Sociobiology 72(3): e11602 (September, 2025)
DOI: 10.13102/sociobiology.v72i3.11602

Sociobiology
An international journal on social insects

SHORT NOTE

# Do Small Social Wasp Colonies Defend Against Large Intruders?

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**Article History**

**Edited by**
Evandro Nascimento Silva, UEFS, Brazil
Received 17 February 2025
Initial acceptance 24 February 2025
Final acceptance 30 March 2025
Publication date 11 July 2025

**Keywords**
Colony defense, *Polistes*, stinging, threats.

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**Abstract**

Against the hypothesis that the ability to defend the brood by stinging is a key enabling mechanism in the origin of sociality in the Hymenoptera, it was claimed that small colonies do not defend the nest against large adversaries. We report on a test of this claim. Using a simulated vertebrate intruder, we provoked early colonies of three species of paper wasps (*Polistes*) until all adult females had either attacked or fled. In each species, a substantial fraction of adult females attacked the intruder, with an approximately linear relationship between the total number of females and the number attacking, consistent with the initial hypothesis. This experimental approach also presents a novel method for comparing attack-readiness between species, developmental stages, or experimental conditions.

It is common to observe that very large colonies of social Hymenoptera tend to be markedly more pugnacious than small colonies, often attacking in mass if one approaches the nest (e.g., Ihering, 1904: 292). This corollary also applies to species with modest mature colony sizes, ranging from tens to hundreds of adult females, including those of the worldwide genus *Polistes*, commonly known as paper wasps. In these, the intensity of a colony's defensive response correlates with colony size (Judd, 1998, 2000; Seal, 2002).

A notable feature of defensive response in all studied *Polistes* is the occurrence of conspicuous visual threats (Starr, 1990; Bruschini et al., 2005; Western & Starr, 2019). These can usually be elicited even from a lone female on the nest, but not if she is away from it (Starr, 1990). However, a given female's readiness to threaten is not a good predictor of attack readiness, as she may instead flee if pressed (pers. obs.).

In hypothesizing that the stinger is a key enabling mechanism in the origin of sociality in the Hymenoptera, Starr (1985) claimed that it has sufficient power to allow even very few females to deter a much larger intruder. Kukuk et al. (1989) disputed this on several grounds. Among others, they maintained that "Only in large colonies in which there is an 'expendable' worker force do bees, wasps, and ants aggressively attack a potential or actual vertebrate predator" so that stinging cannot be an effective deterrent at the earliest stages of sociality. The different predictions of these views are shown graphically in Fig 1.

In a rebuttal, Starr (1989) envisioned a test of this objection using primitively social wasps of the genus Polistes, which involved an intrusion on early colonies with a simulated rat-sized animal.The hypothesis of Kukuk et al. (1989) predicts very little or no defensive response below a certain threshold of colony size (perhaps at least 20 adult females after the emergence of workers), followed by an approximately linear increase with further colony growth (Fig 1b). Against this, Starr predicted that a significant fraction of wasps would attack the intruder even while the colony was very small and without workers, yielding an approximately linear relationship between colony size and response.

Here, we report results from such field tests with colonies of *P. fuscatus* (Fabricius) in Ithaca, USA, and *P. lanio* (Fabricius) and *P. versicolor* (Olivier) in Trinidad, West Indies. The defensive responses of these species to such provocation, including their distinctive threats, are described by Starr (1990) and Western and Starr (2019).

All colonies were in the founding stage of the colony cycle before the appearance of the first adult workers, as evidenced by the absence of cocoon remnants in cells. All colonies were apparently healthy, with at least as many late-brood individuals (apparently in the fourth larval instar or older) as adult females. All colonies were nested on buildings, each at least some meters from another test colony. Those of the two Trinidad species were at the same locality (University of the West Indies Field Station) and so were subject to the same environmental conditions.

Trials were conducted during the active middle part of the day at times of no rain and little wind. In Ithaca, we provoked colonies employing a moderately fuzzy model about the size of a large mouse or small rat, consisting of a cylindrical gray fabric mass about 10 cm long and 3 cm wide, used by honeybee researchers to test colonies' defensive responses (e.g., Nouvian et al., 2016). Lacking access to this model in Trinidad, we used a blackened tennis ball on the end of a long stick. Starting at a distance of at least one meter, we slowly waved the model (of whichever type) increasingly close to the nest until each female had either clearly attacked the model or fled from it. In very few trials, in which not all females could be brought to the decision point by such purely visual provocation, we lightly brushed the nest with the model; this always caused indecisive wasps to either attack or (usually) flee. Aside from differences in the species-characteristic sequence of threats (Starr, 1990; Western & Starr, 2019), there was no discernible difference in responses to the two kinds of models.

Those that walked or flew onto the model were scored as attacking – most of these wasps conspicuously stung the model – while those that walked to the far side of the nest or flew off the nest and away were scored as fleeing. Callow individuals, as seen by their very dark compound eyes, were disregarded.

Figs 2-4 show the fractions of adult females attacking the model from colonies of *P. fuscatus*, *P. lanio,* and *P. versicolor*. Best fit linear regression was used to estimate the association between colony size and propensity to attack (regression curve estimation; SPSS 24, IBM 2016). Values of $F$ for regressions are 48.5, 119.2, and 14.3, respectively; $R^2$ = 0.66, 0.75, and 0.35, respectively ($p < 0.001$ in each case).

The data show that provocation of even small founding-stage colonies often elicits attack from at least one female. This outcome is consistent with Starr's (1985) view and contrary to that of Kukuk et al. (1989). We admit to some surprise at the large fraction of females that attack a simulated vertebrate when pressed to a decision.

The approximately linear relationship between the total number of female wasps and those attacking during the founding stage is noteworthy. Judd's (1998) finding that this increases in the growth stage (with workers present) and then declines sharply in the reproductive stage (when males and new queens are produced) in *P. fuscatus* makes biological sense and is expected to be general for the genus.

Given that the two Trinidad species nested in the same locality and on the same set of buildings, the difference in the slopes of the regression lines corroborates our impression that *P. lanio* (0.79 ± 0.08) is distinctly more pugnacious than the smaller *P. versicolor* (0.49 ± 0.13). No inference should be drawn from comparing the regression lines of either of these and *P. fuscatus*, as the provocation devices differed. However, the *P. fuscatus* results replicate the result that very small colonies attack a simulated vertebrate intruder.

Previous studies of colony-level defensive responses in Polistes have relied solely on the fraction of threatening and/or attacking individuals (e.g., Judd, 1998, 2000; Seal, 2002). This approach has the drawback that the provocation must be well standardized in order to allow reliable comparison between species, colony conditions, and/or observers. The technique of pressing all adult wasps to either attack or flee eliminates any ambiguous or non-responsive individuals. Even so, some standardization is desirable, and we suggest a blackened tennis ball as a provocation device that is easily prepared.

## Acknowledgments

We thank A. Ramcharan and R. Nowogrodzski for field assistance.

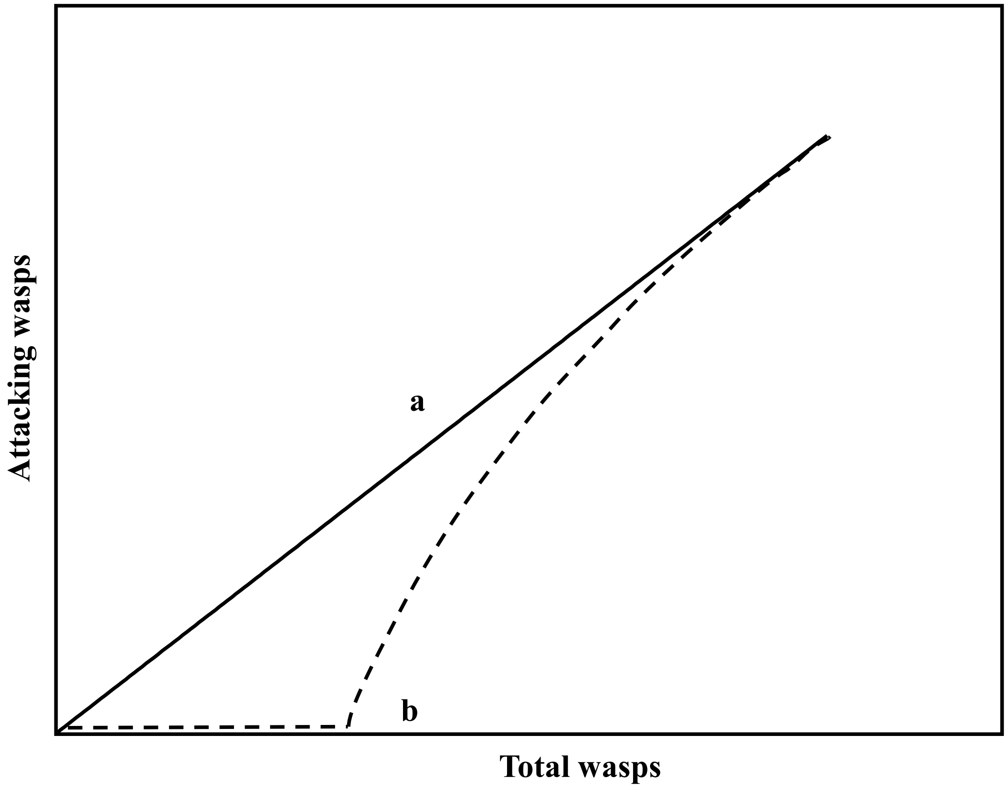


**Fig 1**. Graphic representation of the competing hypotheses of a) Starr (1989) and b) Kukuk et al. (1989). The first predicts a defensive response in the initial stages of colony development, while the second predicts no active defense by very early colonies with few or no workers. The inflection point in the latter might be expected at the beginning of the growth stage, when the first workers are present.

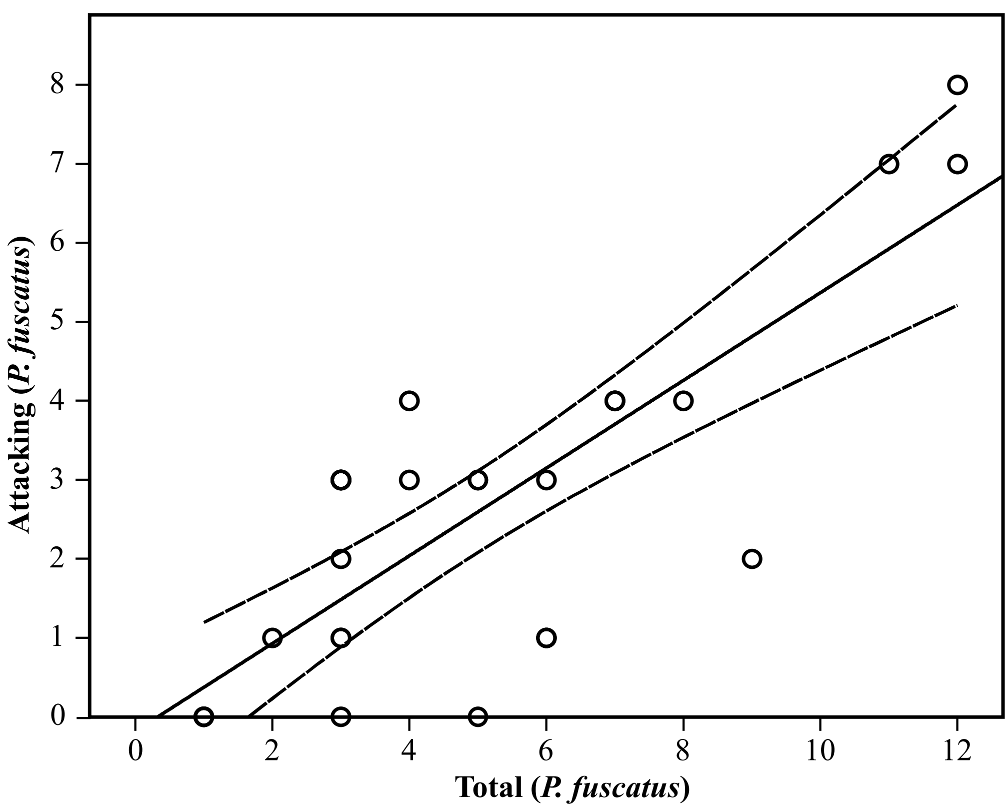


**Fig 2**. Fraction of adult females in 28 founding-stage colonies of *Polistes fuscatus* attacking a simulated vertebrate intruder. Some points overlap and thus represent results from multiple colonies. The solid line represents the best-fit linear regression model with 95% confidence intervals, where $y = -0.181 + 0.555x$ ($R^2 = 0.65$; $P < 0.001$).

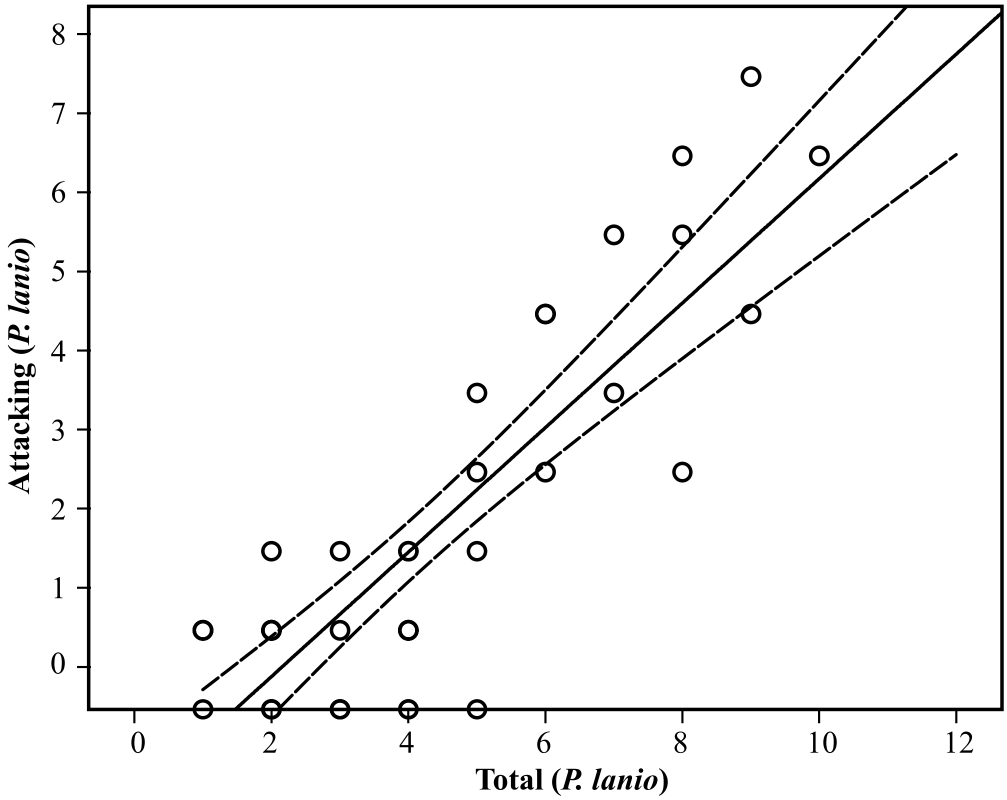


**Fig 3**. Fraction of adult females in 42 founding-stage colonies of *Polistes lanio* attacking a simulated vertebrate intruder. Some points overlap and thus represent results from multiple colonies. The solid line represents the best-fit linear regression model with 95% confidence intervals, where $y = -1.162 + 0.787x$ ($R^2 = 0.73$; $P < 0.001$).

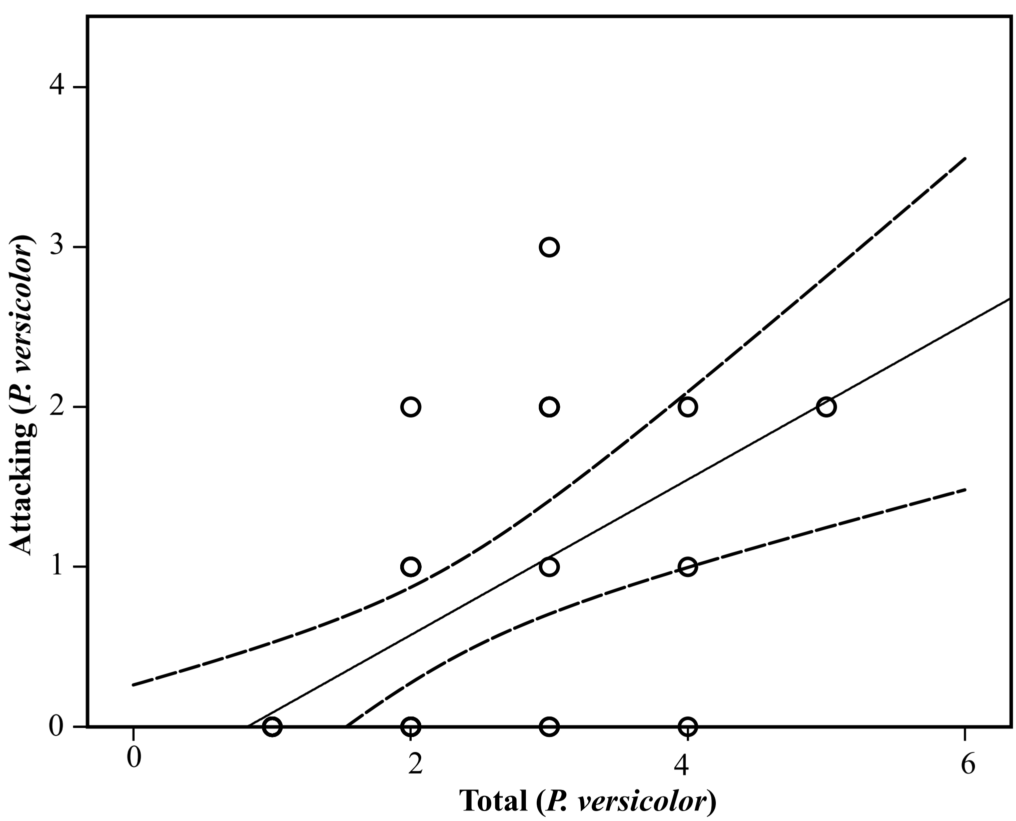


**Fig 4**. Fraction of adult females in 29 founding-stage colonies of *Polistes versicolor* attacking a simulated vertebrate intruder. Some points overlap and thus represent results from multiple colonies. The solid line represents the best-fit linear regression model with 95% confidence intervals, where $y = -0.400 + 0.486x$ ($R^2 = 0.35$; $P < 0.001$).

## References

Bruschini, C., Cervo, R. & Turillazzi, S. (2005). Defensive responses to visual and vibrational stimulations in colonies of the social wasp *Polistes dominulus*. Ethology, Ecology, and Evolution, 17: 319-326. https://doi.org/10.1080/08927014.2005.9522585

Ihering, R. von (1904). As vespas sociais do Brasil. Revista do Museu Paulista, 6: 97-309.

Judd, T.M. (1998). Defensive behavior of colonies of the paper wasp *Polistes fuscatus* against vertebrate predators over the colony cycle. Insectes Sociaux, 45: 197-208. https://doi.org/10.1007/s000400050080

Judd, T.M. (2000). Division of labour in colony defense against vertebrate predators by the social wasp *Polistes fuscatus*. Animal Behaviour, 60: 55-61. https://doi.org/10.1006/anbe.2000.1449

Kukuk, F., Alexander, B., Eickwort, G.C., Gibson, R., Morse, R.A., Ratnieks, F. & Raveret-Richter, M. (1989). The importance of the sting in the evolution of sociality in the Hymenoptera. Annals of the Entomological Society of America, 82: 1-5. https://doi.org/10.1093/aesa/82.1.1

Nouvian, M., Reinhard, J. & Giurfa, M. (2016). The defensive response of the honeybee *Apis mellifera*. Journal of Experimental Biology, 219: 3505-3517. https://doi.org/10.1242/jeb.143016

Seal, J.N. (2002). Does *Polistes instabilis* de Saussure (Hymenoptera: Vespidae) investment predict nest defense? Journal of the Kansas Entomological Society, 75: 335-338.

Starr, C.K. (1985). Enabling mechanisms in the origin of sociality in the Hymenoptera – the sting's the thing. Annals of the Entomological Society of America, 78: 836-840. https://doi.org/10.1093/aesa/78.6.836

Starr, C.K. (1989). In reply, is the sting the thing? Annals of the Entomological Society of America, 82: 6-8. https://doi.org/10.1093/aesa/82.1.6

Starr, C.K. (1990). Holding the fort: Colony defense in some primitively social wasps. In D.L. Evans & J.O. Schmidt (Eds.), Insect defenses. Albany, State University of New York Press (pp 421-463).

Western, C.A. & Starr, C.K. (2019). Array and sequence of visual threats in three neotropical social wasps (Hymenoptera: Vespidae: *Polistes* spp.). Journal of Entomological Science, 54: 288-292. https://doi.org/10.18474/JES18-110