Array and Sequence of Visual Threats in Three Neotropical Social Wasps (Hymenoptera: Vespidae: *Polistes* spp.)[1]

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Abstract The pattern of threats against a simulated large-animal intruder is analyzed in colonies of *Polistes lanio* (F.), *P. major* Beauvois, and *P. versicolor* (Olivier) in Trinidad, West Indies. Four distinct threats were identified, corresponding to four of the five threats previously found in north-temperate species: wing raise, leg wave, abdomen bend, and wing flutter. The first three are common to all three species, while wing flutter typically preceded attack only in *P. versicolor*. Under gradually escalating provocation, threats normally arise in a species-characteristic sequence. The occasional appearance of threats out of sequence is consistent with the hypothesis that the sequence is a product of differing response thresholds.

Key Words defense, eusocial, paper wasps, sting, Trinidad

Colonies of many social wasps have conspicuous responses to disturbance by large animals. However, in most species the signal value of these responses appears to be little more than a show of agitation. In the worldwide primitively social genus *Polistes*, in contrast, colonies respond with visually conspicuous threats (Starr 1990). Each such threat appears to have originated as intention movements associated with readiness to attack, so that they are true displays. To date, four distinct visual threats—known as “wing raise,” “leg wave,” “abdomen bend,” and “wing flutter”—and one apparent auditory threat, “wing buzz,” have been described by Starr (1990). The characteristic array of threats and the sequence in which they arise under escalating provocation allow for a graded response by the wasps. Array and sequence are known to vary among species.

Although threat sequences tend to be species-characteristic, individual threats occasionally arise out of sequence. Analysis of such anomalies in previously studied species is consistent with the hypothesis that the characteristic sequence is a product of differing thresholds among threat behaviors (Starr 1990: fig. 15.6). This goes against the hypothesis that it is a fixed action pattern or a first-order Markov process.

Eight species have been studied heretofore: *P. annularis* (L.), *P. dorsalis* (F.), *P. exclamans* Viereck, *P. fuscatus* (F.), and *P. metricus* (Say) in North America (Starr 1990); *P. dominulus* (Christ) in Europe (Bruschini et al. 2005); and (less rigorously)

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P. erythrocephalus Latreille and *P. instabilis* Saussure in Central America (C.K.S. pers. obs.). Our purpose here is to record the threat patterns in three neotropical species in comparison with what is known from other species and to further test the hypothesis of the threat sequence arising out of different thresholds. In addition, we provide data bearing on the hypothesis (Starr 1990) that differences in threat sequence among species may be explained in part by differences in body coloration.

Materials and Methods

All results are from unconstrained colonies of *P. lanio* (F.), *P. major* Beauvois, and *P. versicolor* (Olivier) in northern Trinidad, West Indies. We spent several hours watching colonies of each species while standing at a distance. This allowed us to acquaint ourselves with the on-nest behavior of adult females in undisturbed colonies and so to discount as possible threats any such behavior pattern.

Following Starr (1990), we later video-recorded the colonies responses to visual provocation, beginning from an undisturbed, at-rest condition and ending when most of the adult females had flown off the nest. Provocation was by a black-painted tennis ball affixed to the end of a long rod, the ball serving to simulate a vertebrate intruder. We moved the ball slowly in a circular motion, gradually approaching the nest until the ball was within about 0.5 m. We analyzed responses by means of slow-motion playback. Only the responses of wasps that flew at the ball are recorded. Our study material comprised eight colonies of *P. lanio*, six of *P. versicolor*, and three of *P. major*. We conducted just one provocation per colony of the first two species, while we provoked each *P. major* colony twice, the two episodes at least a week apart.

Results and Discussion

Polistes lanio, *P. major*, and *P. versicolor* together manifested the same four visual threats described from North American species. These are: wing raise whereby the wings, still longitudinally folded, are raised and held up off the abdomen; leg wave in which the forelegs are raised off the substrate and oscillate at the femur–tibia joint (based on slowed-down playback of several sequences from each species, there is little variation within or between species in the rate of waving, about 8–9 cycles/s); abdomen bend in which the abdomen is twisted to the side and bent so that the tip is directed somewhat anteriorly, often with a probing motion as if stinging; and wing flutter in which the wings, still folded and raised above the abdomen, are rapidly fluttered at low amplitude.

No species manifested a wing buzz that was recorded from *P. dominulus* and occasionally from the *P. metricus* (Bruschini et al. 2005, Starr 1990). We noted no difference in form of any of these threats from what was previously described from North American species. Aside from wing flutter—which depends on the wings being in a raised position—the different threats are physically independent of each other. Accordingly, a wasp may be performing two or more threats at once.

All three species include leg wave, wing raise, and abdomen bend in their characteristic threat arrays, while only *P. versicolor* includes wing flutter (Table 1).

Table 1. Incidence of threats preceding attack in three neotropical *Polistes* species. Sample sizes are numbers of individuals recorded from at-rest condition to attack.

Threat	*P. lanio* (*n* = 107)	*P. major* (*n* = 62)	*P. versicolor* (*n* = 65)
Wing raise	107 (100%)	62 (100%)	65 (100%)
Leg wave	107 (100%)	60 (96.7%)	63 (96.9%)
Abdomen bend	107 (100%)	62 (100%)	65 (100%)
Wing flutter	3 (2.8%)	0	64 (98.5%)

We never saw wing flutter in *P. major*, and it preceded very few attacks by *P. lanio*. Observations of *P. erythrocephalus* and *P. instabilis* indicate that wing flutter is also very uncommon in these species (C.K.S. pers. obs.), and it is not recorded from *P. dominulus* (Bruschini et al. 2005), although it is part of the typical array in the North American *P. exclamans* (Starr 1990).

As seen in Table 2, threats are initiated in a relatively predictable order under gradually escalating provocation. The characteristic threat sequence for both *P. lanio* and *P. major* is: wing raise → leg wave → abdomen bend. For *P. versicolor* the sequence is: wing raise → leg wave → abdomen bend → wing flutter.

With 11 *Polistes* species studied to date, some common features are apparent. In all but one species, wing raise is typically the first threat to arise under gradually

Table 2. Relative precedence of members of the threat array in three neotropical *Polistes* species.* In the threat pair of wing raise and leg wave in *P. lanio*, for example, wing raise began before leg raise in 97 of 107 instances of individual response. Pairs involving wing flutter are relevant only for *P. versicolor*.

Threat Pair		Species		
First Threat	Second Threat	*P. lanio*	*P. major*	*P. versicolor*
Wing raise	Leg wave	97:10	54:6	61:2
Wing raise	Abdomen bend	107:0	62:0	65:0
Wing raise	Wing flutter**	—	—	64:0
Leg wave	Abdomen bend	101:6	55:5	50:13
Leg wave	Wing flutter**	—	—	64:0
Abdomen bend	Wing flutter**	—	—	64:0

* Relative number of precedence of threat pairs is recorded with number of observed threats occurring first in the threat array.

** Wing flutter threat was observed only in *P. versicolor* and is relevant only to that species.

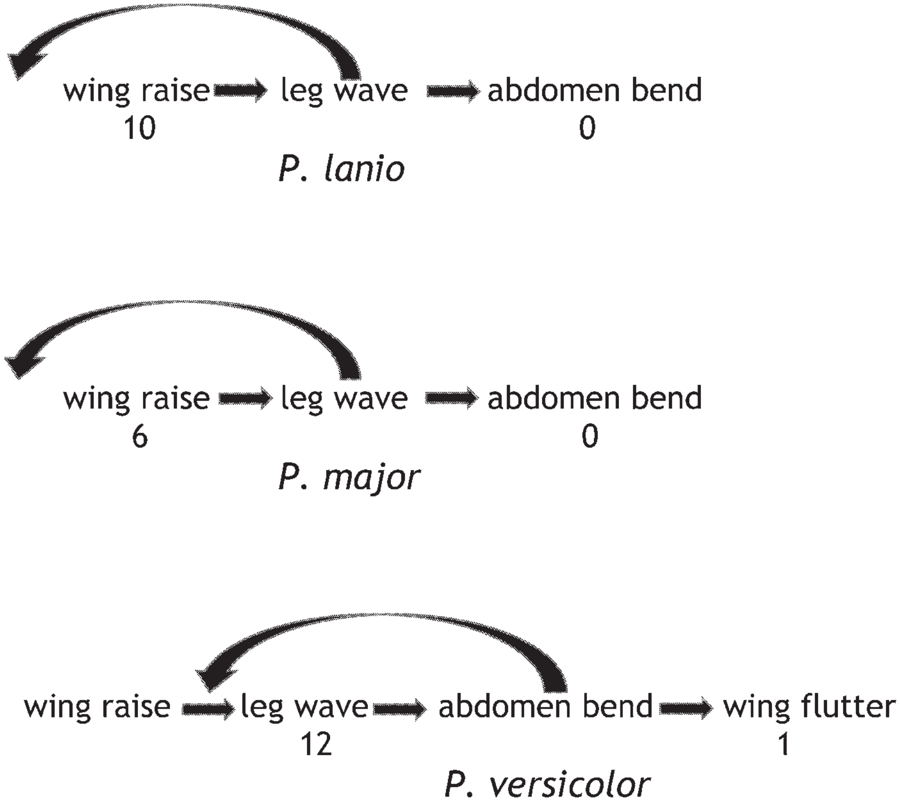

Fig. 1. Frequency of threats immediately following a threat arising out of the species-characteristic sequence in three neotropical *Polistes* species. The curved arrow above the line indicates the displacement of a threat ahead of its usual position. Numbers indicate the frequency with which other threats followed the displaced threat.

increasing provocation, followed by leg wave. However, differences among species in the array or sequence are not evidently correlated with taxonomic relationships. That is, neither the species groups recognized by Richards (1978) nor the emerging cladistic pattern (Pickett and Wenzel 2004) appear to predict the known differences.

Alone among the 11 species, *P. annularis* typically initiates its threat sequence with leg wave, followed by wing raise. Starr (1990) hypothesized a relationship with this species color pattern, in which the forelegs are contrastingly yellow, while the top of the abdomen (exposed by wing raise) is mostly dark brown, giving leg wave greater conspicuousness. This hypothesis is undermined by the observation that, in *P. lanio*, which is colored much like *P. annularis* and appears to be very closely related (Richards 1978), it is wing raise and not leg wave that initiates the sequence.

Occasionally a threat arises out of its species-characteristic sequence (Table 2). When a threat that does not normally come last arises early, this raises the question of which one will follow it. In all but one of the 29 cases in which this occurred, the displaced threat was followed by the one that it displaced, instead of the one that would normally follow it (Fig. 1). This is consistent with results from North America (Starr 1990) and with the hypothesis that the threat sequence is a simple product of differing thresholds among behavior patterns.

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