainfall (see [31]). The density of individuals in a population can be surprisingly high, which is somewhat unexpected for an insect group that has been overlooked for such a long time period. The genus *Striatophasma*, which was mainly collected south/southeast of the *Mantophasma* distribution, typically inhabits dry regions with scattered vegetation, and specimens have often been collected from dwarf bushes. In the Gamsberg/Hakos Mountains, *Mantophasma* and *Striatophasma* are sympatric. Austrophasmatidae, which live in the winter-rain South African region, were typically found in habitats with sparse to scattered vegetation. Eberhard et al., [44] reported a preference of *Viridiphasma clanwilliamense* to a small tree (*Euclea recemosa*), but for most species, we did not observe a preference for hiding on a specific plant species; clearly, Austrophasmatidae select dense bushes or grass tussocks, which provide camouflage and a sufficient prey spectrum. The Kraalbos *Galenia africana*, a bush that is poisonous to sheep and is common in overgrazed or otherwise disturbed Western/ Northern Cape areas, appears to be particularly attractive to mantophasmatodeans. The occurrence of heelwalkers in strongly disturbed areas suggests that these insects are less sensitive to environmental damage as long as prey is available. At least for the *Austrophasma* and *Hemilobophasma* populations, we found that nymphs prefer bushes, whereas adults were typically collected from large grass tussocks. Copulating heelwalkers have regularly been observed in these grasses. Most Austrophasmatidae clades were collected from low altitudes to mountainous locations up to 2000 m, which indicates that different altitudes with changing vegetation types are not effective dispersal barriers for heelwalkers.

Only few *Praedatophasma maraisi* specimens have been detected in the Richtersveld/Ai-Ais region in the Orange River/Fish River vicinity. The first specimen was collected in 1990 by E. Marais (Windhoek, Namibia) on the Namibian side of the Orange River when it approached a light trap (see [38]); two additional specimens were collected by the authors nearby on the South African Orange River site (Richtersveld). However, this species' distribution appears larger because scholars from Namibia detected a putative *Praedatophasma* specimen in 2005 in the dry Gaub/Fish River region, which is approximately 90 km NW of the confirmed localities (H. Vollbrecht, EduVentures Namibia; pers. communication). It is currently unclear whether these large heelwalkers (Figure 5) hide in vegetation similar to the other mantophasmatodeans. Extensive collection activities in the Richtersveld have yielded three additional and distantly related taxa (see Figure 1) with limited ranges. The succulent Karoo in the Richtersveld/Ai-Ais region, where these four mantophasmatodean taxa have been identified, is only sparsely covered with vegetation and represents the most desert-like habitat in which mantophasmatodeans have been found to date. The Richtersveld is the only recognized arid biodiversity hotspot [61] and is located in the summer- and winter-rain transition zone.

Figure 5 Mating pair of *Praedatophasma* spec. collected during an EduVentures expedition with scholars from Windhoek in the Fish River catchment region. Photo courtesy of Telané Greyling, Namibia Horse Safari Company, Aus, Namibia.

General habits

Klass et al., [4] Wipfler et al., [45] Wipfler [62] have provided detailed descriptions of mantophasmatodean morphology; here, we focus on certain characteristics related to the ecological and behavioral aspects of their biology. Adults in all Mantophasmatodea species are in the 13-26 mm range, except for the larger species *P. maraisi* and *T. gladiator* (up to 35 mm). In all species, mature females with developed eggs are substantially larger than males (see below). Both sexes are secondarily wingless and highly flexible along the longitudinal axis. This flexibility enables the species to clean their external genitalia with their mouthparts (Figure 6), but it is also used to attack large prey (Figure 7). The known species' ground color is brownish, grey, or greenish, which indicates camouflage. The *Mantophasma, Tanzaniophasma, Pachyphasma, Viridiphasma, Striatophasma,* and *Austrophasma*/*Lobatophasma* species are typically green; however, the *Austrophasma gansbaaiense* and *Lobatophasma redelinghuysense* specimens have been observed with different ground colors (green or brownish) in the same local population, and the *Mantophasma* specimens have regularly been identified with uniform pale-brown, pale-yellow, or whitish coloring (see also [4,33]). The type of ground color is consistent during nymphal development and cannot be changed, but no detailed information is available regarding the heredity of color frequencies at the population level. Under laboratory conditions without vegetation, many specimens (particularly *Mantophasma*) became paler, and it is advantageous

Figure 6 Abdomen grooming by a female *T. gladiator* (N 38, Brandberg), which shows the flexible body axis. Note the use of a single arolium to adhere the heavy body to the wall of the plastic container (photo taken in the laboratory).

to document the color of specimens in the field. In addition to these general color types, the insect's body might be covered by many spots and median stripes (for a detailed description, see [4]). A number of greenish species exhibit color polymorphism within a population and vary in color and markings. Brownish dorso-median stripes are typical of a few species (Figure 8). In *Striatophasma*, only males show the brownish stripe; the coloration is from brown pigments in the dorsal diaphragm. Other species with brownish stripes (e.g., *Austrophasma* and *Lobatophasma*) belong to Austrophasmatidae, and both sexes have these stripes. In general, whereas there appears to be no specific link to a particular plant species, for most species, the color matches the habitat structure. Green species occupy the more mesic fynbos vegetation in the Cape region, savanna, and hilly grasslands in Namibia and East Africa, and the grey or drab brown morphs occupy more arid habitats in the succulent Karoo, such as many Austrophasmatidae and *P. maraisi*. A good example for color adaptation are the Western Cape's green *Viridiphasma clanwilliamense* and the sympatric *Karoophasma biedouwense* which were mainly collected from green bushes or low-growing grey and brown karooid shrubs; respectively. In *Lobatophasma redelinghuysense*, brown and grey striped morphs dominate in dry sandplain fynbos vegetation, while green striped nymphs dominate in more mesic mountain fynbos vegetation [44]. The only greyish/brownish species north of the winter rainfall South African region is *T. gladiator*, which has a restricted distribution in the Brandberg Massif.

Figure 7 Green morph of a non-pregnant *Austrophasma gansbaaiense* female (S32, Gansbaai) attacking a pregnant female from an undescribed Austrophasmatid species (S18; Vanrynsdorp). The sequence demonstrates the use of the flexible body axis and the arolia in a vigorous attack, as well as the ability to strike extremely rapidly (image from a video recorded in the laboratory).

Apart from hunting, when Mantophasmatodea stalk or walk quickly over very short distances to catch their prey, they predominantly sit and hide, and they rarely walk in vegetation. Most species, at least in the family Austrophasmatidae, hide in the centers of bushes or grass tussocks during the day. Night observations verified the presence of Mantophasmatodea in the periphery of bushes or grasses during feeding or mating. Whereas most specimens that were detected with an electric torch tried to hide themselves (Figure 9), one *H. montaguense* male was observed drumming on a grass stalk (Figure 10). Heelwalkers that were caught and held in hand rarely showed fast escape behaviors. However, in certain cases, we observed a strange "curling" behavior when the specimens were knocked out of a bush. This behavior was particularly conspicuous because, after dropping, Mantophasmatodea typically do not immediately move away. Heelwalkers sometimes jump for small distances, such as a few centimeters (Figure 11; see Additional file 2: Videos 1A, Additional file 3: Video 1B, Additional file 4: Video 1C, Additional file 5: Video 1D), however, we did rarely observe 10 cm distances as described in [5] for *Mantophasma*.

Occasionally, Mantophasmatodea actively drop in the vegetation. In most cases, they land upright on their legs ("cat-like") on the ground or in the correct direction in small branches of shrubs and grasses. Experiments using high-speed cameras suggest that heelwalkers actively influence the landing position due to their highly flexible body axis (see Additional file 6: Video 2A and Additional

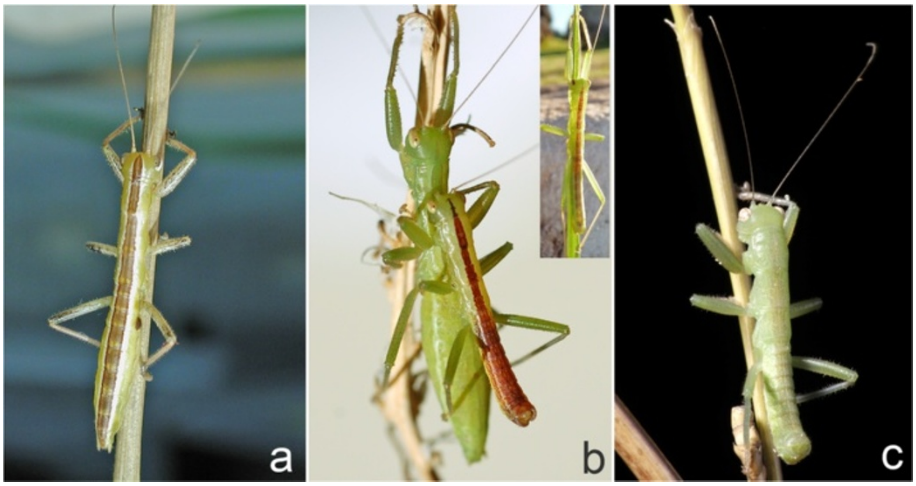

Figure 8 Development of brownish dorso-median stripes in different Mantophasmatodea taxa. a) Female *Austrophasma gansbaaiense* (S32, Gansbaai); the brownish stripe with white margins. **b)** *Striatophasma naukluftense;* the brownish stripe is only developed in males; females with less distinct green stripe. Western population (Gamsberg) with posteriorly broadened stripe. The inset shows a male from an eastern population (70 km E of Rehoboth) with distinctly outlined abdominal stripe. **c)** An undescribed species from the Richtersveld with weak male dorsal stripe development.

file 7: Video 2B). Similarly sized unwinged mantises and phasmids were unable to behave similarly; however, the mantises attempted to perform a 'loop', but required much more distance between the start and end points (Predel, unpublished). In the field and in captivity, healthy heelwalkers are reluctant to immediately walk away after dropping. When these insects did not land on their legs but on their backs, they changed their positions with a sudden movement immediately after landing and stopped again (see Additional file 8: Videos 3A and Additional file 9: Video 3B). Due to this behavior, which may be maintained for 30 sec or even longer, it is sometimes difficult to detect heelwalkers in detritus after beating a bush; many arthropods, such as ants, beetles, cockroaches, and spiders, run around actively under these circumstances. In nature, this strategy likely prevents detection by insect-hunting mammals or birds.

Both sexes possess very large arolia on the pretarsi of all legs (see [1,13-15]), which are, however, mostly held in an upright position; this highly characteristic position ("heelwalker") is quite unique among insects. Studies have shown that arolia are rarely used for walking, if at all, and are not necessary to produce, detect, or respond

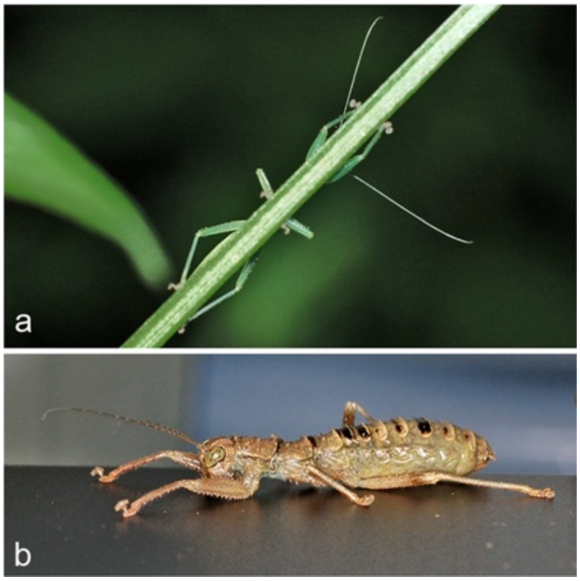

Figure 9 Mantophasmatodea females attempting to avoid detection under sudden light exposure. a) *Mantophasma* spec. (N15, Waterberg) on a grass stalk at 11 p.m. (field observation); **b)** *T. gladiator* (N 38, Brandberg) (photo taken in laboratory).

Figure 10 ***H. montaguense*** **male (S29, Calitzdorp) in the field drumming at night (11 p.m.) on a grass stalk.**

Figure 11 ***T. gladiator*** **male (N 38, Brandberg) forced to jump from a glass slide.** In contrast to grasshoppers, for example, Mantophasmatodea are typically reluctant to jump. (images from a video recorded in the laboratory).

to vibrational communication signals [15]. We observed arolia use when walking or adhering to smooth surfaces. For example, when cleaning body parts or eating large prey, the animals sometimes hung upside-down (Figures 6 and 12) and often used only a single hindleg arolium to adhere to smooth plastic surfaces. We also observed the insects using arolia to stabilize their position after landing or when a large prey was attacked (see Figure 7). Effective adhesion is supported by secretions produced in large glands in the arolia [15]. Secretion production is typically energy-consuming, which may be one reason to maintain the large arolia in an upward position when not in use. All species that have been maintained in our laboratory frequently clean their arolia but also antennae and genital segments using their mouthparts (see Additional file 10: Video 4; also [5] for. *T. gladiator*)); tarsi were not used to clean any body part.

Figure 12 ***T. gladiator*** **female (N 38, Brandberg) using hind leg arolia to adhere to the wall of a plastic container while eating a cricket.** The fore- and hind legs were used to fix the prey (photo taken in the laboratory).

The Mantophasmatodea antennae are long, filiform, and have a flagellum well separated in basi- and distiflagellum; unique feature among insects [4,17,18]. While walking or hiding, these insects continuously wave their antennae in a manner similar to that of cockroaches (i.e., both antennae alternatively move up and down) (see Additional file 11: Video 5). During these motions, the flagellomeres are typically bent downwards. Antenna-flickering has been observed upon contact with a sexual partner and prey. This behavior indicates intensive chemical signal use. Potential glandular structures have been identified in two of the distal flagellomeres [4,18,36]. Occasionally, males walk with their abdomens upwards, similarly to scorpions (e.g., when approaching a sexual partner).

A diurnal habit has been observed in *Mantophasma* specimens (see also [5]). Occasionally, we found these insects sitting in the upper parts of grasses and outer shrub branches during the hottest portion of the day (11 a.m. - 5 p.m.); however, the *Mantophasma* specimens were more abundant in these locations after nightfall. In the laboratory, *Mantophasma* specimens showed greater activity during the day compared with Austrophasmatidae species, including foraging and sexual behaviors (see [33] and below). For all species, mating and drumming behaviors were predominantly observed at night in the laboratory, including dusk and dawn.

Life cycle, growth, and life history

Mantophasmatodea are annual and univoltine species. Females oviposit in pods of foam that form a cocoon, which hardens due to incorporated sand and contains eggs from both ovaries (in *T. gladiator* 26-30, in *Mantophasma* females 20-24; Figures 13 and 14). Tojo et al., [19] reported 10-12 eggs in pods from *K. biedouwense* (Austrophasmatidae), which indicates that these insects may occasionally oviposit eggs from a single ovary (the egg number per ovary is similar to that of *Mantophasma*). These pods are laid superficially (0.5 - 2 cm deep) in sandy soil (Figure 15; see also [33]). In the field, we identified two empty pods

Figure 13 **Female *Mantophasma kudubergense* (N21, Erongo Mts.) abdominal body cavity with 20 large eggs from both ovaries.**

Figure 15 ***Mantophasma kudubergense* female (N21, Erongo Mts.) laying an egg pod under laboratory conditions.** The soil is not from the sample location.

close together, which suggests that females do not hesitate to lay eggs at approximately the same spot. The pods are formed from sand and a secretory liquid to protect the eggs. In the pods, the eggs exhibit a regular vertical arrangement similar to that of bottles in a beer crate (see Figure 14). We did not observe sterile egg pod deposition, which is commonly observed in praying mantises [63].

Mantises and cockroaches, which were often collected at the same location as the heelwalkers, laid eggs/egg cases even under simplified laboratory conditions (e.g., in plastic boxes without a soil cover), but for Mantophasmatodea, oviposition was not observed under these simplified conditions. This reluctance to oviposit was evident. However, Mantophasmatodea specimens readily copulated in the laboratory if provided the opportunity (see below). Pregnant *Mantophasmatodea* females laid eggs almost immediately if sufficient soil was provided, and we obtained more than 30 pods with fertile eggs from 20 *T. gladiator* females after copulation in the laboratory. Uchifune [64] obtained multiple egg pods from *Karoophasma biedouwense* (Austrophasmatidae); individual females laid up to four egg pods over a short period, i.e., a few days, and 50 - 100 eggs total during their adulthood [19]. In this species, oviposition was observed in September and typically occurred in the morning when the temperature was low and the humidity was high [64]. Under artificial laboratory conditions, Mantophasmatodea breeding was unsuccessful in most cases. We tested different dormancy scenarios using *T. gladiator* egg pods (G. Köhler, unpubl. data). Neither a dry and warm period over several months nor dry conditions followed by a cooling (4°C) period over several months initiated hatching. In all scenarios, a water supply was used to terminate dormancy, which simulated the rainy season and appeared to initiate hatching in the field. The egg fertilization rates varied from 48-95% in our experiments, and the embryos reached the anatrepsis phase. From these observations, we assumed a diapause. However, successful rearing in *Sclerophasma paresisense* and *Praedatophasma maraisi* (in fact, *Tyrannophasma gladiator*, see locality) was reported by [17], who used increased moisture and rising temperatures following a cold period.

Figure 14 ***T. gladiator* (N39, Brandberg) egg pod with 29 eggs laid into sand provided in the laboratory.** Note the regular and vertical arrangement of the eggs, which became visible after the removal of the lower sand layer.

In nature, the egg stages survive at least eight months of a dry summer (Austrophasmatidae) or winter (Mantophasmatidae, Tanzaniophasmatidae) within the resistant egg pods, and the first instar nymphs hatch the following year during the rainy season (i.e., in mid-summer for Namibia/East Africa and autumn/winter (May or later) for South Africa) (see also [17,19]). In the Naukluft Mountains (Namibia), we identified multiple (n > 20) first instar *Striatophasma naukluftense* nymphs [45] in the morning

14 days after a strong summer rain; scattered along a section of 200 m. The same section was searched the previous evening without success. This finding suggests highly synchronized egg hatching from different pods during the night (see also [17] for observations on *Karoophasma*). Analyzing the occurrence of nymphs and adults of different Austrophasmatidae species in South African sample sites, we found that development varied considerably at the local scale throughout two subsequent years (Figure 16), depending on the local rainfall patterns and latitude. These observations indicate highly variable life history patterns on both species and population levels as an adaptation to local climate heterogeneity. In Namibia at the end of March 2014, we collected *Striatophasma* (Hakos Mountains) and *Mantophasma* (Emeritus farm) adults and first instar nymphs in the same habitat. For the Hakos locality, detailed precipitation recordings exist and verified strong rainfall at the end of December 2013 and again in mid-March (see Figure 16). Therefore, facultative bivoltine behavior may occur during a long rainy season but this scenario needs to be verified experimentally. Other than the direct influence of rainfall on egg development, there is no information on which additional factors induce the end of dormancy in eggs after the dry period. Under dry experimental conditions and room temperature, most *T. gladiator* embryos remained alive after two years. Similarly prolonged egg dormancy is also known from other Polyneoptera inhabiting semi-deserts; in Southern Africa eggs of the armoured ground cricket *Acanthoplus bechuanus* (Orthoptera) are able to undergo dormancy at least for two years [65].

T. gladiator nymphs that hatched reached adulthood after 3.5-4 months [5]; the adults survived at least two months in our laboratory. First instar *Striatophasma naukluftense* nymphs were collected and reared; the oldest adult died at 136 days (4.5 months). For the winter-

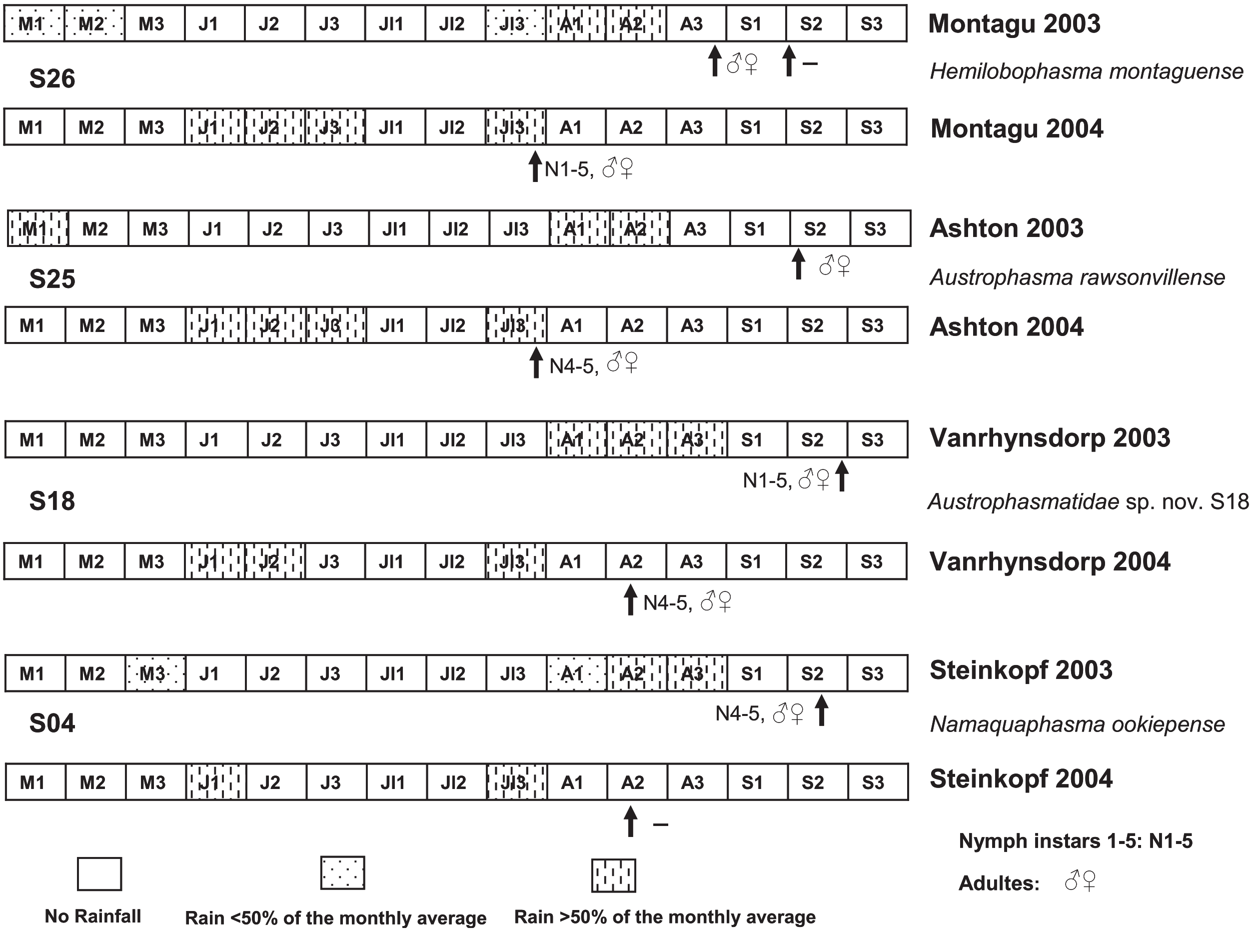

Figure 16 Mantophasmatodea phenology at four sample sites as a function of rainfall patterns in 2003 and 2004. Time scale is in periods of ten days from May through September. For each year and sampling site (sample code see [31], the rainfall per period is ranked into 3 categories: no rain, <50%, or ≥50% of the monthly average rainfall (1962-1990; South African Weather Service [http://www.weathersa.co.za/]). The sampling days are provided for each locality (arrow) and the detection of adults and nymphs is given, respectively. The data indicate a life cycle that responds to the period and amount of rain during spring.

active Austrophasmatidae species, the developmental period appears to be shorter, but the unpredictable weather conditions strongly influence their life spans. Drilling and Klass [17] indicated approximately 55 days (excluding the first instar phase) in *L. redelinghuysense*; our laboratory experiments (21-23°C) have shown that third instar Austrophasmatidae larvae (localities: S04, S15, S18, S26, S32; see Figure 1) reached adulthood within less than a month. In the laboratory, we observed a shorter life span in males compared with fertile females. Typically, Mantophasmatodea molted during the night and ingested their exuviae; therefore, counting the number of instar stages for these insects was difficult. In only a few cases, the fragile Mantophasmatodea exuviae were found hanging on the top or wall of the rearing container. Hockman et al., [17] used antenna development (i.e., the increasing number of basiflagellum annuli) as the criterion for assessing instars and reported 5 nymph instars in *L. redelinghuysense*. The first instar nymphs possessed four annuli in the basiflagellum and seven hairy annuli in the distiflagellum. For each instar, two additional annuli were derived from the most basal annulus (meriston); therefore, the number of annuli in the adult *L. redelinghuysense* basiflagellum was 14. Because consistent antennal development was also observed for other mantophasmatodean taxa [17], the assumed 8-10 instars in *T. gladiator* [5] is likely an overestimate.

There is no available information on mortality factors, including predation and parasitism, in the field. Camouflage appears to be important for these small predators, which are vulnerable to attack by birds, lizards, and predaceous insects that are present in the same microhabitat. Escape behavior, i.e., jumping away from a bush or grass tussock, was rarely observed. However, heelwalkers can jump for a short distance (see above). In particular, the summer-active Mantophasmatidae species regularly co-occur with mantises, mainly the genus *Miomantis*, which were collected using the same collection method. However, on the microhabitat scale, we found that a high heelwalker density was primarily linked to relatively low mantis abundance, even if mantises were more frequent elsewhere in the immediate neighborhood. Although we did not perform quantitative studies, this observation indicates extermination or possible avoidance of intra-guild predation between these insects.

Prey and feeding behavior

Mantophasmatodea are carnivorous insects. Similarly to many other predatory insects, they may be generalists regarding their prey [66] because they consume different types of arthropods, mainly spiders and insects. Mantophasmatodea clearly coincide with microhabitats that have a high arthropod density. Co-occurrence with other predators, as mantises, was rare in the winter rainfall range (Austrophasmatidae), but common in Namibia; however, co-occurrence was not observed in the same microhabitat (see above). We did not observe heelwalkers in bushes with high ant abundance. However, this phenomenon does not exclude ants as prey. We investigated the gut content of 14 specimens from *Mantophasma* spec. (N15, Waterberg) at different nymphal stages and in adults collected at 5:30 p.m. and 11:00 p.m.; we primarily found remains of ants, other adult Hymenoptera, Diptera, caterpillars, and moths, as well as different size spiders. In a single sample, oribatid mite remains were detected. However, phytophagous locusts, bugs, or beetle remains were not observed. Four of the 14 *Mantophasma* specimens did not contain food remains in their gut (3 × 11:00 p.m., 1 × 5:30 p.m.). In an investigation under laboratory conditions, fasting *Mantophasma* sp. males from Waterberg (N15; N = 5) were fed small crickets and dissected at 1 h intervals. After two hours the mid-gut contained considerable quantities of partially digested cricket (Figure 17). However, the foregut stored food remains for many hours. Therefore, food in the foregut does not necessarily reflect recent intake. From these experimental data, we concluded that at least two out of eight (25%) *Mantophasma* specimens (N15) collected at 11 p.m. consumed a meal a few hours in advance. In contrast, the six specimens collected at 5:30 p.m. did not show signs of a recent meal. One specimen from the same location was collected at 7 a.m., and both the foregut and mid-gut were entirely filled with food particles. These experiments indicate hunting activity during the evening and at night.

To further survey the Mantophasmatodea food spectrum, we investigated the potential prey from a single bush (*Suaeda fruticosa*, Amaranthaceae) at 8 a.m. in the dry Richtersveld (South Africa), which yielded four adult specimens from an undescribed Mantophasmatodea taxon (Figure 18). In total, we collected 12 mites (2 species), 2 pseudoscorpions, 32 spiders (6 species; most individuals

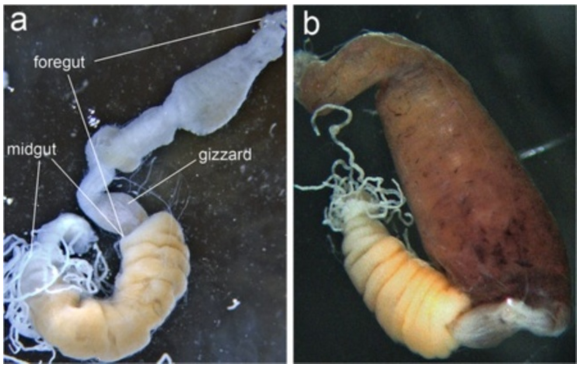

Figure 17 Dissected adult *Mantophasma* spec. (N15; Waterberg) gut tissues before (a) and 2 h after (b) feeding with crickets. In the latter specimen, the gizzard and mid-gut contained food particles 2 h after the meal.

Figure 18 A *Suaeda fruticosa* (arrow) sample site with four adult Mantophasmatodea specimens (8 a.m.). In addition to the Mantophasmatodea, we collected the remaining arthropods from this bush to survey the potential prey spectrum. Subsequently, the gut content of the four Mantophasmatodea specimens and the identity of the collected arthropods were analyzed in the laboratory.

less than 3 mm), a single termite, 7 adult Psocoptera, 19 small, adult Heteroptera (likely Geocoridae), 3 Homoptera nymphs, 1 myrmicine ant, 1 caterpillar, 1 plume moth, 9 adult Coleoptera (7 Curculionidae, 1 Nitidulidae, and 1 Latridiidae), 2 phytophagous beetle larvae, and 4 winged Diptera (3 Brachycera and 1 Nematocera); a few Diptera escaped. The prey remains in the guts of the four Mantophasmatodea collected from the same bush indicated that each specimen consumed a meal the night before, but the gut contents did not entirely reflect the potential prey spectrum (the prey spectrum that was present in the morning). In the gut lumen of these Mantophasmatodea, we found brachyceran fly remains; additional remains were assigned to a caterpillar, a spider, and a few small adult insects (likely Holometabola) that were not identical to the species listed above.

The literature includes only a few observations on how Mantophasmatodea find and handle their prey in the field [5,33]. A hide and wait strategy (in combination with slow stalking) is very likely and is concordant with the nocturnal activity of most species. In the laboratory, Mantophasmatodea nymphs and adult Austrophasmatidae were mainly fed different *Drosophila* species. Larger Mantophasmatidae and Tanzaniophasmatidae specimens were fed house and flesh flies, as well as different size *Gryllus* nymphs. Additional prey that were successfully provided in captivity include mosquitos, plant hoppers, booklice, moths (including larvae), termites, bush crickets, antlion lacewings, may flies, and small earthworms. Adis et al., [33] also fed the insects dead mealworms (*Tenebrio*). In captivity, crickets were refused as prey by many Austrophasmatidae, but not Mantophasmatidae. For *T. gladiator,* [5] suggested that cockroaches and moths were prey in the Brandberg area. In a single experiment, we placed two late instar *Mantophasma* spec. nymphs (N21, Erongo Mountains) with a mantis nymph (*Miomantis* sp.) of the same size and from the same locality in a plastic box (100x100x40). The mantis was the prey. Cannibalism among nymphs and adults (also between females) has been regularly observed in captivity (see also [19,33]). In certain instances, females have successfully attacked males after mating or without mating contacts in both small pots and larger cages.

When hunting *Drosophila*, Mantophasmatodea waited or sometimes walked a few millimeters to the flies. With a sudden motion, they moved forward and caught the prey with their mandibles (see Additional file 12: Videos 6A, Additional file 13: Videos 6B, Additional file 14: Videos 6C and Additional file 15: Videos 6D). Thus, small prey, such as fruit flies, can be caught without using the legs. Occasionally, we observed that Mantophasmatodea used the tarsi of a foreleg to catch a fruit fly and bring it to their mouthparts. The insects embrace (face-to-face) larger prey using their spiny forelegs and, often, their mid-legs (Figure 12; see also [5] for *T. gladiator*); the prey is immediately consumed. In a single case, we removed an *A. gansbaaiense* female's victim (a male of the same species) immediately after the first attack to the neck and found the ventral nerve cord severed. This behavior was not consistent, but [5] also reported initial neck bites with larger flies. Meal consumption requires a short time and does not necessarily exclude body appendages (see Additional file 16: Video 7). Adis et al., [33] observed that Mantophasmatodea occasionally bite their prey's head off (e.g., *Musca*). We occasionally observed this behavior when we fed the Austrophasmatidae specimens using *Drosophila*. In few cases, the heelwalkers only used the heads for eating/feeding and neglected the remaining bodies from up to ten fruit flies.

Sexual behavior

General remarks

All Mantophasmatodea species exhibit strong sexual dimorphism in the external genital structure [4], and males are, on average, smaller and more slender compared with females. The male reproductive system includes testes, a deferent duct, seminal vesicles, and accessory glands [7] and is proliferated in the abdomen. Depending on the species, pregnant females have 8-15 eggs per ovary, which are surrounded by a thin cover of tissue and typically oviposited in a single pod (but see also [19], which includes a description of pods with 10-12 eggs). The female's weight increases remarkably during egg maturation (wet weight in g) (e.g., *Mantophasma kudubergense* (0.14-0.22) [5] and *Austrophasmatidae* sp. n. (0.063-0.152; S18, Vanrhynsdorp)). For *Karoophasma biedouwense* and *Hemilobophasma montaguense*, 50-100 eggs total per lifetime have been reported [19]. Under laboratory conditions, Mantophasmatodea mate readily; therefore, we observed different aspects of their sexual behavior, such as sexual communication, partner finding, courtship, and copulation, in several species and compared these data with previous descriptions in [20].

Drumming behavior

Both sexes use single vibrational calls, which are produced by tapping the abdomen onto the substrate (see Additional file 17: Videos 8A and Additional file 18: Video 8B), for mate location and recognition [20]. The male subgenital plate has a semicircular lip-like process of taxon-specific extension ([1,4]; Figure 19), which temporarily contacts the surface during drumming (='drumstick'). Females do not develop this abdominal process and tap with the middle part of their ventral abdomen. Female calls consist of single repeated pulses, whereas male calls are more complex pulse trains that likely contain coding for species recognition. Eberhard and Picker [20] detailed a behavior associated with duet drumming in *K. biedouwense*. The males randomly emitted drumming calls to test their environment for receptive females, whereas the females typically drummed in response to the male calls. After stimulation by a male, the females stopped walking, began drumming, and rapidly moved their antennae. In response, males initiated rapid antennal movement, rubbed their abdomen on vertical stems before drumming, and, finally, began their partner-searching behavior. Rubbing the abdomen appears facultative because we did not observe this behavior before drumming in our laboratory experiments. Substrate vibration is likely detected by leg scolopidial organs [21].

An analysis of two sympatric Austrophasmatidae (*Viridiphasma clanwilliamense* and *Karoophasma biedouwense* [20,44] species revealed different call parameters in both species and a clear preference for conspecific calls. However, most Mantophasmatodea species are not sympatric [31], and species recognition via species-specific call parameters may be relatively unimportant. This assumption was partially confirmed by [22], who analyzed vibrational communication in 13 Mantophasmatodea species, which included 11 Austrophasmatidae and two Mantophasmatidae species from Namibia. Nevertheless, slightly different call parameters were reported for all species studied. For females, a greater pulse repetition time in Austrophasmatidae was observed compared with species from Namibia [22]. For our report, we studied vibrograms and temporal call characteristics for male *Striatophasma naukluftense* from Namibia (Figure 20, Table 1). We studied the following five parameters for the male calls: 1) pulse repetition time (the time between single beats), 2) number of pulses per pulse train, 3) pulse train duration, 4) inter-pulse train intervals (the time between the end of one pulse train and the beginning of the next pulse train), and 5) pulse train repetition time (the time between initiating two pulse trains). For reasons explained below, only the first three parameters are presented here (see Table 1). In addition, we analyzed six males from the *Mantophasma/Sclerophasma* clade, which currently consists of *Sclerophasma paresisense* and several *Mantophasma* species. In contrast to the specimens studied in [22], our six *Mantophasma/Sclerophasma* specimens originated from different localities/populations (see Figure 1). The calls from these males were similar in structure, but the temporal patterns of all measured characteristics (see Table 1) differed significantly (Kruskal-Wallis test results are not shown). When comparing coefficients of variation (CV) values of the measured calls with those reported for other Mantophasmatodea species (CVs for all parameters <15%, see [22]), we found similar CV values for the duration of pulse trains and the number of pulses/train (CVs: 0.4-17%, see Table 1). In contrast, the pulse repetition time had much higher CVs on inter-individual level (38% and 57% for *Striatophasma* and *Sclerophasma/Mantophasma*, respectively) in our analysis compared with the study by [22]. Because the intra-individual comparisons did not demonstrate this variation, we excluded a systematic error. The number of individuals investigated was low and further specimens have to be investigated, but the obtained intra-specific variability in *Striatophasma* and *Mantophasma* already suggests variation at the population level. A direct comparison of call parameters obtained in our analyses with those reported in [22] is complicated by incorrect assignments (and GPS data) for their Namibian species; the calls assigned to specimens from the Brandberg should be from *Tyrannophasma gladiator* instead of *Sclerophasma paresisense*, and the calls assigned to specimens from Paresisberge should be from *Sclerophasma paresisense* instead of *Praedatophasma maraisi*. A notable

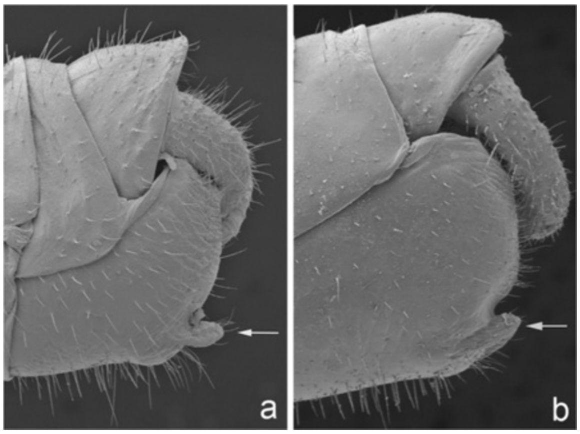

Figure 19 SEM micrographs showing taxon-specific development of male subgenital plates (arrow) from *Pachyphasma brandbergense* and *Striatophasma naukluftense*. (modified from [45]).

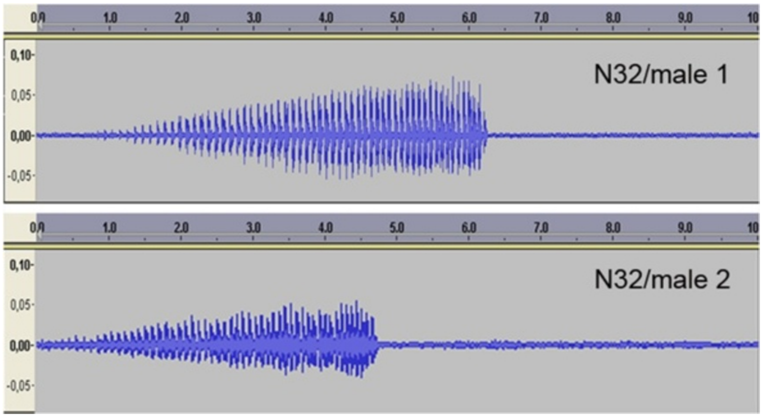

Figure 20 Vibrogram of substrate vibrational signals of two male *Striatophasma naukluftense*. The specimens were caught at Gamsberg Pass, Namibia (N32); the signals were recorded at ca. 20°C in the laboratory. The male call consists of repeated pulse trains and one pulse train for each individual is shown. The duration of pulse train is about 6000 ms (male 1) and 4500 ms (male 2), respectively. Note the increasing amplitude in the first segment and the more constant amplitude in the second segment of the pulse train.

difference between our analyses and [20,22] is that their recordings were collected during the day, and the insects were stimulated. In our recordings, the Austrophasmatidae species (not shown) drummed spontaneously, but only during the evening, at night, and, occasionally, in the morning. In contrast, both sexes in *Mantophasma* were also observed drumming during the day (see also [5]); however, the main drumming activity occurred at night without a detectable activity window. In general, the intra- and inter-individual variability in call parameters were

Table 1 Temporal characteristics of vibrational signals for three males of *Striatophasma naukluftense* and six males from the *Sclerophasma/Mantophasma* clade

Taxa	Pulse repetition time (ms)/CV(%)	Pulse train duration (ms)/CV(%)	Number of pulses per pulse train/CV(%)
***Striatophasma* (N32)**	19.46 ± 2.16/11%	5365.4 ± 409.6/7%	57.4 ± 5.38/9%
	n = 70	n = 7	n = 7
***Striatophasma* (N32)**	19.2 ± 2.41/125%	4395.7 ± 221.7/5%	50.2 ± 3.3/7%
	n = 40	n = 4	n = 4
***Striatophasma* (N33)**	35.6 ± 2.43/6%	2537.5 ± 323.3/13%	28.8 ± 2.93/10%
	n = 60	n = 6	n = 6
Average (N32,N32,N33)	**24.75 ± 9.39/38%**	**4099.53 ± 1437.02/35%**	**45.46 ± 14.8/32.5%**
***Sclerophasma* (N14)**	21.03 ± 3.77/17%	1300 ± 122.5/9%	14.89 ± 1.17/7%
	n = 90	n = 9	n = 9
***Mantophasma* (N9)**	not analyzed	1939.2 ± 266.7/13%	20.7 ± 2.6/12.5%
		n = 11	n = 11
***Mantophasma* (N10)**	24.05 ± 7.5/31%	2059.5 ± 277.8/13%	24 ± 3.0/12.5%
	n = 60	n = 6	n = 6
***Mantophasma* (N15)**	39.03 ± 3.65/9%	1689 ± 83.3/4%	19 ± 0.9/5%
	n = 60	n = 6	n = 6
***Mantophasma* (N20)**	74.08 ± 4.7/6%	1628.6 ± 111.3/7%	12.1 ± 0.9/7%
	n = 70	n = 7	n = 7
***Mantophasma* (N31)**	78.5 ± 2.12/2%	3205 ± 15/0.4%	13 ± 0
	n = 20	n = 2	n = 2
Average (N9,N10, N14, N15, N20, N31)	**47.34 ± 27.33/57%**	**1970.22 ± 660.1/33.5%**	**17.33 ± 4.79/28%**

The data are the mean ± standard deviation; n = number of measured values analyzed per individual. For pulse repetition times, each pulse train was measured 10 times and then averaged. CV = coefficient of variance (i.e., standard deviation/mean (rounded)); localities (N9-N33) in accordance with [31]).

expressed as CVs that ranged from 10-40% ([22]; this study) and were in the variation range for communication in other insects (23.6% average CV; [67]).

Based on the studies conducted using Mantophasmatodea, the following questions remain. 1) It is not clear whether repetitive pulse trains constitute a single call, as proposed in [20] and [22]. Alternatively, repetitive pulse trains could compose consecutive calls. 2) Certain parameters studied ([20,22], and this study) are inter-correlated. The number of pulses per pulse train might depend on the pulse train duration. As another example, the pulse train repetition time is the sum of the inter-pulse train interval and pulse train duration. It is difficult to determine which parameter is most important for females to discriminate among male calls from different species because of these strong inter-correlations. 3) In insect communication, call performance also depends on the specimen condition and ambient temperature (Boumans, pers. communication). Stonefly studies have demonstrated that temperature has an important impact on the frequency but not the number of pulses [68]. However, physical constitution affects the number of pulses per pulse train (Boumans, in prep.). After submitting the manuscript, the authors collected in the Richterveld (South Africa) males of two different species *(Namaquaphasma ookiepense; Austrophasmatidae* gen. n. sp. n. S01) in the same bush and placed them in separate plastic boxes in the field. The *N. ookiepense* males produced short pulse trains of about a second (see also [22]). In striking contrast to these short signals were the pulse trains of the second species which lasted 4-6 sec.

Courtship and mating behavior

If maintained in spacious cages, mating in Austrophasmatidae species primarily begins in the evening or at night. In contrast, mating of several *Mantophasma* specimens was observed at any time of day. Eberhard and Picker [20] hypothesized that males were attracted chemically through female pheromones over a long range and through continuous vibrational communication in a median range, such as where both partners are in the same bush. However, even if vibrational communication is part of a heelwalker's sexual behavior, it is not an obligate behavior for locating a sexual partner in the laboratory (see also [20]). If males and females were placed at different edges of a cage (200 × 200 × 300, with a grass tussock structure), they found each other without drumming. Sexual partners seemed to notice each other from approximately 8-10 cm. As they neared each other, rapid antennation (i.e., flickering of their antennae) occurred (see [20]), which indicates odor-mediated sexual communication. This approach was often interrupted by phases without movement. In most cases, the antennae did not directly contact the partner (see also [5]), but occasionally, contact was made. We frequently observed the males moving their abdomens up and down, while the females approached the males over a short range or continuously beat their abdomens on the surface/substrate. In one case, we observed a *Hemilobophasma montaguense* female that walked back and forth 3 cm in front of a male; suddenly, the female stopped and moved her abdomen up, and immediately, the male moved closer and mounted. Males mount rapidly. If the male's head was initially directed towards the tip of the female abdomen, the male quickly rotated until their heads were aligned (see Additional file 19: Video 9). Copulation occurs through a false male-above mating superposition, and males hold the females with their fore- and midlegs. Eberhard and Picker [20] reported arolia use during copulation, but this behavior was only observed (if ever) during the first second(s) of mounting to stabilize their position. Shortly after mounting, the males hold their arolia upwards again. For copulation, males extend their abdomen to the right side of the females, forming an "s" shape, while females project their abdomen upwards. Fixing the genitalia on the left side of the body was not observed (see also [20]). The male cerci are used as claspers to bring the genitalia of sexes close together. The large male genitalia evaginate and insert into the vagina (morphological description in [4]). During prolonged mating (see below), males remain mounted regardless of the female's behavior. During copula, we observed females walking, stalking, catching prey (see Additional file 20: Video 10), and excreting (see also [20]). Even if a female dropped down from the grass, the male remained sitting on the female's abdomen afterwards. Occasionally, we found males mounted on dead females. Both partners groomed during copula. When cleaning the forelegs, males occasionally stood with only their midlegs on the females, while the hind legs were held upwards. Under these circumstances, we observed that male midleg arolia contacted the female body. Except for grooming, the males did not move during copula; even the antennae did not flicker (see Additional file 11: Video 5). This observation might be interpreted as a behavioral adaptation to minimize the energy loss during the extended copulation time. The position of males during copulation was typical of Mantophasmatodea (Figure 21) and included upholding the hind legs, as well as resting from antenna flickering.

The males generally appear to be at risk of attack by the female, as indicated by their rapid mounting. Zompro et al., [5] reported that *Mantophasma kudubergense* males retreated by jumping away if the females appeared agitated after mounting. In *Austrophasmatidae* sp. n. (S18, Vanrhynsdorp), we observed that a female defended herself against a mounted male by both leg kicking and biting (see Additional file 21: Video 11). The elements of sexual behavior, such as drumming, antennae flickering for chemical cues, and antennae contact, can be interpreted

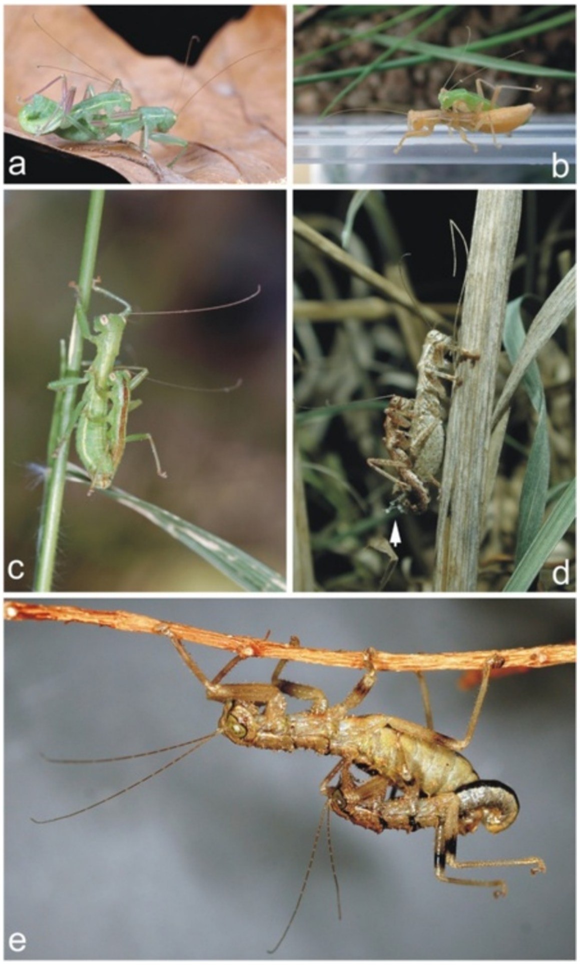

Figure 21 Typical mating position of Mantophasmatodea. (a) *Mantophasma* spec. (N15, Waterberg); righthand view. **(b)** *Mantophasma kudubergense* (N21, Erongo Mts.) with different color morphs; lefthand view. **(c)** *Striatophasma naukluftense* (N35, Naukluft Mts.; from [45]). **(d)** *Austrophasmatidae* sp. n. (S18, Vanrhynsdorp), with a conspicuous semi-liquid and gelatinous substance (arrow) between the external genital structures. **(e)** *T. gladiator* (N 38, Brandberg). Note the uniform position of the hind legs and antennae in males.

as species recognition behavior [20] or courtship behavior to reduce female attacks; the elements might be involved in both behaviors. As described for *Mantophasma kudubergense* by [33], we observed intense pumping movements at the tip of the abdomen for Austrophasmatidae males; thereafter, spherical eversion of the phallic lobes was observed. Eberhard and Picker [20] considered this action an indication of direct sperm transfer from males to females. This behavior was observed during the first 1-2 min of copulation and at least three times during the first hour of copulation. In our observations we did not identify similar time patterns for pumping in Austrophasmatidae. Pumping occurred at different periods during prolonged copulation. In *Austrophasmatidae* sp. n. (S18, Vanrhynsdorp) we observed a semi-liquid, gelatinous substance between the external genital structures of males and females during the last phase of copulation (Figure 21C). We assume that this substance was released by the male and that it was a type of mating plug, not a spermatophore.

Copulation frequency and time

Heelwalkers typically exhibited extended copulation times ([20,33]; our observations are summarized in Table 2). However, we do not know exactly when the sperm transfer occurred. Thus, we do not know if the prolonged mating time should be considered as mate guarding and which role prolonged copulation plays in the male and female Mantophasmatodea sexual strategies. Currently, there is no evidence that the copulation time depends on the sexual partners' mating status. Adis et al., [33] reported remating for *Mantophasma kudubergense*; we observed remating in other species, such as *A. gansbaaiense*, *K. botterkloofense*, and *Austrophasmatidae* sp. n. (S18, Vanrhynsdorp). Remating 24 - 48 h after the first mating has been observed both with different partners and the same partner, but no partner choice experiments have been conducted. *Austrophasmatidae* sp. n. (S18, Vanrhynsdorp) males occasionally began drumming 4 h after mating. In September 2003, in Little Karoo, we observed that 20.8% of all *H. montaguense* individuals were in copula during the day, which included 10 (i.e., five pairs) out of 48 (25 males, 23 females) individuals.

Mating costs

In captivity, female heelwalkers in copula were regularly observed hunting and feeding on insects. Therefore, the extra costs from mating may be low for females. In contrast, males do not eat during copula. Thus, males lose a significant amount of weight during copulation. We assume that a short starvation period is a natural phenomenon in Mantophasmatodea, similarly to other carnivorous arthropods (e.g., [69-71]). In addition to starvation and dehydration, transferring substantial amounts of protein and liquids to the females must also be considered. We attempted to assess the costs to males by comparing weight loss during copula versus weight loss during a similar starvation/dehydration period. The weight lost was considered an indicator of the cost to a male during prolonged mating. Weight loss during mating that exceeds a similar starvation period indicates remarkable protein transfer. Therefore, we compared the costs during mating with other biological periods of energy depletion to assess the consequences of prolonged mating for the male energy budget and fitness. In our experiments, *Austrophasmatidae* sp. n. (S18, Vanrhynsdorp) male weight loss was measured after starvation/dehydration for one group of males (starvation group, N = 6) and after mating for a

Table 2 Copulation times for several Mantophasmatodea species in the laboratory

Species	Observed copulation times in hours	Number of observed copulations
Karoophasma botterkloofense (S16)	> 29	1
*Karoophasma botterkloofense**	68.5 (S.E. ±4.56)	7
Austrophasmatidae sp. n. (S18)	7.5-31.5	17
Hemilobophasma montaguense (S26)	20-54	4
Austrophasma gansbaaiense (S32)	24 [R], 24 [R], 64	3
Mantophasma spec. (N21)	18-28	6
*Mantophasma kudubergense***	12-72	12
Hemilobophasma sp.n.[1] x *H. cf. montaguense*[2]	< 24	1
Mantophasmatodea in general***	Up to 96	-

*Data from [19].
**Data from [5], species assignment according to [46].
***Data from [36].
[R] Data from a remating pair of *A. gansbaaiense* (S32, Gansbaai).
[1] *Hemilobophasma sp. n.* - male (S31, De Rust).
[2] *Hemilobophasma cf. montaguense* - female (S29, Calitzdorp).

second group (mating group, N = 7). Starvation and mating were conducted under the same experimental conditions (temperature 22-24°C, 12 h light). Preliminary experiments showed 1) that males can lose up to 50% of their initial body mass within 24 h of starvation and dehydration, and 2) a significant positive correlation between initial body mass and percent of weight lost was identified (Spearman rank test: r = 0.89, N = 10, p = 0.01). Therefore, in the following experiments, we only used males with the same body class and feeding status (i.e., both groups did not differ significantly in their average initial weight) (starvation group: 0.033 g, s.d. 0.004/mating group: 0.0325 g, s.d. 0.003; t-Test: t = 0.226, df = 11, p = 0.82). Mating was not artificially interrupted, and we assumed copulation with sperm (and protein) transfer in all cases. As a result, the copulation times varied among tested males and were in the 11-21 h range (average 14.7 h), whereas the starvation time was 24 h for all individuals in the starvation group. The starving males lost body weight in the range of 2.6-29.6% (average: 13.29, s.d. 11.37), and the males in copulation lost body weight in the range of 3.5-9.0% (average: 6.38, s.d. 0.81). An analysis of variance confirmed that 1) the initial body weight had a positive effect on the percentage of body weight lost (i.e., the heavier individuals lost relatively more weight), 2) the weight lost between both experimental groups (starving/desiccating males versus mating males) did not differ, and 3) the treatment time (starvation or copulation time) did not affect the results (Table 3). Altogether, our data show that body weight lost during mating does not differ significantly from loss during a similar starvation and desiccation timeframe. Considering that males do not feed (and most likely do not take in water) during prolonged copulation, the data suggest that proteins are not excessively transferred from males to females.

Conclusions

Only a few years after the first Mantophasmatodea was described, the literature includes an impressive scientific knowledge on its diversity and biology. In contrast to the well-known distribution range in Southern Africa, however, the Mantophasmatodea range and diversity in East Africa have not been explored as extensively. In addition, the assignments of the known genera to different erected families must be clarified in a thorough revision. Future novel discoveries regarding general aspects of their biology will largely depend on successful breeding in captivity. One particular aspect of their biology is their tendency toward broad species distribution with many local populations. This phenomenon is, in part, due to low dispersal abilities (winglessness, low mobility, and low chance of dispersal for all stages, including eggs). Using mass fingerprints of peptide hormones to map the different populations, it appears possible that intraspecific migration/replacement/hybridization can be followed over a long time period, which is another unique possibility provided by these fascinating insects.

Table 3 Analysis of variance to determine the effects of 1) initial body weight (in g), 2) treatment duration (in hours), and 3) treatments (starvation/desiccating vs. mating) on the percentage of body weight lost in *Austrophasmatidae sp. n.* males (S18, Vanrhynsdorp)

Source of Variation	Sum of square	DF	Mean square	F	P
Corrected Model	554.466[a]	3	184.822	5.964	0.016
Intercept	276.439	1	276.439	8.921	0.015
Main Effects					
Initial body weight	385.618	1	385.618	12.444	0.006
Duration of treatment	129.356	1	129.356	4.174	0.071
Treatment	016.256	1	016.256	0.525	0.487
(Starvation/mating)	278.885	9	030.987		
Error	2037.005	13			
Total	833.351	12			
Corrected total					

[a] $R^2 = 0.665$ (adjusted $R^2 = 0.554$).

Sampling and export permissions

The insects were captured and exported with permission from the Western and Northern Cape Nature Conservation Boards (no. 2297/2003, 0697/2004, 0554/2004), the Ministry of Environment and Tourism of Namibia (research/collecting permits 891/2005, 1041/2006), and Malawi (Government Document: Department of Forestry Specimens Collection Permit 21/01/2011/no.1).

Additional files

Additional file 1: **Methods.**

Additional file 2: **Video 1A - Jumping male; *Tyrannophasma gladiator*.** Note: movement of antennae is artificially affected by airflow using a blow-dryer.

Additional file 3: **Video 1B - Jumping male; *Tyrannophasma gladiator*.** Note: movement of antennae is artificially affected by airflow using a blow-dryer.

Additional file 4: **Video 1C - Jumping male; *Tyrannophasma gladiator*.** Note: movement of antennae is artificially affected by airflow using a blow-dryer.

Additional file 5: **Video 1D- Female is jumping over a male which tries to mount and copulate afterwards; *Karoophasma botterkloofense*.**

Additional file 6: **Video 2A- Flexible body whilst jumping; *Tyrannophasma gladiator*.**

Additional file 7: **Video 2B- Flexible body whilst jumping; *Tyrannophasma gladiator*.**

Additional file 8: **Video 3A - Landing behavior after dropping; *Tyrannophasma gladiator*.**

Additional file 9: **Video 3B - Landing behavior after dropping; *Tyrannophasma gladiator*.**

Additional file 10: **Video 4 - Grooming behavior; *Austrophasmatidae* sp. nov. (S18, Vanrhynsdorp).**

Additional file 11: **Video 5 - Antenna-flickering, *Austrophasmatidae* sp. nov. (S18, Vanrhynsdorp).**

Additional file 12: **Video 6A - Foraging behavior; *Karoophasma botterkloofense*.**

Additional file 13: **Video 6B - Foraging behavior; *Austrophasmatidae* sp. nov. (S18, Vanrhynsdorp).**

Additional file 14: **Video 6C - Foraging behavior; *Austrophasmatidae* sp. nov. (S18, Vanrhynsdorp).**

Additional file 15: **Video 6D - Foraging behavior; *Austrophasmatidae* sp. nov. (S18, Vanrhynsdorp).**

Additional file 16: **Video 7 - Foraging behavior (details); *Pachyphasma brandbergense*.**

Additional file 17: **Video 8a, Drumming behavior; *Austrophasmatidae* sp. nov. (S18, Vanrhynsdorp).**

Additional file 18: **Video 8B - Drumming behavior; *Austrophasmatidae* sp. nov. (S18, Vanrhynsdorp).**

Additional file 19: **Video 9B - Mating behavior; *Austrophasmatidae* sp. nov. (S18, Vanrhynsdorp).**

Additional file 20: **Video 10 - Female foraging whilst in copula; *Austrophasmatidae* sp. nov. (S18, Vanrhynsdorp).**

Additional file 21: **Video 11 - Female defense against male; *Austrophasmatidae* sp. nov. (S18, Vanrhynsdorp).**

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

SR and RP conducted field samplings and observations. Rearing, laboratory observations including video and vibrational signal tapping were performed by RP and partly by SR. The mating cost experiment was carried out and analyzed by SR. JM analyzed the vibrational signals. Data interpretation and preparation of the manuscript was done by SR, RP and JM. The final manuscript was written by RP and SR. All authors read, commented on and approved the final manuscript.

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