Social wasps are effective biocontrol agents of key lepidopteran crop-pests

Robin J. Southon[1]; Odair A. Fernandes[2]; Fabio S. Nascimento[3*]; Seirian Sumner[1*]

*equally contributing authors

[1]Centre for Biodiversity and Environmental Research, Department of Genetics Evolution and Environment, Division of Biosciences, University College London, Gower Street, London, WC1E 6BT, United Kingdom

[2]School of Agricultural and Veterinarian Sciences, São Paulo State University (UNESP), 14884-900, Jaboticabal, SP, Brazil

[3]Departamento de Biologia, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, 14040-900, Ribeirão Preto, SP, Brazil

R.J.S.: University College London – rjsouthon@gmail.com
O.A.F.: São Paulo State University (UNESP) – odair.fernandes@unesp.br
F.S.N.: Universidade de São Paulo – fsnascim@usp.br
S.S.: University College London – s.sumner@ucl.ac.uk
Corresponding Author: Robin J. Southon – rjsouthon@gmail.com

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Abstract

Biocontrol agents can help reduce pest populations as part of an integrated pest management scheme, with minimal environmental consequences. However, biocontrol agents are often non-native species, require significant infrastructure, and overuse of single agents results in pest resistance. Native biocontrol agents are urgently required for more sustainable multi-faceted approaches to pest management. Social wasps are natural predators of lepidopteran pests, yet their viability as native biocontrol agents is largely unknown. Here we provide evidence that the social paper wasp *Polistes satan* is a successful predator on the larvae of two economically important and resilient crop pests, the sugarcane borer *Diatraea saccharalis* (on sugarcane *Saccharum* spp.) and the fall armyworm *Spodoptera frugiperda* (on maize *Zea mays*); *P. satan* wasps significantly reduce crop damage sustained by these pests. These results provide the much-needed baseline experimental evidence that social wasps have untapped potential as native biocontrol agents for sustainable crop production and food security.

1. Introduction

Satisfying the food demands of a globally growing human population in a sustainable way requires the preservation and restoration of terrestrial ecosystems, as highlighted by the United Nation's 2030 Agenda for Sustainable Development. Concurrent with this are concerns over agricultural practices that focus on short-term economic gains with long-term detrimental impacts on productivity, ecology, and the environment. Arthropod pests alone are thought to be responsible for losses of 18–26 % of annual crop yield worldwide, at an economic cost in excess of US$ 470 billion [1,2]. Chemical pesticides and genetically engineered annual crops have been the main approaches to reducing the damage caused by insect pests as part of the Green Revolution [3,4]. However, overuse of these tools can lead to the development of resistant pest populations, jeopardizing the sustainability of control strategies and crop production [5]. There is a call for alternative methods of effective pest control with long-term sustainability that works with ecosystems, rather than against them [6].

Integrated pest management (IPM) provides a promising approach to sustainable farming if it embraces the use of biocontrol (i.e. the use of other species as natural enemies of pests). Despite its promise and apparent increasing popularity, the use of biological control in IPM remains modest and inconsistent

[7]. Exploiting biocontrol agents is not always straightforward as species are often non-native; moreover such pest control systems often require substantial costs and infrastructure to implement and maintain. There is a need to identify native biocontrol agents that are locally abundant, and that are relatively cheap and easy to employ and maintain. The tropics, where biodiversity is at its most diverse, is a promising oasis for discovering and exploiting native agents [8]. It is also in developing tropical countries that natural biocontrol is likely to have the biggest impact on farmers' livelihoods and the environment, due to the current misuse of pesticide treatments in these regions [9]. Here we provide the much-needed experimental evidence that predatory social wasps can contribute to ecological solutions for sustainable agriculture as biocontrol agents.

Parasitoid wasps have long been utilised as biocontrol agents of agricultural insect pests [10–12], and recently also in livestock hygiene management [13]. Some species of parasitoid wasps can be reared easily on an industrial scale, providing a ready source of pest control on demand [14]. By contrast, the predatory power of hunting wasps (which feed meat protein – often derived from other insects – to their developing brood) in biocontrol is almost entirely overlooked, despite the recognised impact of predatory wasps on wild insect populations [15,16]. There are several reasons why social wasps have not been exploited for biocontrol: unlike some parasitoids, they are difficult to successfully rear on a large scale in captivity [17]; they are perceived by humans as dangerous due to their stings [18]; we lack the baseline knowledge on their effectiveness as biocontrol agents. Predatory wasps may be good candidates for biocontrol agents as they are thought to have a generalist diet, feeding especially on Lepidoptera and Diptera (the main insect Orders of crop pests). Social wasps may be especially beneficial due to their large population sizes, central place foraging, and the ease of establishing high density populations in artificial shelters [19–26]. The potential in harnessing predatory wasps in biocontrol was recognised over a century ago when *Polistes* paper wasps were identified as important predatory enemies of cotton worm *Alabama argillacea* [19,20,27]. More recent work has shown that wasps are common in a range of agricultural environments [28–33], and that pest lepidopterans form a main or significant portion of wasp forage [21,24,34–36]. One concern is that the overall impact of predatory wasps on crop pests may be limited, as many pests hide within the plant, potentially making them inaccessible to hunting wasps. This raises the question of whether wasps as predators are only effective on pests that are exposed on the plant [22]. Therefore, critical knowledge gaps that currently preclude the use of predatory wasps as biocontrol agents include determining the efficacy of wasp predation on hidden prey and quantifying the impact of wasps in reducing pest populations and crop damage.

We tackled these outstanding questions by studying the foraging behaviour and efficacy of a *Polistes* paper wasp, and its impact on two critical lepidopteran crop pests which infest two of the world's most economically important crop plants - sugarcane *Saccharum* spp. and maize *Zea mays*. Our experiments were conducted in Brazil, which is the world's largest producer of sugarcane, the third largest global producer of maize [40,41], and where US$ 17.7 billion worth of crop (7.7 % of annual harvest) is lost to insect pests annually [42]. Common pests of these crops are (respectively) the lepidopteran sugarcane borer *Diatraea saccharalis* (henceforth referred to as SB) and the lepidopteran fall armyworm *Spodoptera frugiperda* (henceforth referred to as FAW) [43,44]. These two pests have a similar life cycls: eggs are laid exposed on the leaf and upon hatching larvae move into the plant to shelter and feed [45–47]. Here we propose the use of *Polistes satan* as a biocontrol agent of SB and FAW. Several traits of *P. satan* suggest it may be a good biocontrol agent: previous experiments have highlighted the potential of *Polistes* in pest-control [22,23,48]; colonies are medium sized with up to 72 adult female wasps (mean 30 adult females and 97 cells in established colonies [49]), hence a significant amount of prey is required to sustain the demands of developing brood; it is native to Brazil, and so does not present the issues that an alien biocontrol agent may, whilst also being common in agricultural landscapes [50].

We conducted two experiments to test the overarching hypothesis that *P. satan* has the potential to be an effective biocontrol agent of SB on sugarcane and FAW on maize. We used a behavioural experiment (Experiment 1) to test the prediction that *P. satan* predates on SB and FAW on their respective host plants, even when hidden under the leaf-sheath (sugarcane) or in the whorl (maize) (Prediction 1). We then conducted an exclusion experiment (Experiment 2) to test the prediction that *P. satan* can significantly reduce the pest population and associated damage of FAW on maize (Prediction 2). Our results provide quantitative evidence that *P. satan* can be an effective biocontrol agent on economically important lepidopteran crop pests. We discuss the benefits and challenges of exploiting social wasps for sustainable agriculture and landscape management.

2. Material and methods

(a) Experimental animals and plants

Ten mature post-emergence colonies (median number of adult females per colony = 24, interquartile range = 17, range = 10–38) with brood of *P. satan* were collected on the 8th July 2018 near Pedregulho, Brazil (20°9'45.87"S, 47°30'1.95"W), transported to the Universidade de São Paulo at Ribeirão Preto, and housed individually in wooden boxes with two wire mesh sides (33 x 31 x height 51 cm; combs attached to the roof of the box) (see Figure S1A). Upon collection, adult wasps received a unique identification mark using extra fine tip Uni POSCA markers. Colonies were kept in wooden boxes for up to 21 days (as per [51], wasps were provided with *ad libitum* water, honey water consisting of 50/50 honey/water, and given dead *Zophobas morio* larvae twice per day on the nest, using forceps), after which time boxes were moved to an outdoor screenhouse (6.5 x 9.1 x highest-height 5.0 m; see Figure S1C); each box was placed approximately 1 m off the ground and separated by 1 m from other nest boxes. Boxes were opened, allowing wasps free access to leave their nest boxes and explore the screenhouse for the remainder of the experiment. Wasps foraged freely on *ad libitum* water and food (see above) placed on a table 4.0–7.5 m away from the nest boxes before experimental trials. At the time of set up, the screenhouse contained at least 251 adult wasps (239 females and 12 males), and each colony contained brood of all stages (eggs, larvae, and pupae).

For Experiment 1, we used 64 SB and 64 FAW larvae at 3rd–4th and 5th–6th instar respectively. Prior to experimental trials, larvae were measured to the nearest millimetre. For Experiment 2, 90 FAW egg masses 2–3 days post-oviposition were used. Sugarcane *Saccharum* sp. and maize *Z. mays* plants were used approximately 5 weeks from seed planting. In Experiment 1, we used 96 sugarcane and 96 maize plants. The mean height at the end of the first experiment for sugarcane was 13 ± 1 cm from soil surface to top visible dewlap, and of maize 57 ± 2 cm from soil surface to highest leaf arch (sample of 20 plants each to nearest integer). In Experiment 2, we used 30 maize plants with a mean height of 64 ± 1 cm.

(b) Prediction 1: *P. satan* are predators of hidden lepidopteran pest species

Experiment 1 consisted of a series of behavioural trials to determine whether *P. satan* foragers were capable of predating on both ‘concealed’ and ‘unconcealed’ (i.e. hidden and not) SB and FAW larvae on their host plants. We explored two conditions that mimicked the different stages of the larvae’s life cycle: larvae that were unconcealed on the leaf (large larvae do sometimes appear exposed on the plants in both species – O.A.F. *pers. obs.*) and larvae that were hidden concealed within the plant (as is typical for older large larvae). Trials for each pest species were conducted over a period of five days (31st July 2018 to 4th August 2018 for SB larvae on sugarcane; 13th to 17th August 2018 for FAW larvae on maize). Each day was divided into four experimental time slots (at 09:30, 11:30, 13:30, and 15:30 hours). For each time slot, a corner of the screenhouse was selected randomly for a trial (single corner used per day). Each trial consisted of six plants of the same species (either sugarcane or maize), arranged in pairs (2 x 3 plant layout, 50 cm apart from each other, see Figure S1D). Each pair was given one of three treatments: (1) unconcealed – a single larva placed in an exposed position in the centre of one of the uppermost leaves; (2) concealed – a single larva hidden within the plant (SB larvae were hidden by gently prying the leaf-sheath slightly from the stem of a sugarcane plant, placing a larva inside, and then closing the sheath against the stem such that the end of the larva was just under the sheath edge to the open leaf; FAW larvae were hidden by dropping a larva into the innermost whorl of a maize plant); (3) a control – no larva present on the plant. We also tested for any potential effects of the methods used to conceal larvae; specifically, we compared sugarcane plants which were subjected to the methods used to conceal larvae (as above) but without the placement of a larvae – against control plants which were untampered (n = 12 plants per treatment, Wilcoxon rank-sum test $\alpha = 0.05$). Pest larvae were placed on plants outside the screenhouse immediately prior to trials, to avoid any demonstration effects.

Each trial lasted for 45 min, during which an observer (positioned approximately 100 cm away) recorded predation and visitation behaviours of wasps on the plants. Data recorded included: (1) individual identification marks of successful predators; (2) time taken for a wasp to grasp a pest larva in its mandibles; (3) number of visits made by wasps to the plant before a successful predation event occurred, visitation being defined as a wasp placing her tarsi on the plant for more than ½ second. In total, there were 16 trials per pest species (2 replicates per trial, 32 replicates per treatment). Additionally, the temperature (in ^{o}C, 1 d.p.) was recorded from the start of the observation, and at 15 minute intervals thereafter until the end of the 45 minute observation period (four recordings per trial; digital temperature probe held 50 cm from plants). Statistical analyses used the mean value of these air-recordings.

Wasp interactions with SB and FAW were analysed separately. Models used the fixed effects of treatment (unconcealed/concealed larvae), and scaled (as per R function ‘scaled’) pest size and temperature. Random effects included in the models were date of observation, position in the screenhouse nested within session time (accounting for treatments being represented by pairs of plants during trials), and number of leaves on maize plants (see Table S1 for random effect variance and random factors that were subsequently removed from the final models due to having minimal variance). In total, we ran four models with specific response variables (Models 1–4). To test whether *P. satan* predates upon each of the pest species, we ran two logit binomial generalized linear mixed models (GZLMM-binomial), with the binary response variable of success or failure of predation for each individual pest larva within the 45 min period (Model 1). We tested whether pest conditions influence the time taken for a successful predation event using two measures of search time – time taken to predate (i.e. a wasp removes prey from the plant) (Model 2), and the number of visits to a plant prior to predation (Model 3). The response variable for Model 2 was time taken (in seconds, log10 transformed) for a wasp to predate upon a pest larva; for this we ran two general linear mixed models (GLMM). The response variable for Model 3 was a total count of wasp visitations to a host plant prior to predation; we ran two negative binomial generalized linear mixed models (GZLMM-nbinomial). Model 4 consisted of two negative binomial generalized linear mixed models (GZLMM-nbinomial), testing total visitation rates within the 45 min period between all three treatments (including controls).

(c) Prediction 2: *P. satan* is effective in reducing plant-damage caused by FAW

As SB typically bores inside of the sugarcane stem from the leaf-sheath, whilst FAW remains in and around the maize whorl (i.e. being more realistically accessible to wasps) [45–47], we decided to test whether the presence of *P. satan* foragers could have an overt impact on a FAW infestation and damage. Experiment 2 assessed the damage caused by FAW on maize under controlled conditions in the presence and absence of *P. satan* foragers. The experiment was conducted between 13th to 28th August 2018. Plants were infected with eggs of FAW on the 13th August. To infect the plants, egg masses were cut from a nylon mesh that FAW adults had laid eggs on; glue was applied to the underside of the cut mesh (in such a way to avoid seepage to the egg mass on top) in order to attach to a leaf. A standardised area of egg mass was attached to the top side of the upper most leaves, approximately one third distance from the stem; one egg mass was applied to each of three leaves per plant (see supplementary data for egg mass sizes). Plants were then randomly assigned to one of two treatment groups: (1) a ‘wasp-exposed’ treatment consisting of 15 plants placed 15 cm apart in two different corners of the screenhouse (of eight and seven plants respectively); (2) a ‘wasp-exclusion’ treatment consisting of an equal number of plants placed directly alongside each of the wasp-exposed treatments but enclosed inside a wasp-proof wire mesh exclusion cage (77 x 81 x height 79 cm). The plants were watered daily and protected from ants by being raised off the floor, but otherwise left undisturbed for 15 days – after which plants were removed from the screenhouse for analysis.

The effectiveness of wasp predation on FAW was assessed in two ways. First, damage to the plant by FAW was scored (blind to treatment by a single observer) using the Davis et al. [52] scale (ranging from 1–9, with 9 being the highest damage rating); differences between treatments were analysed with a Wilcoxon rank-sum test (α of 0.05). Second, plants were dissected in order to count the remaining FAW larvae number, weight (wet weight, mg, 1 d.p.), and length (mm, 0 d.p). To test the direct effect of wasp treatment on FAW infestations on the plants, we ran a negative binomial generalized linear model (GZLM-nbinomial), with the number of larvae recorded per plant as a response variable (Model 5). We also tested whether there was any significant effect of wasp treatment on the weight and length of the FAW larvae using separate general linear mixed models (GLMM) (Models 6 and 7 respectively). We accounted for pests coming from the same plant by including plant ID as a random effect.

(d) General statistical analyses

Generalized linear model fits were assessed by comparing residual deviance with the residual degrees of freedom. Histograms and Q-Q plots were used to determine normal distributions, and general linear model fits assessed by plotting residual versus fitted values. *P* values for models were calculated with a likelihood ratio test of the model with and without target factor (except for negative binomial models, using *Z*-values), and tested to α of 0.05. Descriptive values of transformed and scaled variables are provided pre-modified. All analyses were performed in R 3.3.3 [53], using the packages 'lme4' [54] and 'glmmADMB' [55,56]. Means reported with ± standard error and medians with interquartile range (IQR).

3. Results

(a) Prediction 1: *P. satan* are predators of hidden lepidopteran pest species

A total of 47 uniquely marked *P. satan* foragers (18 on SB and 29 on FAW) were observed predating on larvae placed on experimental plants; the wasps originated from eight (SB) and nine (FAW) colonies. We observed that 44 % (SB) to 48 % (FAW) of known foragers predated on both unconcealed and concealed pest larvae, whilst the remainder were only observed predating on unconcealed pests. We found no suggestion that concealment protocol alerted wasps to the presence of pest larvae (Wilcoxon rank-sum test $W = 71.50$, $p = 1.000$).

P. satan hunted larvae of both pest species successfully: 67.19 % SB and 79.69 % FAW used in Experiment 1 were predated on in 43 and 51, out of 64 experimental plants. Although both unconcealed and hidden concealed pests were successfully predated upon, treatment (i.e. hidden or not) had a significant effect on the success of predation events on both pest species (Model 1 GZLMM-binomial, SB: $\chi^2_1 = 20.76$, $n = 64$, $p < 0.001$; FAW: $\chi^2_1 = 24.03$, $n = 64$, $p < 0.001$; Figure 1). For SB and FAW respectively, 90.63 % and 100.00 % of unconcealed pests were predated upon, compared to 43.75 % and 59.38 % of concealed pests; suggesting that unconcealed pests of both species were more readily taken by the wasps, but that wasps were also able to find and access hidden concealed prey (to a lesser extent). Pest size had no significant effect on the success of predation events for either pest species (SB: $\chi^2_1 = 0.64$, $p = 0.425$, mean size = 15 ± 0.4 mm; FAW: $\chi^2_1 = < 0.01$, $p = 0.973$, mean size = 29 ± 0.6 mm). Temperature had a significant effect on predation events occurring on SB, but not FAW, larvae (see Table S2); for SB there were significantly more visitations (total) to concealed treated plants within the 45 min period than control plants, whilst for FAW there were significantly more visitations to both concealed and unconcealed treated plants than control plants (see Table S3).

We examined which factors influenced the search effort required by the wasps to successfully predate on unconcealed or concealed larva using two measures of effort – time to predation and number of visitations to the plant – but found no significant effects. Treatment did not influence time taken for successful predation in either pest species (Model 2 GLMM, SB: $\chi^2_1 = 1.29$, $n = 43$, $p = 0.257$, mean time to predate = 611 ± 103 seconds; FAW: $\chi^2_1 = 1.23$, $n = 51$, $p = 0.267$, mean time to predate = 318 ± 56 seconds). Likewise, pest size had no significant effect on time taken for successful predation in either pest species (SB: $\chi^2_1 = 3.75$, $p = 0.053$; FAW: $\chi^2_1 = 0.23$, $p = 0.629$). Successful predation events on hidden concealed prey were not explained by visitation rates (Model 3 GZLMM-nbinomial, SB: $Z = -1.80$, $n = 43$, $p = 0.071$, median = 1 visit, IQR = 1; FAW: $Z = -1.32$, $n = 51$, $p = 0.186$, median = 1 visit, IQR = 0). There was no significant effect of pest size (SB: $Z = -1.35$, $p = 0.178$; FAW: $Z = 0.27$, $p = 0.790$) on visitation rates before a successful predation event. Temperature had a significant effect on time to predate SB larvae, but not FAW or visitation rates for either species (see Table S2).

(b) Prediction 2: *P. satan* is effective in reducing plant-damage caused by FAW

Maize plants that were exposed to wasps incurred significantly less damage by FAW compared to plants in which wasps were excluded. Davis et al. [52] scale ratings for plants exposed to wasps ranged from 3–5 (median = 3, IQR = 1), whereas the range for plants that were excluded was 6–8 (median = 6, IQR = 1) (Wilcoxon rank-sum test, $W = 15.50$, $n = 30$, $p < 0.001$; Figure 2).

Wasp treatment affected the FAW larvae populations remaining in plants at the end of the experiment. FAW larvae were found present in 9 of the 15 of plants that were exposed to wasps, and all 15 plants from which wasps were excluded; there were significantly fewer larvae present in plants exposed to wasps (median number of larvae per plant = 1, IQR = 1), than those where wasps were excluded (median = 2; IQR = 2) (Model 5 GZLM-nbinomial: $Z = 3.09$, $n = 30$, $p = 0.002$). We also found a significant effect of treatment on the weight and size of the pest larvae on the plants at the end of the experiment; larvae found on plants that were exposed to wasps weighed (5.4 ± 1.5 mg) significantly less than those found in plants from which wasps were excluded (25.5 ± 1.8 mg) (Model 6 GLMM, $\chi^2_1 = 26.37$, $n = 49$, $p < 0.001$). Likewise, larvae found in wasp-exposed plants were significantly shorter (7 ± 0.6 mm) than those on wasp-excluded plants (12 ± 0.4 mm) (Model 7 GLMM, $\chi^2_1 = 28.10$, $n = 49$, $p < 0.001$) (see Figure 3).

4. Discussion

There is an urgent need for the development of more sustainable food production for the growing global population under the pressures of climate change [57]. Social wasps make good contenders for managed biocontrol agents, due to higher foraging rates than solitary wasps [58], their tendency to fixate on the most abundant prey source [48], and already being a model species in the study of animal behaviour [59]. Moreover, there are in excess of 1,500 species of social wasps, with many genera distributed in a cosmopolitan fashion across the globe; appearing to thrive in disturbed and agricultural habitats [28–33]. We conducted a controlled experiment which provides evidence that native social wasps could be effective future biocontrol agents of lepidopteran pests in economically important crops. We show that these wasps can predate on pests that are hidden in the plant, and that plants exposed to wasps sustained less damage with fewer and smaller pest larvae present. These results provide the proof-of-concept required to demonstrate that predatory wasps offer an important ecosystem service to agriculture, through biocontrol of pests.

Our experiments show that *P. satan* predates successfully on two of the world’s most important crop pests – SB and FAW. Previous evidence of predation on these pests was limited to observational studies which found that FAW was the most common prey carried by foraging *Polistes* wasps returning to their nests from kale (37 % of prey [38]) and maize (23 % of prey [24]) plantations in Brazil. Wider-scale field experiments on the biocontrol value of wasps in a handful of studies from over 35 years ago have had mixed results, due to the difficulty of controlling biotic and abiotic factors in field experiments [22,23]. Our experiments controlled for these factors, and provide the evidence-base for exploring further use of social wasps in biocontrol.

In contrast to bees and ants, wasp foraging behaviour is poorly studied [60]. The search effort for successful predation of hidden prey in Experiment 1 appeared to be no different to that for exposed (i.e. unconcealed) prey. Wasps are thought to use both visual and olfactory cues to hunt prey [60]. Our experiment manipulated the quality of prey visual cues (as exposed-unconcealed larvae were visible, whilst hidden-concealed larvae were not – at least to the human eye); this suggest that these wasps may be primarily using olfactory cues in hunting. In Experiment 2, FAW larvae that survived on plants exposed to wasps were significantly smaller in size than those on plants that were not exposed. This may be a behavioural response by the FAW larvae to the presence of hunting wasps, whereby they spend more time hiding than feeding [61]; alternatively, wasps may have preferentially predated upon larger larvae, as the speed-accuracy/handling trade-off of hunting less conspicuous smaller prey may be too great in terms of energy/time expenditure [62].

The most common mode of biocontrol in crops such as sugarcane and maize are parasitoid wasps. Although highly effective, parasitoid wasps are only able to lay their eggs in larvae that are exposed on the plant – limiting their window of active parasitism to the early larvae stages [63, 64]. Our study reveals several behavioural traits of *P. satan*'s foraging behaviour that makes them complementary to current modes of biocontrol. Firstly, *P. satan* can predate on multiple immature stages of the FAW lifecycle; in Experiment 1 larvae predation was confirmed, and in Experiment 2 occasional feeding on egg masses was also observed (R.J.S. *pers. obs.*). A second trait of *P. satan* that affords advantages over the use of parasitoids concerns its hunting ability, as we found that *P. satan* foragers prey upon both concealed and unconcealed SB and FAW larvae. Having multiple biocontrol agent species (such as generalists and specialists) imposes a range of contrasting selection pressures on pests in the evolution of resistance, reducing the risk of specialist-parasitoid biocontrol resistance developing [65]. However, social wasps are not easily reared in the laboratory. Adopting management practices that either boost local natural populations, or developing husbandry methods for farming social wasps (e.g. in 'vespiaries' [66]), similar to the way honeybees are farmed for their pollination services could be a viable alternative to laboratory mass-rearing.

Despite *P. satan* being native within Brazilian agricultural environments, several factors may limit population numbers and nest activity. These include misuse of pesticides (as a non-targeted species) [67]; lack of suitable nesting sites (e.g. buildings and trees) among large crop monocultures [68]; public health policies (e.g. in Brazil 'instrução normative IBAMA no 141/2006') that result in the removal of wasp nests from buildings – regardless of nest size and potential risk to humans [69]. Evidence-based public education schemes on the value of social wasps as pest controllers is likely to encourage a more tempered public response to wasps [18,58] such that social wasps are tolerated, and their populations encouraged in suitable locations that maximise impact on pest populations but minimise human contact.

this study provides a springboard evidence-base for further research on the efficiency of wasp predation in field realistic agricultural settings. One potential issue with our controlled experiments was the density of wasps within the screenhouse. Dense nesting aggregations of *Polistes* are common in nature and can persist for several years (e.g. [70]). However, such aggregations may be less common in large-scale agricultural environments due to scarcity of nesting sites. However, social wasps are commonly sampled in Brazilian agricultural surveys [31, 50], suggesting their foraging range is large; moreover, positive correlations have been found between plant growth and wasp species richness [31]. Tropical/sub-tropical *Polistes* are especially promising biocontrol agents due to their need to provision larvae throughout extended nesting cycles. IPM schemes that manipulate and inflate wasp populations by translocating colonies to suitable locations within agricultural landscapes may be especially effective (and low cost) for smallholder farms, where areas of high wasp abundance can be engineered within small plots using artificial vespiaries [68]. A second issue was that wasps were given a limited choice of prey, and other competing predators were excluded. In a more natural setting, there will be other prey available which could reduce the impact of the wasps as targeted biocontrol agents.

5. Conclusion

Developing a wider evidence-base on the ecosystem services of social wasps as biocontrol agents is one essential step forward in tackling the poor pubic image that wasps suffer from, and persuading farmers to embrace the natural capital that native predatory wasps offer [18,58]. Future work is required to determine the general value of social wasps as biocontrol agents (e.g. how much variation in efficiency is there across crop types, pest species, wasp species, and climate), to identify the most appropriate complementary biocontrol agents to use alongside the wasps (e.g. parasitoids and pathogens) in an IPM practice, and to determine the extent to which these practices can be generalised across geographical regions. Integrated crop management that exploits the natural capital of native insects, such as social wasps, is timely and essential in an era of global declines in insect populations, and when there is an urgent need to re-evaluate the reliance of our current agricultural practices. Harnessing the power of native biocontrol agents is one way by which we can achieve better stewardship of the natural world, and work with the capital provided by biodiversity.

Data accessibility

The datasets supporting this article have been uploaded as part of the supplementary materials.

Authors’ contributions

S.S. and F.S.N. conceived the project and acquired funding. All authors contributed to designing the study and writing the manuscript. R.J.S. and F.S.N. collected wasp colonies and constructed nest boxes. O.A.F. raised fall armyworm and grew maize plants. R.J.S. conducted experiments and data analyses.

Competing interests

We declare no known competing interests.

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FIGURE LEGENDS

Figure 1. Percentage of successful *P. satan* predation events on *D. saccharalis* (SB) and *S. frugiperda* (FAW) larvae in unconcealed verses concealed larvae treated plants across 45 min trials (Model 1, *** sig. $p < 0.001$).

Figure 2. Median *S. frugiperda* (FAW) damage rating per Davis et al. [52] scale in wasp-exposed verses wasp-excluded maize *Z. mays* plants (error bars denote IQR) (*** sig. $p < 0.001$). (left-side). Sample photographs of maize leaf damage in a plant by FAW with scale rating (right-side). Photograph credit: A.R. de Souza.

Figure 3. (top-left) Median number of *S. frugiperda* (FAW) found in wasp-exposed verses wasp-excluded maize *Z. mays* plants (error bars denote IQR). (top-right) Mean wet weight, and (bottom-centre) mean length of FAW found in wasp-exposed verses wasp-excluded maize plants (error bars denote standard error) (Models 4–6, ** sig. $p < 0.05$; *** sig. $p < 0.001$).

SUPPLEMENTARY FILES

‘projectdata’ – raw data file

‘supplementaryfiguretables’ – supplementary Figure S1 & Tables S1–3, detailed:

Figure S1. (A) Nests of the study species *P. satan* are clusters (i.e. satellites) of brood-containing combs, with adults which can be easily translocated into nest boxes; (B) *P. satan* readily hunt larvae of *D. saccharalis* (SB) and *S. frugiperda* (FAW) in the semi-natural environment of a (C) large screenhouse; (D) set up for behavioural observations of *P. satan* foraging on pests of sugarcane and maize. Photograph credits: A, B, D – S.S.; C – F.S.N..

Table S1. Random effect variance and standard deviation in models (2 d.p.), factor was dropped if variance equalled zero and the model re-ran without effect (** sig. $p < 0.05$; *** sig. $p < 0.001$).

Table S2. Temperature effect in models 1-3 (^{o}C) (** sig. $p < 0.05$; *** sig. $p < 0.001$).

Table S3. Test of total visitation rates within 45 min between unconcealed, concealed, and control treatments in Experiment 1 (negative binomial generalized linear mixed models, with random effects - date of observation, position in the screenhouse nested within session time, and number of leaves (maize); ** sig. p < 0.05; *** sig. p < 0.001).

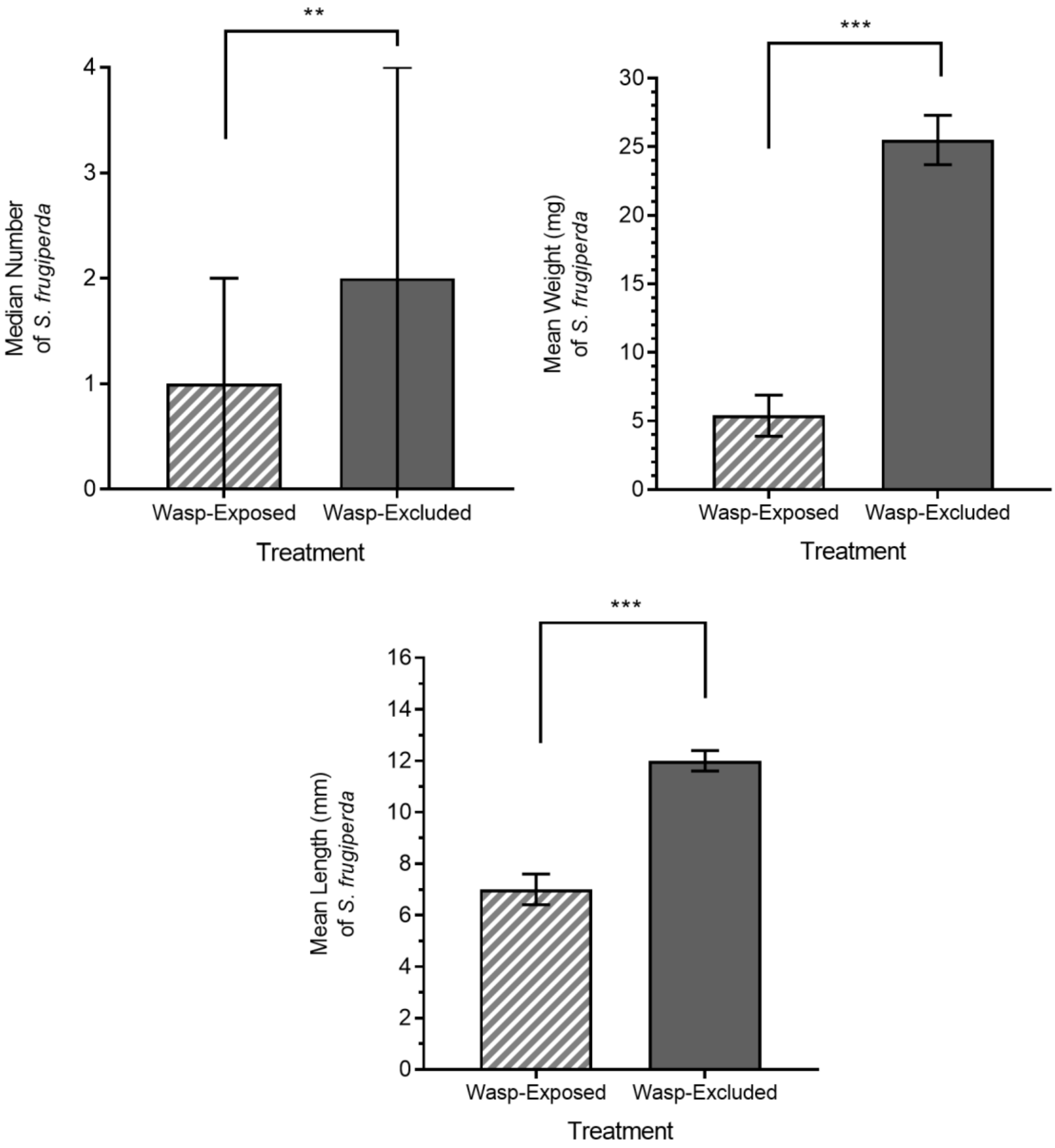
Figure 1

***
***
100
80
60
40
20
0
Percentage Predated
D. saccharalis
S. frugiperda
Pest Species
Unconcealed
Concealed

Figure 2


***
8
6
4
2
0
Median
Damage Rating
Wasp-Exposed
Wasp-Excluded
Treatment
3
4
5
6
7
8

Figure 3


**
Median Number of S. frugiperda
0
1
2
3
4
Wasp-Exposed
Wasp-Excluded
Treatment
***
Mean Weight (mg) of S. frugiperda
0
5
10
15
20
25
30
Wasp-Exposed
Wasp-Excluded
Treatment
***
Mean Length (mm) of S. frugiperda
0
2
4
6
8
10
12
14
16
Wasp-Exposed
Wasp-Excluded
Treatment