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Novel Wing-Flashing Behavior in a Scorpionfly (*Panorpa debilis*) May be Competitive

Brian R. Magnier[1] · Graham A. Montgomery[1]

Abstract Scorpionflies (Mecoptera: Panorpidae) are important models for studying sexual selection and mating strategies. However, much is still unknown about their behavior and natural history. Here we describe a wing-flashing behavior in a population of *Panorpa debilis* Westwood from central New York. Wing-flashing has been previously observed, but not described in Mecoptera. We use a combination of direct observation and video analysis in an attempt to understand the motivation behind this behavior: is wing-flashing behavior used for attraction of mates, for control of food resources, or perhaps neither? If wing-flashing is involved in mate attraction, we would expect skewed wing-flashing ratios between males and females and a high rate of wing-flashing aimed at conspecifics of the opposite sex. If the behavior is instead used for intraspecific competition for resources, we would expect a high degree of wing-flashing aimed at conspecifics of the same sex or indiscriminate of sex. We demonstrate that this behavior is nonrandom — and most likely competitive in nature — by showing that wing-flashing preferentially occurs near other individuals, and by comparing wing-flashing rates across males and females in a variety of situations. Both sexes used wing-flashes in response to the opposite sex, though most wing-flashes were female to female signals. Wing-flashing was even observed as a response to potentially competitive arthropods like harvestmen (*Leiobunum* spp.). In addition to their suitability as study organisms for mating behavior, *P. debilis*, may be a useful organism for studying animal communication and signaling.

Keywords Antagonistic behavior · mecoptera · *panorpa* · scorpionfly · signaling · wing-flash

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Introduction

Characterization and study of animal behaviors is vital, not only in the field of animal communication, but also in diverse fields from psychology to evolutionary biology. One of the most useful models for understanding animal communication and information transfer between individuals is the signal-cue model: signals are behavioral or morphological adaptations evolved to convey information to a receiver, while cues are unintentional traits or actions that a receiver can pick up (Guilford and Dawkins 1991). Intraspecific competition for resources is common in nature, and has lead to the evolution of aggressive interactions and behaviors, often in the form of signals and cues (Bakker 1962; Endler 1992; Searcy and Nowicki 2005). Besides mediating competitive interactions, signals and cues can also serve an important function in mating systems, eg. in peacock spiders of the genus *Maratus* (Salticidae; Girard et al. 2015).

In the context of intraspecific competition, bold patterns and spread limbs, often wings, can be used as signals that establish dominance (Ficken 1962; Simpson 1968). Taxa across the animal kingdom utilize patterns as deceptive or startling behaviors in competition against rivals: cephalopods (Adamo and Hanlon 1996), birds (Aves: Eurypygidae; Thomas and Strahl 1990), and especially insects. Within insects, competitive signaling is widespread and has been described in Blattodea (Barth 1964), Orthoptera (Alexander 1961), and Diptera (Briceño et al. 1996; Burk 1983; Alcock and Pyle 1979), sometimes with reference to competition over "personal space" (Biggs 1972).

Panorpa debilis, a species of panorpid scorpionfly found in the northeastern US, has a high-contrast black-and-white pattern on its wings, which it frequently raises, perhaps as a signal. As a member of the order Mecoptera, *Panorpa debilis* is a holometabalous insect closely related to fleas (Siphonaptera) and flies (Diptera) (Misof et al. 2014). The order Mecoptera contains relatively few species (~600 worldwide; Whiting 2002), and most are economically unimportant, thus mecopteran groups are often overlooked compared to larger insect orders. Within the family Panorpidae, most species prefer moist woodlands (Byers 1963) and most, like *P. debilis,* are short-lived scavengers (Byers and Thornhill 1983), perhaps bringing them into competition for resources with harvestmen (Opiliones: *Leiobunum spp.*) that occupy a similar niche. Scorpionflies are also well known for their nuptial displays and interesting courtship behavior (Engqvist and Sauer 2003; Engqvist 2009; Hartbauer et al. 2015; Rupprecht 1974; Steiner 1929), wherein males present a nuptial gift to a female prior to copulation. Scorpionflies have a resource-defense polygyny mating strategy (Thornhill 1980; Thornhill 1981), in which males compete for resources to present to females. Males will present a salivary secretion as a "nuptial gift" to a female. The quantity of saliva presented is related to the male's condition, driving the need for a productive territory (Engqvist 2009). It has also been shown that males utilize pheromones in their courtship display (Thornhill 1979).

The reason why *P. debilis* "wing-flashes," raising its wings in a way that seems to advertise their high-contrast patterning, is unknown. Here we aim to describe this previously undescribed behavior and to interpret its function. Video recordings combined with direct observation allow us to conduct basic inquiries into the potential motivations behind this wing-flashing behavior. We aim to answer one primary question: Is wing-flashing primarily related to attracting mates (as in peacock spiders), or is it competitive in nature, involved with securing food resources (as in many flies)?

To address this overarching question, we ask the following: 1) Is wing-flashing a random behavior, or is it a function of proximity to the nearest individual? If it is indeed a non-random signal to other individuals, it might serve a competitive or reproductive purpose; if it is randomly given it must serve another function. 2) Are there sex-based differences in wing-flash rate? A differential wing-flash rate between sexes could suggest that this behavior is involved in reproduction. Scorpionfly mating behavior primarily takes place at night (Byers 1963; Engqvist and Sauer 2003; Engqvist 2009; Thornhill 1981), but we might still expect to detect frequency differences in wing-flashing during the day if it were primarily a behavior restricted to one sex. 3) Is wing-flashing only observed in response to conspecifics, or do we observe it in interactions with other species as well? Use of this behavior in response to species with similar niches could support the hypothesis that wing-flashing is competitive. An increase in wing-flashing rate at the site of resources could also support this hypothesis.

Methods

Study Site

The study site was a poorly drained patch of mixed deciduous forest in the Mundy Wildflower Garden on the campus of Cornell University in Ithaca, New York (42.44993, −76.46956). The survey area was a 5-by-10 m rectangular area, adjacent to a trail, that appeared to be a site of high *Panorpa* density. To roughly estimate population size at the site, scorpionflies were captured and marked with a unique color combination of paint. 34 individuals were marked in this way, then daily counts of marked and unmarked individuals showed that individual turnover was relatively high: the day after marking individuals, we observed over 40 individuals in the study site, only 4 of which were marked (10% resight rate). This mark-resight experiment combined with daily counts of individuals allowed us to estimate that at least 80 individuals were present in this area during the study period in late summer. Capture of multiple male and female specimens enabled us to determine our study species to be *Panorpa debilis* based on morphology. At least one other *Panorpa* species (*Panorpa nebulosa* species group, cf. *nebulosa*) was present at the field site, but in low numbers, and was not included in any videos or analyses. Cryptic species could have been present, but methods to detect them (eg. mitochondrial barcoding) were beyond the scope of this study. Voucher specimens were deposited in the Cornell University Insect Collection (CUIC Lot # 1272).

Observations

We observed behavior via two methods: Five-minute individual observations and video recording. All observations occurred in late summer 2014 between 10:00 and 18:00 h in order to avoid the possibility of sluggish behavior in early morning. Unfortunately, logistics made nocturnal observations impossible for this study. For each five-minute observation ($n = 7$), one *Panorpa debilis* individual was chosen at random within the study-site. Using a stopwatch, we observed its behavior for five minutes, noting the time of each wing-flash given by the individual and assigning a distance rating of 1–6

based on proximity to the signal recipient. Distance categories were classified as: *1*: <2 cm, *2*: 2-5 cm, *3*: 5-10 cm, *4*: 10-15 cm, *5*: 15-25 cm, *6*: >25 cm. We also noted if/ when the individual was feeding or drinking during the observation.

Video Recording and Analysis

We recorded nearly one hour of video footage (62 videos) using a Canon EOS 6D DSLR camera (Ota, Tokyo, Japan). We randomly chose individuals within the study area for recording over the course of 3 days. Due to the high rate of individual turnover (based on resighting rates of marked individuals), we believe our video sampling represents a large subset of the individuals present: likely between 50 and 60 individuals. The length of each clip varied considerably, with a maximum video length of ~6 min and a minimum of 7 s, though most were around one minute long. We did not focus on individuals displaying certain behaviors and all videos were shot to include nearby individuals in the frame.

   Two datasets were created from this one hour of footage; the first to determine the rate of wing-flashing in various contexts, and the second to determine if wing-flashing was given randomly or non-randomly (closer to other individuals). To create the first dataset, we assigned each segment of video to one of four categories of interactions — alone, conspecific, harvestman or harvestman + conspecific. We then noted the number of wing-flashes observed during the time spent in that context. The "alone" context was assigned if distance to the nearest individual was >15 cm; this distance was assigned as the cutoff due to the low visibility of the signal to other individuals in the dense undergrowth at greater distances. The "conspecific" context was assigned if distance to the nearest conspecific was <15 cm. The "harvestman" context was assigned if a harvestman was <15 cm away, and "harvestman + conspecific" was likewise assigned if a harvestman and conspecific were both present. Many videos were comprised of individuals in multiple contexts; eg. a scorpionfly could begin the video in an alone context, but then move into the conspecific context if a conspecific approached. Any time the context changed, a new data entry began. If a situation was ambiguous (eg. the signal recipient was not clear, as was often the case if multiple conspecifics/ harvestmen were present) the segment of video was excluded from analysis. For each video segment, we also noted sex, signal recipient sex, feeding/not feeding, and physical contact presence/absence. We determined sex by noting the presence or absence of the elongated abdomen and clasping genital bulb in male scorpionflies, an obvious feature. Focal individuals were chosen at random and individuals part of an interacting pair were not counted twice. This dataset allowed us to compare the rates of wing-flashing among the four contexts we defined.

   We also wanted to determine if wing-flashing rates were higher when individuals were closer together, and created the second dataset to answer this question. We started by digitally measuring the distance to the recipient individual in ImageJ (v. 1.48 Abramoff et al. 2004) whenever an individual flashed its wings in a video. We calibrated our measurements to the size of an average individual of *Panorpa debilis* (roughly 1.5 cm), and rounded the distance to the recipient individual to the nearest centimeter. From these data, we were able to create a distribution of distances to the nearest neighbor when individuals were wing-flashing ("Wing-flashing"). For

comparison, we next created a distribution of distances to the nearest neighbor when individuals were *not* wing-flashing ("Not Wing-flashing").To do this, we took multiple distance measurements for each video. Distances to the nearest neighbor were taken at the beginning of the video and at 15 s intervals until the clip ended, thus giving more weight to longer videos. Finally, we compared the distributions and means of "Wing-flashing" and "Not Wing-flashing", allowing us to determine if wing-flashing usually occurred when individuals were closer together than normal.
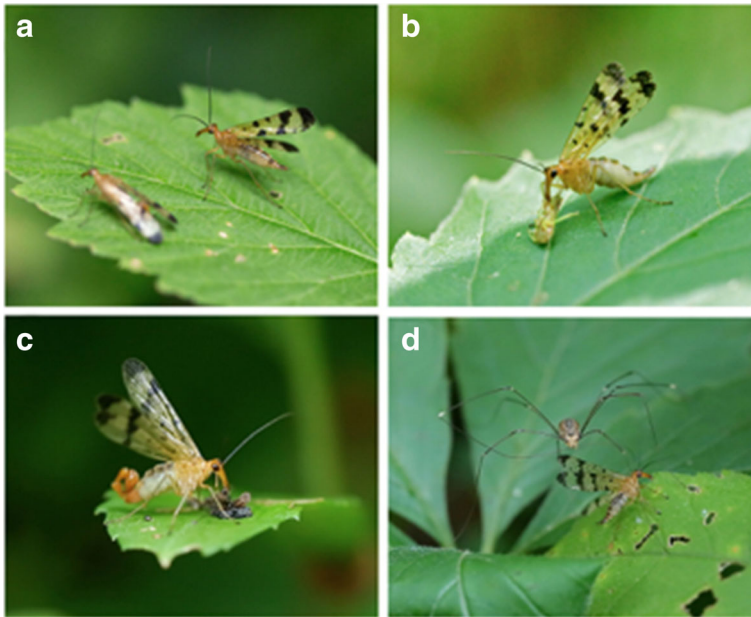
Description of Wing-Flashing Behavior

P. debilis wing-flashing behavior consists of raising and lowering both fore- and hind-wings, often in response to approaching conspecifics or while feeding or drinking (Fig. 2). During a typical wing-flashing event, an individual will start with wings held at rest, parallel to the body, then raise all four at once, with the front pair rising to nearly a 45 degree angle to the coronal axis of the body (see Figs. 1 and 2). The wings are then lowered more slowly than they were raised. Wing-flashing behavior appears to fall on a gradient from subdued raises to fully-spread flashes. At one end of the spectrum, the movement is quite slow, with both pairs of wings held together as they are raised. At the other extreme, both pairs of wings are raised quickly, and all four wings separate slightly. Both males and females exhibit slow and fast wing-flashes; the average duration of a single wing-flash is 0.95 s, with a range from 0.28 to 2.09 s ($n = 30$). Wing-flashing can occur frequently, often many times per minute, and wings seem to be more fully-spread during aggressive interactions than during feeding or drinking.

We also rarely observed abdomen quivering during wing raises. Abdomen vibration has been described during courtship and aggressive interactions in *Panorpa* previously (Thornhill 1981; Hartbauer et al. 2015), and it has been suggested that vibrations are generated by both sexes prior to copulation to locate each other (Rupprecht 1974). Hartbauer et al. (2015) noted slow "wing-waving" in *Panorpa,* accompanied by abdominal vibrations, related to mating, but this behavior appears to be distinct from the "wing-flashing" observed in *P. debilis*. The abdominal vibrations described therein appeared to be associated with a sex-pheromone emitted by males prior to copulation; we also observed females performing this abdominal vibration behavior.

Fig. 1 Photographs of a captured female *Panorpa debilis* **a** at rest and **b** wing-flashing

Fig. 2 Images of wild *Panorpa debilis* exhibiting wing-flashing behavior. **a** A female wing-flashing in response to nearby male. **b** A female eating a cicadellid. **c** A male eating a dead arthropod. **d** A female wing-flashing towards a harvestman. All images are frames from our video observations

Results

Direct Observations

Direct observations are presented as five-minute time-lines to show the context of wing-flashes in seven individuals (Fig. 3). Distance between individuals not wing-flashing was not recorded, limiting the utility of these data, but we note that most wing-flashes occurred when conspecifics were nearby or during feeding/drinking.

First Dataset - Generalized Linear Model

Data were analyzed in JMP 10 Pro (JMP®). We analyzed our first dataset, focused on wing-flash rate in different contexts, by using a generalized linear model based on count data, with a Poisson family and log linkage. The response variable was the count of the number of wing-flashes observed during the video. Log(time) was used as an offset to account for differences in sampling effort, as we assume the expected number of wing-flashes to be proportional to observation time. We included the following variables in the analysis: sex, context of the video segment, presence of feeding/drinking, and the interaction terms sex*context and feeding/drinking*context. Insignificant interaction terms were excluded from the model to prevent over-parameterization and the optimized model was chosen based on the AIC score. Post-hoc pairwise comparisons were performed, with a Bonferroni correction for multiple comparisons. We performed a total of 10 comparisons,
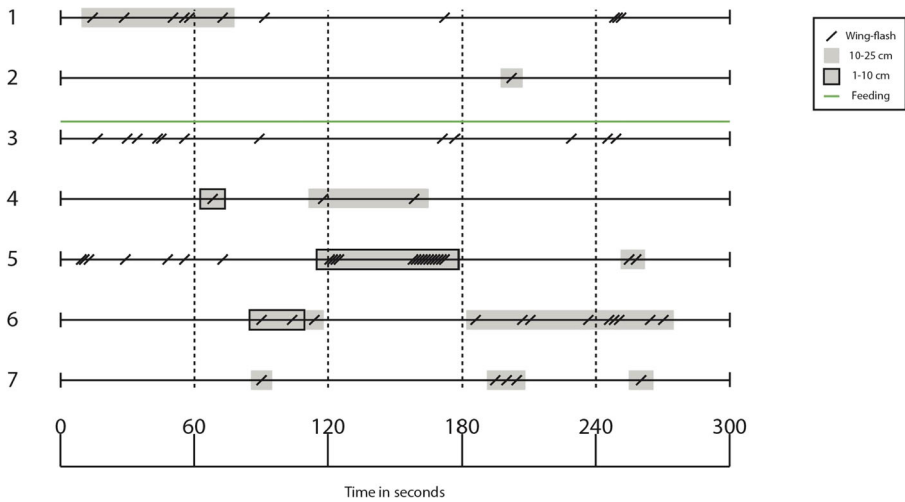
Fig. 3 Summary of direct observations. Individual number is shown on the y-axis. Slashes (/) denote wing-flashes. *Shaded regions* and *outlined/shaded* regions show proximity to the nearest conspecific (10–25 cm, and 1–10 cm, respectively and a *green line* above a timeline denotes feeding. Note that distance to the nearest conspecific between bouts of wing-flashing was not recorded. For instance, in observation 4, a conspecific could have been closer than 25 cm in between the first and second wing-flash

yielding a new alpha level of 0.005. Additionally, using the linear model and a Prediction Profiler in JMP, expected values of wing-flashes per unit time for each context were generated (Fig. 4). The high rate of individual turnover at the study site (as demonstrated in our mark-sight study) allows us to assume independence between samples.

Average rates of wing-flashing in each context are presented in Table 1. Overall, we found that females near conspecifics (in the conspecific context) showed significantly higher rates of wing-flashing than when alone (in the lone context), when excluding individuals that were feeding/drinking ($\chi^2 = 10.89$ [DF = 1], $p = 0.0010$). Males, however, did not exhibit a significant difference. When feeding/drinking, lone individuals showed significantly higher rates of wing-flashing than when alone and not feeding/drinking ($\chi^2 = 19.24$ [DF = 1], $p < 0.0001$), and individuals feeding/drinking while alone did not show a significant difference in wing-flash rate compared to individuals near conspecifics ($\chi^2 = 0.023$ [DF = 1], $p = 0.879$). Aacross all contexts (alone, conspecific, harvestman or harvestman + conspecific), there was no significant difference in wing-flashing rate between males and females ($\chi^2 = 1.38$ [DF = 1], $p = 0.24$). In some contexts, however, there was a significant difference. Males showed significantly higher wing-flash rates than females when alone ($\chi^2 = 12.98$ [DF = 1], $p = 0.0003$). Additionally, female scorpionflies had a significantly higher rate of wing-flashing when near harvestman than when alone ($\chi^2 = 42.51$ [DF = 1], $p < 0.0001$), but this difference was not significant in males ($\chi^2 < 0.0001$ [DF = 1], $p = 0.99$).

Across the footage, we recorded 258 wing-flashing events given near a single conspecific 'target' individual. Of these, 225 (87.2%) were given by females in close proximity to another female. Females signaled to males in 16/258 (6.2%) of wing-
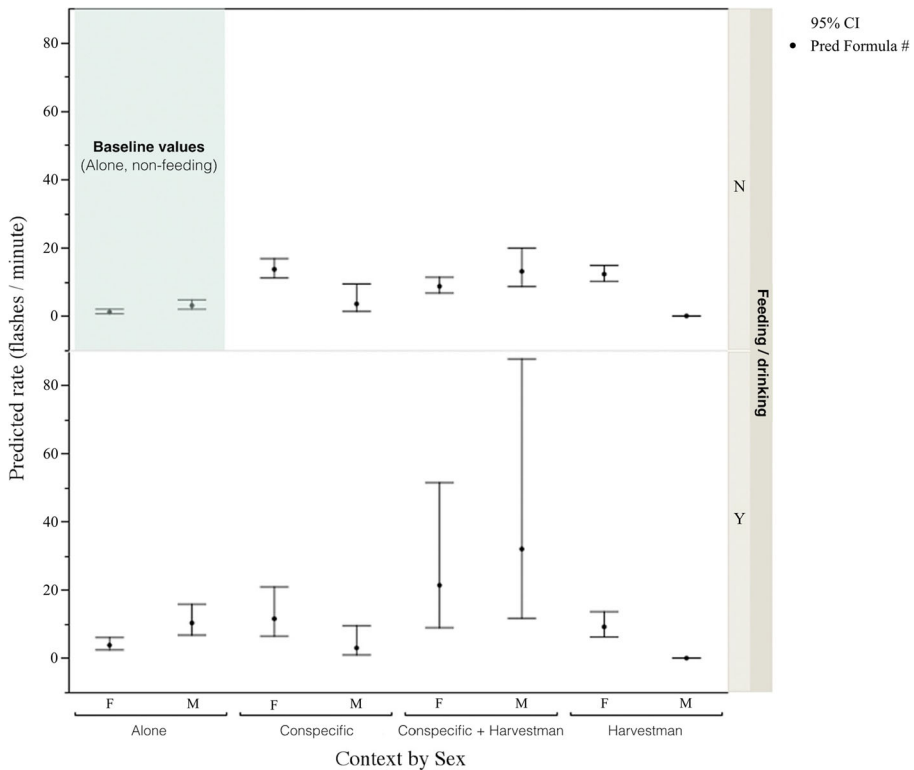
Fig. 4 Graph of predicted wing-flash rate by sex, context, and feeding/drinking or not. Mean predicted rates and 95% CI reported, generated from our generalized linear model. Rates are expected wing-flash values per minute

flashing events, and males signalled to females in 17/258 (6.6%) of wing-flashing events. No exclusively male-male wing-flashing was recorded. Wing-flashes were omitted from these statistics when two or more possible signal recipients were present r, making it impossible to judge which individual was the intended receiver.

Second Dataset - Distance Analysis

Using a student's t-test (DF = 319), we found that the average distance between between a wing-flashing individual and its nearest neighbor was significantly lower than the average distance between an individual and the nearest potential signal receiver ($p < 0.0001$) when not wing-flashing. The mean distance between individuals at a random point in time was 8.6 ± 4.9 cm ($n = 161$), while the mean distance between a wing-flashing individual and the nearest potential signal receiver was 6.8 ± 5.0 cm ($n = 341$).

Overall, 51% of wing-flashes occurred within 4 cm of a potential receiver, and 79% occurred when the individual was within 15 cm. When looking at distances taken at standard points in time, as opposed to whenever a wing-flash was given, we found that scorpionflies spent approximately 25% of their time within 4 cm of potential receivers, and 70% within 15 cm (Fig. 5).

Table 1 Predicted rate of wing-flashing per minute of observation by sex, context, and feeding

Sex	Context	Feeding/drinking	Predicted rate (Wing-flashes/min)
F	Alone	N	1.1
F	Alone	Y	3.8
F	Conspecific	N	13.6
F	Conspecific	Y	11.5
F	Conspecific + Harvestman	N	8.7
F	Conspecific + Harvestman	Y	21.3
F	Harvestman	N	12.2
F	Harvestman	Y	9.1
M	Alone	N	3.0
M	Alone	Y	10.2
M	Conspecific	N	3.5
M	Conspecific	Y	3.0
M	Conspecific + Harvestman	N	13.0
M	Conspecific + Harvestman	Y	31.8
M	Harvestman	N	-[a]
M	Harvestman	Y	-[a]

Predicted values were generated from the generalized linear model created from the first dataset. [a] Males were never observed wing-flashing in response to harvestman alone

Discussion

Through our analyses, we found that 1) Wing-flashing is more likely to occur when individuals are in close proximity, supporting that this behavior is non-random, especially in combination with the finding that scorpionflies have higher rates of wing-flashing while feeding or drinking. 2) Wing-flashing behavior in *Panorpa debilis* occurs frequently in both sexes (Fig. 4) in response to multiple contexts, weakening support for the "mate attraction" hypothesis. 3) Wing-flashing rate did increase when harvestmen were nearby, but this increase was only significant in females. Based on these results, we conclude that wing-flashing is a versatile antagonistic signal aimed at potential competitors and is not primarily a mating signal.

In the characteristic scorpionfly "resource-defense polygyny" reproductive strategy, males compete with other males to defend resources in order to gain access to females (Thornhill 1981). While we never observed any mating behavior, due to the timing of our observations (scorpionflies usually mate at night), it is possible that wing-flashing is related to this resource-defense strategy of reproduction. Without observing mating, we can't rule out the use of wing-flashing; future studies should include mating observations. However, if mating were the main motivation behind wing-flashing behavior, we might expect to find males exhibiting higher wing-flashing rates than females. We found that male and female wing-flashing rates are not significantly different overall, although rates did vary in different contexts. Males wing-flash more when alone than females do, while females wing-flash more when near conspecifics;
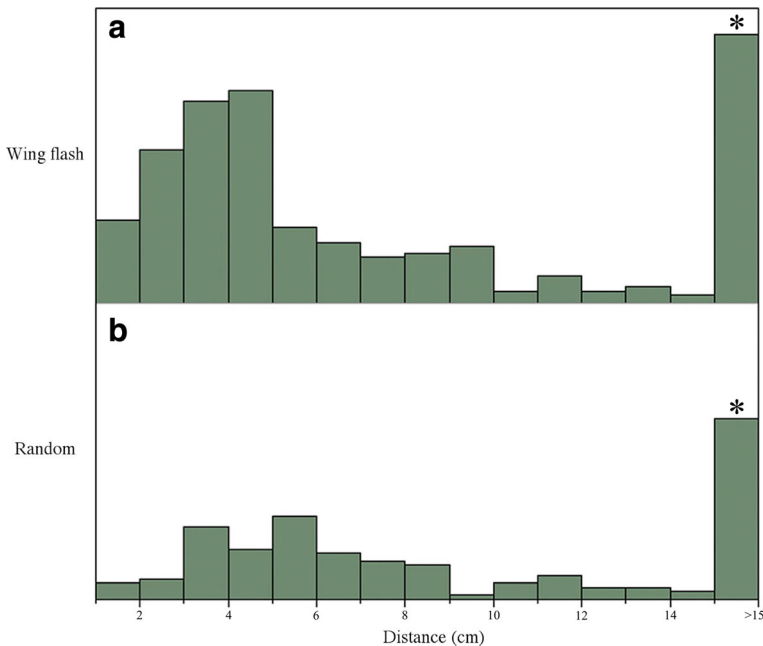
Fig. 5 Histogram of distances from one scorpionfly to the nearest signal receiver. All distances are rounded to the nearest cm. Cut-off for accurate measurement was 15 cm. Note that all larger distances are treated as 15 cm. **a** Count data during wing-flashing. **b** Count data from "random", i.e. non-wing-flashing, times

females also wing-flash more when near harvestman (Opiliones: *Leiobunum* spp.) than when alone. None of these findings suggest a link to mating. Looking more closely at wing-flashing contexts, by far the most wing-flashes observed between conspecifics were female-female signaling pairs (87.5%). Females and males both wing-flashed in response to individuals of the opposite sex, but males were never seen wing-flashing specifically to another male. Females far outnumbered males in the field, and subsequently in video samples, which suggests females may be more numerically common, or at least more visible; we have a smaller sample size for males. Males did, however, have lower wing-flashing rates than females when conspecific were present; Females often wing-flashed when conspecifics were present, a finding supported by context-specific wing-flash rate data. This suggests that wing-flashing could signify competition over resources. Females may need to zealously protect resources to increase fecundity/egg production; males, on the other hand, may not be so resource-stressed, and thus may not need to defend resources and personal space so actively.

Harvestman frequently elicited wing-flash responses coupled with apparently aggressive physical contact from the scorpionfly, further suggesting that wing-flashing is not solely an intraspecific behavior related to courtship or mating. Harvestman are scavengers in direct competition with scorpionflies for resources, namely dead arthropods (Halaj and Cady 2000; Wijnhoven 2011), and so scorpionflies may use wing-flashing as a competitive resource-defense signal. We did not detect a significant difference between male wing-flash rate when alone and when in the presence of a harvestman, but we again did find a significant difference

for females. This result, similar to our finding that female wing-flash rates are higher in the presence of conspecifics, could support the idea that females protect resources more strongly than males.

Overall, the wing-flashing behavior described here in *Panorpa debilis* (Fig. 1) appears most similar to the agonistic wing displays found in tephritid flies in the genus *Rhagoletis* (Tephritidae; Aluja and Norrbom 1999; Bush 1969). Although it does occur during mating, wing-waving documented in *Rhagoletis pomonella* does not appear to be directly related to reproduction. Wing-waving in this species is often coupled with charging attacks and direct contact with conspecifics and appears to be related to "personal space" rather than fixed territories (Biggs 1972). Like many other wing-signaling insects, including *P. debilis*, *R. pomonella* possess boldly patterned black and white wings, which may have evolved to increase signaling distance and intensity. Similar to *Rhagoletis*, we conclude that wing-flashing in *Panorpa debilis* appears to function as a versatile antagonistic signal between individuals, and may also play an important role in resource defense, especially in females.

References

Abramoff MD, Magalhaes PJ, Ram SJ (2004) Image processing with image J. Biophoton Int 11:36–42

Adamo SA, Hanlon RT (1996) Do cuttlefish (Cephalopoda) signal their intentions to conspecifics during agonistic encounters? Anim Behav 52:73–81

Alcock J, Pyle WD (1979) The complex courtship behavior of *Physiphora demandata* (F.) (Diptera: Otitidae). Z Tierpsychol 49:352–362

Alexander RD (1961) Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). Behaviour 17:130–223

Aluja, M., & Norrbom, A. (Eds.). (1999). Fruit flies (Tephritidae): phylogeny and evolution of behavior. CRC Press, Boca Raton, FL, 376–401.

Bakker K (1962) An analysis of factors which determine success in competition for food among larvae of *Drosophila melanogaster*. Arch Néerl Zool 14:200–281

Barth RH Jr (1964) The mating behavior of *Byrsotria fumigata* (Guerin) (Blattidae, Blaberinae). Behaviour 23:1–30

Biggs JD (1972) Aggressive behavior in the adult apple maggot (Diptera: Tephritidae). The Canadian Entomologist 104:349–353

Briceño RD, Ramos D, Eberhard WG (1996) Courtship behavior of male *Ceratitis capitata* (Diptera: Tephritidae) in captivity. Fla Entomol 79:130–143

Burk T (1983) Behavioral ecology of mating in the Caribbean fruit fly, *Anastrepha suspensa* (Loew)(Diptera: Tephritidae). Fla Entomol 66:330–344

Bush GL (1969) Mating behavior, host specificity, and the ecological significance of sibling species in frugivorous flies of the genus *Rhagoletis* (Diptera: Tephritidae). Am Nat 103:669–672

Byers GW (1963) The life history of *Panorpa nuptialis* (Mecoptera: Panorpidae). Ann Entomol Soc Am 56: 142–149

Byers GW, Thornhill R (1983) Biology of the Mecoptera. Annu Rev Entomol 28:203–228

Endler JA (1992) Signals, signal conditions, and the direction of evolution. Am Nat 139:125–153

Engqvist L (2009) Should I stay or should I go? Condition- and status-dependent courtship decisions in the scorpionfly *Panorpa cognata*. Anim Behav 78:491–497

Engqvist L, Sauer KP (2003) Influence of nutrition on courtship and mating in the scorpionfly *Panorpa cognata* (Mecoptera, Insecta). Ethology 109:911–928

Ficken MS (1962) Agonistic behavior and territory in the American redstart. Auk 79:607–632

Girard MB, Elias DO, Kasumovic MM (2015) Female preference for multi-modal courtship: multiple signals are important for male mating success in peacock spiders. Proc R Soc B 282:2015–2222

Guilford T, Dawkins MS (1991) Receiver psychology and the evolution of animal signals. Anim Behav 42:1–14

Halaj J, Cady AB (2000) Diet composition and significance of earthworms as food of harvestmen (Arachnida: Opiliones). Am Midl Nat 143:487–491

Hartbauer M, Gepp J, Hinteregger K, Koblmüller S (2015) Diversity of wing patterns and abdomen- generated substrate sounds in 3 European scorpionfly species. Insect science 22:521–531

JMP®, Version 10 [Computer software]. SAS Institute Inc., Cary, NC, 1989–2007. Available from http://www.jmp.com

Misof B, Liu S, Meusemann K, Peters RS, Donath A, Mayer C et al (2014) Phylogenomics resolves the timing and pattern of insect evolution. Science 346:763–767

Rupprecht R (1974) Vibrationssignale bei der Paarung von Panorpa (Mecoptera/Insecta). Experientia 30:340–341

Searcy WA, Nowicki S (2005) The evolution of animal communication: reliability and deception in signaling systems. Princeton University Press, Princeton, NJ

Simpson MJA (1968) The display of the Siamese fighting fish, *Betta splendens*. Anim Behav Monogr 1:1–73

Steiner P (1929) Studien an *Panorpa communis* L. Z Morphol Okol Tiere 17:1–67

Thomas BT, Strahl SD (1990) Nesting behavior of sunbitterns (*Eurypyga helias*) in Venezuela. Condor 92:576–581

Thornhill R (1979) Male pair-formation pheromones in Panorpa scorpionflies (Mecoptera: Panorpidae). Environ Entomol 8:886–888

Thornhill R (1980) Competition and coexistence among *Panorpa* scorpionflies (Mecoptera: Panorpidae). Ecol Monogr 50:179–197

Thornhill R (1981) *Panorpa* (Mecoptera: Panorpidae) scorpionflies: systems for understanding resource-defense polygyny and alternative male reproductive efforts. Annu Rev Ecol Syst 12:355–386

Whiting MF (2002) Mecoptera is paraphyletic: multiple genes and phylogeny of Mecoptera and Siphonaptera. Zoologica Scripta 31:93–104

Wijnhoven H (2011) Notes on the biology of the unidentified invasive harvestman *Leiobunum* sp. (Arachnida: Opiliones). Arachnologische Mitteilungen 41:17–30