Why we love bees and hate wasps

SEIRIAN SUMNER,¹ GEORGIA LAW¹

and ALESSANDRO CINI^{1,2}[®] ¹Centre for Biodiversity & Environment Research, Department of Genetics, Evolution & Environment, University College London, London, U.K. and ²Dipartimento di Biologia, Università degli Studi di Firenze, Via Madonna del Piano 6, 50019, Sesto Fiorentino, Florence, Italy

Abstract. 1. Bees and wasps are important facets of natural capital to be valued by human societies: bees pollinate wild flowers and agricultural crops; wasps regulate arthropod populations, including insect vectors of human diseases and crop pests. Despite the importance of both taxa, bees are universally loved whilst wasps are universally despised. This study explores some of the reasons behind this.

2. Here data are presented from almost 750 members of the public on their perceptions of insects, including bees and wasps. In addition, an analysis is conducted of researcher effort on bees and wasps, using publication numbers of peer-reviewed papers over the last 37 years, and unpublished conference proceedings at specialist international conferences over the last 16 years.

3. The results show that wasps are indeed universally disliked by the public and moreover are unpopular research taxa among researchers. Words used to describe wasps are emotive and negative, whilst those describing bees are functional and positive. A low level of interest in nature and a lack of knowledge (among the public) and research effort (among scientists) regarding the ecosystem services of wasps are likely to be at the root of the negative perception. Whilst the ecosystem services of bees are well understood by the public, those provided by wasps are poorly understood.

4. Positive action to promote research on wasps and to overhaul the public image of wasps via outreach and the media could help to reset the imbalance in appreciation of two of the world's most ecologically important taxa. Cultural shifts to a more positive attitude towards wasps could be pivotal in working with these facets of natural capital, rather than against them.

Key words. Aculeate wasps, ecosystem services, pest control, pollinators, social insects.

'Hornets and wasps ... are devoid of the extraordinary features which characterize bees; this we should expect, for they have nothing divine about them as the bees have.' (Aristole, c. 300 BC)

Introduction

It is a truth universally acknowledged that people like bees and dislike wasps. This imbalance in emotion does not accurately

Correspondence: Seirian Sumner, Centre for Biodiversity & Environment Research, Department of Genetics, Evolution & Environment, University College London, Gower Street, London, WC1E 6BT, U.K. E-mail: s.sumner@ucl.ac.uk

reflect the importance of both taxa in the environment. We value bees as pollinators and enjoy a long history of co-habitation and domestication with a few bee species. In contrast, wasps are not valued (despite their role as apex predators), and human–wasp interactions are usually not enjoyable. The root of the problem appears to be our longstanding, culturally ingrained lack of appreciation for their role in ecology and economy. We lack quantitative assessment of the extent to which these stereotypes are upheld by the general public, and an evaluation of why wasps are so socially maligned. Perhaps if we valued wasps as we do bees, we would dislike wasps less.

Our disgust with regard to certain arthropods is deeply rooted in our culture and psychology (Lockwood, 2013). Wasps, spiders, cockroaches, fleas, mites and flies are among the most revolted; they are the 'children of filth' (Lynd, 1921); God

836 © 2018 The Authors. *Ecological Entomology* published by John Wiley & Sons Ltd on behalf of Royal Entomological Society This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited. sends hornets as punishment in three books of the Bible (*New Jerusalem Bible*, Deuteronomy 7:20; Exodus 23:28; Joshua, 24:12). Reasons for our revulsion are likely to have an evolutionary basis: there is strong selection to learn to recognise, avoid and fear organisms that could inflict pain (stings or bites), spread disease, or kill. Even committed wasp researchers recognise the negative emotions that wasps evoke in humans:

... they terrorize housewives, ruin picnics, and build large aerial nests that challenge fleet-footed stone-throwing boys the world over. (Evans & Eberhard, 1970)

Social wasps are among the least loved insects ... yet, where statistics will not alter a general impression, another approach might. Every schoolchild ... ought to sit watching a Polistes wasp nest for just one hour ... I think that few will be unaffected by what they see. (W.D. Hamilton, 1996)

Our dislike of wasps is largely shaped by a group of wasps that represent less than 1% of the aculeate (stinging) wasps - the Vespines. These consist of 67 species of social wasps which most commonly come into contact with humans vellowjackets (Vespula, Dolichovespula spp.) and hornets (Vespa, Provespa spp.) (Carpenter & Kojima, 1997). There are at least another 850 species of social wasps [Stenogastrinae (Carpenter & Kojima, 1996) and Polistinae (Ross & Matthews, 1991)]. However, the vast majority of wasps (an excess of 75 000 species) are solitary - these include at least 4000 species of solitary Vespidae [e.g. pollen wasps (Masarinae) and potter wasps (Eumenidae)], over 9000 species of Crabronidae, and some 5000 species of Pompilidae (Spradbery, 1973). There are at least another 650 000 species of parasitic wasps (Parasitica), many of which are undescribed (Aguiar et al., 2013); these insects are small, solitary and mostly lack a stinger and so are not largely recognised as 'wasps' by the public. The public's opinion of wasps, therefore, is limited to their experience with less than 1% of this highly diverse and specious group, and more specifically a handful of species (Lester, 2018).

Thanks to the Vespines, wasps are perceived as more dangerous than bees. All aculeate wasps sting, as do all bees, and bee and wasp stings are equally likely to illicit severe allergic reactions in humans. However, wasp stings are perceived as more of a threat than bee stings: over 2300 years ago Aristole (the first published entomologist) described the stings of Vespines (hornets and yellowjackets) as being 'stronger' than those of honey bees. More recently, Justin Schmidt has given us quantitative affirmation of Aristotle's observation: in his personal pain calibration scale of insect stings, wasps span the full range of the Schmidt pain scale (0.5-4) whilst bees are relatively less painful (Schmidt scale 0.5-2.5) (Schmidt, 2016). This is, perhaps, a quantifiable reason to dislike wasps more than bees.

Insects provide vital ecological functions in the natural systems on which we depend: they pollinate our crops, regulate populations of arthropod pests and vectors of disease, decompose organic matter and till soils (Losey & Vaughan, 2012; Schowalter *et al.*, 2018). They are pivotal to the balance of our subsistence on this planet. The value of ecosystem services is defined as the benefits that people obtain from ecosystems, and include provisioning, regulating, supporting and cultural services (Millennium Ecosystem Assessment, 2005). Pollination is a 'headline' ecosystem service that has enjoyed a long history of research interest and financial investment into understanding the ecological value of bees as pollinators (Dicks et al., 2013; Vanbergen & Initiative, 2013; Hanley et al., 2015); at least 1500 crop types depend on pollination (Klein et al., 2007) and 3-8% of global crop production depend on insects for this (Aizen et al., 2009). Pollination services are estimated to be worth annually \$3 billion in the US alone (Losey & Vaughan, 2012) and upwards of \$130 billion globally; but this is likely to be an underestimate, as putting a monetary value on ecosystem services is complex and overlooks the additional impact on people's well-being (Hanley et al., 2015). Moreover, pollination services are not limited to bees: hoverflies, beetles, butterflies, wasps and bugs all contribute to pollination, but their contributions are not well recognised (Rader et al., 2016). A recent study found that in certain environments the social wasp Vespula pennsylvanica was a more effective pollinator than the honey bee (Thomson, 2018). Ecologists have a responsibility to ensure that the full potential of insects is realised in the health and economy of the global ecosystem (Prather & Laws, 2017).

Insect ecosystem services other than pollination are relatively poorly studied; this includes the regulatory services of insect carnivores, such as predatory and parasitic wasps, which are effective agents of biocontrol. The value of the Parasitica wasps as biocontrol agents is well studied (Narendran, 2001). In contrast, we understand little about the biocontrol potential of the Aculeata wasps. Most aculeate wasps are predatory, hunting other arthropods and feeding them to their brood (Grissell, 2010). The solitary species tend to be specialists (e.g. Pompylidae hunt spiders almost exclusively) whereas social species are thought to be generalists (Grissell, 2010). It is the social wasps (the ones that are so feared by the public), therefore, that are likely to provide important services as regulators of a wide range of insect pests and vectors of disease. By regulating both carnivorous and phytophagous arthropod populations, wasps also indirectly deliver protection to lower invertebrate taxa and various plants. Limiting arthropod population growth is essential as arthropods can reproduce rapidly, reaching population sizes that can have knock-on detrimental effects on plants and other invertebrate taxa (Gaston & Lawton, 1988). Insectivorous birds, mammals and amphibians are important regulators of insect populations. However, the predatory impact of wasps is likely to be equal or more effective because of their short generation times; thus, insect predator populations can closely match fluctuations in prey populations (Archer, 1985). Social wasps are also likely to be important as biocontrol agents. The ecosystem services provided by biological control has an estimated value of US\$417 billion a year (Costanza et al., 1997), and in America alone the value of natural control provided by insects was estimated at US\$4.5 billion annually (Losey & Vaughan, 2012). But these estimates overlook the potential contributions to be made by predatory social wasps. Wasps clearly hold high potential for these ecosystem services. Why, therefore, do the public not value wasps as they do their stinging, pollinating counterparts?

Insect populations across taxonomic groups are declining at alarming rates due to land-use change and/or climate change

(Prather *et al.*, 2013; Ollerton *et al.*, 2014; Hallmann *et al.*, 2017); such declines are likely to be affecting the associated ecosystem services (Prather *et al.*, 2013; Oliver *et al.*, 2015). Bee declines are a cause of great concern, with estimates of up to 75% population declines over the last few decades (Senapathi *et al.*, 2015; Woodcock *et al.*, 2016). Wasps are likely to be affected by the same anthropogenic challenges that bees currently face (e.g. agricultural practices, habitat loss) (Isaac *et al.*, 2013; Senapathi *et al.*, 2015) and the data suggest that wasps may be declining at similar rates to bees (Isaac *et al.*, 2013). We cannot afford for cultural stigma to obscure scientific and societal efforts in understanding and conserving insects and the ecosystem services they offer (Hochkirch, 2016; Noriega *et al.*, 2017).

The degree to which the public are informed about the ecological and/or economic value of biodiversity has a strong influence on their attitude and engagement with the environment (Novacek, 2008; Lewandowski & Oberhauser, 2017; Loyau & Schmeller, 2017). This is especially concerning at a time when human-nature interactions are rapidly declining - the 'extinction of experience' (Soga & Gaston, 2016). The public's passionate embrace of the importance of bees is one of the few natural world experiences that may not be in danger of extinction. Global societal concerns about the decline of our pollinators has led to a ground-swell of action from the public, non-governmental organisations and charities. Scientists have taken advantage of the public's keen interest in bees using citizen science approaches to gather data on bee populations and response to land-use change. As a result, bees have received a great deal of public exposure and are very popular subject choices for science engagement activities, popular science books and community projects. In contrast, media coverage of wasps is largely negative and restricted to the nuisance they cause in late summer (Sumner & Brock, 2016), or as inspiration for the latest Sci-Fi movie (Ant-Man and The Wasp, 2018) or blockbuster thriller (Dhand, 2018). The high (and positive) engagement agenda and media profile of bees and their importance as pollinators are therefore likely to engender positivity among the public towards bees. Equally, the low (and exclusively negative) engagement agenda and media profile of wasps and the lack of information in the public arena on their role in ecosystems are likely to drive the negativity among the public towards wasps (Livingstone et al., 2018). Scientists have the potential to drive the publicity and engagement agenda with respect to the public's exposure to biodiversity issues; the level of research effort on bees and wasps may therefore help to explain the imbalance of exposure that bees and wasps have in the public arena.

We conducted a survey of 748 members of the public to determine whether the contrasting perceptions of wasps and bees are upheld by data, and to better understand the reasons behind the differences. Specifically, we predicted that people would feel more positive to bees and butterflies, and less positive towards wasps and flies (Prediction 1). We then focused on the pairwise comparison of bees and wasps: we tested the prediction that the general public recognises ecosystem services that wasps offer (i.e. as natural pest controllers) less than they do the ecosystem services of bees (i.e. as pollinators) (Prediction 2). Next, we examined to what extent these biases were upheld among the scientific community: we test the prediction that research effort on wasps in general and with respect to ecosystem services is under-represented relative to that on bees (Prediction 3). The results show that wasps are unpopular among both the public and scientists; the data suggest that lack of knowledge (among the public) and lack of research effort (among scientists) with regard to the ecosystem value of wasps are likely to be at the root of the negative perception.

We discuss how the general negative emotion toward wasps is likely to be a form of the culturally ingrained implicit bias, and that this is being perpetuated by the lack of sufficient scientific research on the ecosystem value of wasps; this may reinforce a positive feedback loop between the public (through their dislike of wasps) and the scientists (through their reluctance to study wasps). We suggest that positive action to overhaul the public relations image of wasps via outreach and the media could help to reset the imbalance in appreciation of two of the world's most ecologically important taxa. Shifting cultural perceptions of wasps will encourage conservation and management strategies that work with these important facets of natural capital, rather than against them.

Materials and methods

Public perception of insects survey

Over a period of 2 months (December 2017 to January 2018), members of the public were asked to fill in an online survey. Although our ultimate aim was to compare the public's opinion of bees and wasps, we included two other insect groups in our survey in order to avoid leading questions: flies were included as a 'disliked' insect corollary to wasps, and butterflies as a 'loved' corollary to bees. The survey was shared via email and social media (Twitter and Facebook) by the authors and their communities. We deliberately did not define what we meant by a 'wasp', as the point of the study was to capture the public's understanding of wasps.

Prediction 1: There is taxon-level variation in the public's emotion towards insects. Data for all four insect groups were used to test this prediction. To obtain a qualitative assessment of emotion for each insect group, we asked respondents to provide up to three words that they would use to describe each insect in turn. Words were corrected (e.g. for spellings) and collated into common stems (e.g. 'flower' and 'flowers' were combined; 'hate', 'hateful' and 'hatred' were combined) and the frequency of occurrence of each word per taxa was counted and visualised in a word frequency diagram ('Wordle'), where the size of the word text indicates the relative frequency with which the words were used in each insect category. Word clouds were generated using the algorithm implemented in the website https://www .jasondavies.com/wordcloud/, using the following visualisation parameters: rectangular spiral, -60° to $+60^{\circ}$ orientation, and scale = n. The 10 most commonly used words were collated for a qualitative assessment of how descriptions were mostly emotive (e.g. 'scary', 'pretty') or indicative of value or function (e.g. pollinator).

To obtain a quantitative assessment of people's emotion in respect of each insect group, we asked the question, 'If you see one of these insects, how does it make you feel?' This response aims to detect the participant's immediate feelings towards each insect regardless of the insect's importance in ecosystems and the environment. Respondents rated each insect on a Likert scale, from -5 to -1 [negative emotion from strongly (-5) to weakly (-1) negative], 0 [neutral emotion (i.e. neither positive nor negative), +1 to +5 (positive emotion from strongly (+5) to weakly (+1) positive]. In order to gauge the demographic we were sampling, respondents were also asked to report their personal level of interest in nature [from 0 (no interest) to 10 (extremely strong interest)] and the highest level of education (from a choice of 'school leaver', 'undergraduate degree', or 'postgraduate degree').

We used generalised linear mixed models with negative binomial distribution and log-link function to assess what factors might explain differences in emotion; the response variable was the emotion score (recalibrated from -5 to +5 to 1-10); explanatory factors were species (categorical variable – four levels) and interest in nature (continuous variable – on a scale of 1-10), and respondent ID was included as a random factor to account for individual-level bias. We included the interaction term: 'species' × 'interest in nature'. Level of education was not included in this analysis as it was positively correlated with interest in nature and thus violated the assumptions of the model; moreover, it had a low predictive power as there were only three levels. Sequential Bonferroni correction was used to account for multiple *post hoc* pairwise comparisons.

Prediction 2: Interest in nature influences the public's appreciation of ecosystem services by bees and wasps. We sought to determine the extent to which the public appreciate the ecosystem service value (ESV) of wasps (as predators of arthropods) and bees (as pollinators of plants). We asked people to score (1-10) their responses to the questions: 'To what extent do you regard these insects as predators?' to assess knowledge on the main ESV of wasps, and 'To what extent do you regard these insects as pollinators?' to assess knowledge on the main ESV of bees. Respondents indicated a score between 1 (indicating 'no value as pollinator/predator') and 10 (indicating 'highest possible value as pollinator/predator'). In the survey, these questions were posed in respect of all insect groups, but we only included data for bees and wasps in our analyses as this was the focus of our comparison. A generalised linear mixed model with negative binomial distribution and log-link function was used to determine difference in the public's perception of ESV for bees and wasps. The response variable was the ESV score given for predation (for wasps) and pollination (for bees). As in the model on emotions, the explanatory variables were species (categorical variable - four levels) and interest in nature (continuous variable - on a scale of 1-10), and respondent ID was included as a random factor to account for individual-level bias. We included the interaction term 'species' \times 'interest in nature'. For reasons explained earlier, level of education was not included in the model. Sequential Bonferroni correction was used to account for multiple post hoc pairwise comparisons.

Prediction 3: Research effort on wasps is under-represented relative to bees. We addressed this prediction in three ways. First, we focused on general biological research topics for which bees or wasps are study subjects. We conducted Web of Science searches to compare the number of published research articles on bees versus wasps from 1980 to 2017. Papers were selected using the title term 'bee' OR 'bees' (for effort on bee research) and 'wasp' OR 'wasps' (for effort on wasp research); they were then filtered by Web of Science Category (to include ecology, biological conservation, environmental science, agronomy, agriculture interdisciplinary, horticulture, environmental studies, zoology, evolutionary biology); finally, we filtered out papers on parasitoid wasps, as these are not likely to be the insect that is relevant to the public's understanding of what a wasp is. We plotted the data as a cumulative sum of the number of papers on each taxonomic group from 1980 until 2017. The search was conducted in July 2018, but we excluded data from 2018 as it is an incomplete year of sampling.

Secondly, we examined whether there is a taxon imbalance in research effort specifically on ecosystem service research on bees and wasps. As a representative sample of this, we searched for the number of papers ('articles') with 'wasp' (in title) AND 'ecosystem service' OR 'biological control' (in topic) to assess the research effort on wasp ESV; similarly, we searched for the number of papers ('articles') with 'bee' (in title) AND 'ecosystem service' OR 'pollination' (in topic) to assess the research effort on bee ESV.

Thirdly, we compared the representation of conference abstracts (including all oral and poster presentations) at five international meetings of the specialist social insect learned society (International Union of the Study of Social Insects, IUSSI) over the last 16 years. We chose this society as it includes researchers across the full taxonomic spectrum of social insect research, including bees and wasps, who are interested in a wide range of evolutionary and ecological questions, including applied ones. The advantage of using oral and poster conference abstracts is that these include unpublished work and this removes any inherent implicit taxonomic bias in publication opportunities and acceptance [e.g. there is a specific journal for bee research (Apidologie) but not for wasps]. Chi-squared tests were used to detect any statistically significant bias with respect to taxon in these datasets, in the pooled datasets across years.

Results

Overall, 748 people submitted responses online from 46 countries, although the majority (70.6%) were from the U.K. The educational levels of respondents ranged from school leavers (14.05%, n = 105) to holders of undergraduate (52.27%, n = 391) or postgraduate (33.72%, n = 252) degrees (File S1). Level of education was strongly positively correlated with level of interest in nature (Spearman $\rho = 0.240$, P < 0.001, n = 748) and so we chose to include only the level of interest in nature for our analyses to avoid using confounding variables and to retain the variable with the most information (10 levels rather than three).

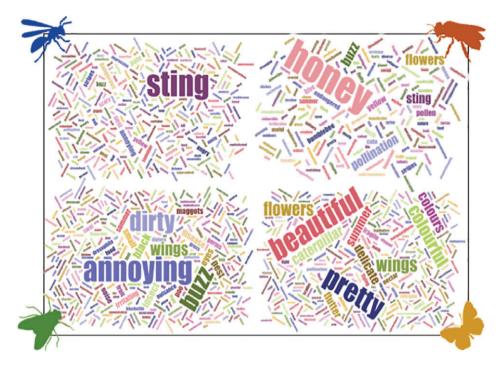


Fig. 1. Words used by the public to describe (clockwise from top left) wasps, bees, butterflies and flies. The size of the word indicates the relative frequency with which that particular word was used, within each taxonomic group.

Prediction 1: Taxon-level variation in the public's emotion towards insects

The 7139 words used by the public to describe the four insects provide qualitative support for the perceived differences in the public's emotions towards insects (Fig. 1; Table 1). Among the 10 most commonly used words, those used for bees reflected the function and usefulness of bees to humans and ecosystems (e.g. 'honey', 'flowers', 'pollen', 'pollination'); this contrasts with the words used to describe wasps and butterflies, which were almost exclusively emotive (e.g. for wasps – 'sting', 'annoying', 'dangerous', 'angry'; for butterflies – 'beautiful',

'pretty', 'delicate', 'colourful') and rarely reflected their ecological value. Words used to describe flies were both emotive (e.g. 'annoying', 'pest') and indicative of their functional impact on human societies, (e.g. 'dirty', 'disease'), but did not reveal much knowledge of the important role played by flies as pollinators and predators (Table 1).

There was a bimodal distribution of emotions towards the insects, which was explained by taxon: butterflies and bees were viewed almost exclusively positively, and flies and wasps almost exclusively negatively (Fig. 2a). Butterflies received the highest level of positive emotion, followed closely by

Table 1. The most common words used to describe wasps, bees, flies and butterflies (n = 1199 words from a total of 7139 unique words proposed by 748 members of the public). Percentages of occurrence for each of the 10 most common words are reported for each taxon.

Rank	Wasp		Bee		Fly		Butterfly	
	Word	%	Word	%	Word	%	Word	%
1	Sting	23.4	Honey	24.0	Annoying	10.3	Beautiful	10.5
2	Annoying	3.6	Flowers	6.9	Dirty	8.3	Pretty	10.0
3	Pain	3.5	Buzz	6.9	Buzz	8.1	Wings	6.1
4	Nest	3.1	Sting	6.2	Wings	5.1	Colourful	5.9
5	Dangerous	2.9	Pollination	6.0	Black	3.2	Flowers	5.9
6	Stripes	2.6	Pollen	3.1	Insect	2.7	Caterpillar	4.5
7	Buzz	2.6	Yellow	3.0	Pest	2.6	Colours	4.4
8	Yellow	2.5	Bumblebee	2.4	Eyes	2.4	Delicate	3.9
9	Angry	2.5	Hive	2.3	Small	2.2	Summer	3.9
10	Scary	2.3	Stripes	1.9	Disease	2.2	Flutter	3.1
Total entries	1894	_	1354	_	1940	_	1951	_
Total words	350	_	186	_	358	_	305	_

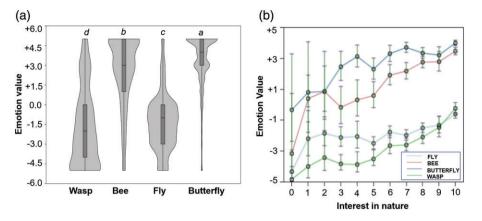


Fig. 2. (a) Emotion scores assigned to each taxonomic group by 748 members of the public: -5 to -1 indicates a negative emotion; 0 indicates neutral/neither like nor dislike; +1 to +5 indicates a positive emotion towards that insect group. Overall significant interaction between species and emotion rating (P < 0.001); all pairwise comparisons are significant. (b) Level of self-reported interest in nature explains the variation in emotion to insects within and among taxa. Estimates with 95% confidence interval of the estimated marginal means from linear mized models are plotted.

bees, and then flies and wasps. All species-pairwise tests were significant: bees are liked more than butterflies, and flies are disliked less than wasps (all tests, P < 0.001 after Bonferroni correction). The level of interest in nature reported by the public was positively correlated with emotion overall (F = 67 477, d.f. = 43, P < 0.001), suggesting that the more interest a person has in nature, the more positively they view insects overall. There was also a significant interaction with species (F = 5934, d.f. = 30, P < 0.001; Fig 2b): the strongest effects were for the more charismatic taxa (bees and butterflies) and the weaker effects were for the less charismatic taxa (flies and wasps). This suggests that a greater interest in nature results in a more extreme emotional feeling towards the charismatic species, than towards the less charismatic species.

Prediction 2: Interest in nature influences the public's appreciation of ecosystem services by bees and wasps

There was a significant effect of species on how people rate the ESV of the insects (F = 157795, d.f. = 1, P < 0.001), with bees rated consistently high and wasps low. As with emotion, self-reported level of interest in nature explained some of the variation in ESV rating: the greater the interest in nature, the higher the ESV given (F = 5826, d.f. = 10, P < 0.001; Fig. 3a). Importantly, there was a significant interaction effect with species: interest in nature had a greater effect on ESV ratings for wasps than for bees (F = 4115, d.f. = 10, P < 0.001; Fig. 3b). This suggests that people understand the ESV of bees even if they do not have a strong interest in nature; however, only those with a high interest in nature are well informed about the ESV of wasps.

Prediction 3: Research effort on wasps is under-represented relative to bees

Three lines of evidence supported this prediction. First, of the 5244 papers in our sample published between 1980 and 2017, 64.3% (n = 3372) have bees as subjects, and 35.7% (n = 1872)

have wasps, with bees thus being significantly over-represented (Yates-corrected $\chi^2 = 218.43$, d.f. = 1, P < 0.001). The bias in research effort is even more apparent when corrected for the number of species (using approx. species numbers as follows: bees, 22 000; wasps, 150 000; Grimaldi & Engel, 2005; Fig. 4a). Moreover, there was a significant correlation with year of the absolute difference in the numbers of papers on bees and wasps (from 1980 to 2017) (Spearman correlation, $r_s = 0.53$, P = 0.0006, n = 38), suggesting that the disparity of research effort on wasps relative to bees has been increasing over time.

Secondly, wasps (excluding parasitoid wasps) had significantly fewer publications than bees on the topic of ecosystem services and their respective ESV (pollination for bees; biological control for wasps) over the last 37 years. In total, 908 papers were sampled. Only 22 (2.4%) publications on wasp ESVs were found since 1980; this is significantly less than was the case for bees (n = 886, 97.6%)) ($\chi^2 = 609.4, d.f. = 1, P < 0.0001$).

Finally, of the 2543 conference abstracts on bees or wasps presented at the international conferences of the IUSSI that took place over the last 5 years, 18.7% (n = 168) were on aculeate wasps and 81.3% on bees (n = 731) ($\chi^2 = 362.62$, d.f. = 2, P < 0.0001]. Interestingly, the bias towards bees has become more extreme over the 16 years, from 1998 to 2014 (Yates-corrected $\chi^2 = 8.28$, d.f. = 1, P = 0.004) (Fig. 4b).

Discussion

We have provided quantitative evidence to support the widespread stereotype that wasps are universally disliked and bees are universally liked by people. We identified two factors that may influence how people feel towards insects, and specifically wasps and bees: how interested people are in nature, and the extent to which people appreciate the ecological value of bees and wasps. Improving people's understanding of the importance of wasps as regulators of insect pests may help the image of wasps and change how human societies value them. In the second part of this study we found that wasps are unpopular study taxa for scientists as subjects in general

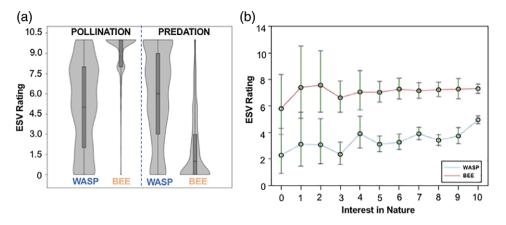


Fig. 3. (a) Scores of ecosystem service value (ESV) assigned to bees and wasps by 748 members of the public: scores ranged from 1 (indicating 'no value as pollinator/predator') to 10 (indicating 'highest possible value as pollinator/predator'). Overall significant interaction between species and ESV rating (P < 0.001). (b) ESV rating for bees and wasps was influenced by a person's self-reported interest in nature (P < 0.001). There was an interaction with species, suggesting that the effect was stronger for wasps (blue) than for bees (red line).

biology but specifically with respect to ecosystem services. We discuss the relationship between these two sets of results and propose ways in which scientists can help improve the public image of wasps. Overturning the poor public image of wasps is important in developing conservation programmes and nurturing the public as guardians of wasps as natural capital, in the same way bees and their services are valued (Novacek, 2008; Loyau & Schmeller, 2017).

People's emotions towards insects were significantly influenced by their self-reported 'level of interest in nature'. The more engaged a person is with natural history and the natural world, the more they may know (or understand) about insects in general and, by extension, the more positive they may feel towards them. The positive effect of human-nature interactions on the expression of pre-environmental behaviour (Soga & Gaston, 2016) and the positive impact of ecological engagement on how people (and stakeholders) value ecosystem services have recently come to light (Livingstone et al., 2018). Our study found a similar result in that there was a significant positive effect of interest in nature on feelings towards all four insect taxa. Intriguingly, the effect was much stronger for the charismatic species (bees and butterflies) than for the less charismatic species (wasps and flies). This suggests that wasps (and flies) are universally disliked, even by people who have a strong interest in nature. Culturing a greater interest in nature among the public per se is not, therefore, going to alter people's feelings towards wasps as much as it would for bees. Engagement, marketing and education are key factors in influencing the public's attitudes to conservation and wildlife management (Sharp et al., 2011; Courchamp et al., 2018); focusing these activities on the less charismatic, less popular and less well-known organisms could have a more profound impact on public support for environmental and conservation programmes and sustainability.

A recurring question asked by members of the public is: 'What's the point of wasps?' The same question is rarely asked about bees, perhaps due to the overwhelming presence in mainstream media of bees, their importance as pollinators, and their plight in the face of environmental change. Our data articulate this sentiment in quantitative terms: the mean ESV given to wasps was consistently lower than that given to bees; even people with a low/no interest in nature rated the ESV of bees as greater than that of wasps. Most intriguing is our finding that an interest in nature results in a bigger boost in ESV rating for wasps than for bees. By engaging the public with the biology and ecological roles of wasps, their image might be improved, but appreciation of bees could already be saturated. Interactions with nature early in life influence environmental attitudes and the pro-environmental behaviour and actions of adults later in life (Soga & Gaston, 2016).

Our second set of analyses revealed that aculeate wasps are under-represented as scientific study organisms in every measure of our analyses. Even though there are over three times the number of species of aculeate wasps compared with bees, there are almost twice as many papers and over four times as many conference abstracts on bees than on wasps. Drilling a little deeper into the literature of ecosystem services, the picture was just as biased, with papers on bee ecosystem services outnumbering those on wasps by 40:1.

The public's dislike of wasps is likely to lie in the deep-rooted cultural perceptions of wasps as unlikeable and in a general lack of appreciation of the ecosystem services performed by wasps, especially among those with little interest in nature generally. This negative cultural stigma could have laid the foundations for the implicit bias against wasp research we detected, even among those already interested in other similar insects, such as bees (most of which also sting). A feedback loop may perpetuate the negative attitudes of both public and scientists to wasps, reinforcing further the lack of research effort in this area (Fig. 5). Such feedback has been suggested previously in light of concerns about the decline in human–nature interactions and the negative impact of this on our attitudes to conservation and environmental issues (Soga & Gaston, 2016).

We suggest two sets of solutions (Fig. 5). The first is to boost the public image of wasps using evidence-based proof of their importance in natural and farmed ecosystems. Positive portrayal of wasps and their ecological and economic importance to the

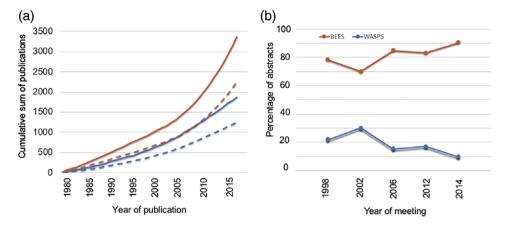


Fig. 4. (a) Cumulative number of papers published between 1980 and 2017 on ecological topics involving bees (red lines) or wasps (blue lines) and the primary study organism. Solid lines are the absolute number of papers; dashed lines are the number weighted by the number of species. (b) Popularity in wasp research has declined over the last 18 years, whereas interest in ants has increased and that in bees has remained unchanged (data from n = 2543 conference abstracts, five conferences between 1998 and 2014).

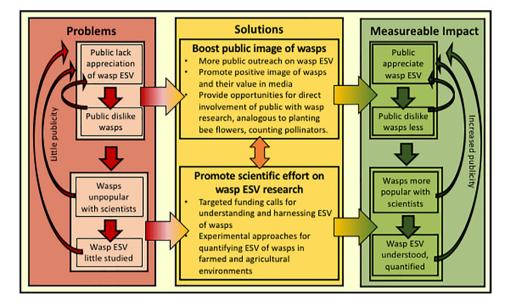


Fig. 5. The paucity of robust scientific knowledge on the ecosystem service value (ESV) of wasps results in lack of media exposure of wasps and of engagement by the public. This drives a positive feedback, reinforcing the cultural norm of disliking wasps and not wanting to study them. Boosting the public image of wasps and research effort will generate the data on wasp ESV that are required to engage the public, society and scientists. Positive feedback of 'knowledge begets knowledge' on wasps will help to rebalance emotions towards these important insects. [Colour figure can be viewed at wileyonlinelibrary.com].

public will help to challenge the stigma that wasps suffer, and could reinforce positive (rather than negative) perceptions of wasps. Bees are an exemplar model for achieving this: in the last few years, positive marketing of the pollination services of bees has led to bottom-up community efforts to create bee-friendly habitats in urban and rural areas across nations. There are few (if any) equivalent wasp initiatives; one exception is the U.K.'s Big Wasp Survey which was set up in 2017 as a citizen science project to sample wasps across the U.K. (Sumner *et al.*). Its success was unexpected given the public's attitude to wasps; it remains to be seen whether this initiative was preaching to the converted, i.e. whether it was the minority of the U.K. public who view wasps positively who self-selected to take part.

In order to help the public understand the value of wasps, however, we require the scientists to value wasps more, and to carry out the required research on the ESV of wasps. Unlike bees, which have the multi-billion-dollar seal of ESV approval, we have no accurate estimates of the economic or ecological value of wasps as natural pest controllers and regulators of arthropod populations. Whilst there are some qualitative studies on what wasps eat (Kasper *et al.*, 2004; Ward &

Ramón-Laca, 2013), quantitative studies are lacking, apart from a handful of invasive populations of Vespula, where colonies are unusually large and exhibit unusual foraging activities and behaviours (Harris, 1991; Harris & Oliver, 1993). Moreover, we lack experimental approaches to determine the predation services of wasps as biocontrol agents (but see correlational studies: Rabb & Lawson, 1957; Picanço et al., 2011) despite their potential as a managed populations (Donovan, 2003). We require experimental studies on native species in their natural and native-farmed habitats, and development of standardised methodologies to quantify the ecosystem services of wasps in both natural and framed ecosystems. Targeting funding routes [as have benefited bee research (e.g. (Vanbergen & Initiative, 2013) and have probably contributed to the increased research effort in bees over the last 10 years] are required to kick-start research into the economic and ecological value of wasps.

All insects are under threat from climate change, habitat loss, fragmentation and deterioration of habitat quality. Maintaining insect abundance and diversity should be a prime conservation priority. Aculeate wasps provide important ESVs as generalist predators with huge potential through managed exploitation for biological control. However, the required research is lacking; robust evidence on their ecological and economic value is required to convince the public to view these insects favourably. An overall increase of scientific understanding could, in turn, help to improve the public's perception of wasps. If this were achieved, we expect that the public would be more accommodating of wasps and more inclined to tolerate wasp nests in their local environment, rather than have them removed. Increased tolerance will benefit the conservation of these important insects. At a time when all insects (including wasps) are experiencing declining populations across the globe, this could have a significant impact on wasp conservation and management strategies. Such a cultural shift in the perception of wasps could thus be pivotal in conserving these facets of natural capital.

And books which told me everything about the wasp, except why. (Dylan Thomas, 'A Child's Christmas in Wales', 1952)

Acknowledgements

We thank the 748 members of the public who took part in this survey and those who helped share it across social media. We also thank Phil Lester and an anonymous reviewer for their comments, which helped to improve the manuscript. SS was funded by Natural Environment Research Council (grant NE/M012913/2) and AC by a Marie Slodowska Curie fellowship (grant no. 706208 SocParPhenoEvol).

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

File S1. Survey responses.

References

- Aguiar, A.P., Deans, A.R., Engel, M.S., Forshage, M., Huber, J.T., Jennings, J.T. *et al.* (2013) Order Hymenoptera. *Zootaxa*, 3703, 51–62.
- Aizen, M.A., Garibaldi, L.A., Cunningham, S.A. & Klein, A.M. (2009) How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. *Annals of Botany*, **103**, 1579–1588.
- Archer, M.E. (1985) Population dynamics of the social wasps Vespula vulgaris and Vespula germanica in England. Journal of Animal Ecology, 54, 473–485.
- Carpenter, W.S. & Kojima, J. (1996) Checklist of the species in the subfamily Stenogastrinae (Hymenoptera: Vespidae). *Journal of the New York Entomological Society*, **104**, 21–36.
- Carpenter, J.M. & Kojima, J. (1997) Checklist of the species in the subfamily Vespinae (Insecta: Hymenoptera: Vespidae). *Natural History Bulletin of Ibaraki University*, 1, 51–92.
- Costanza, R., Arge, R., De Groot, R., Farberk, S., Grasso, M., Hannon, B. *et al.* (1997) The value of the world's ecosystem services and natural capital. *Nature*, **387**, 253–260.
- Courchamp, F., Jaric, I., Albert, C., Meinard, Y., Ripple, W.J. & Chapron, G. (2018) The paradoxical extinction of the most charismatic animals. *PLoS Biology*, **16**, 1–13.
- Dhand, A.A. (2018) City of Sinners. Bantam Press, London, U.K.
- Dicks, L.V., Abrahams, A., Atkinson, J., Biesmeijer, J., Bourn, N., Brown, C. *et al.* (2013) Identifying key knowledge needs for evidence-based conservation of wild insect pollinators: a collaborative cross-sectoral exercise. *Insect Conservation and Diversity*, 6, 435–446.
- Donovan, B. (2003) Potential manageable exploitation of social wasps, Vespula spp. (Hymenoptera: Vespidae), as generalist predators of insect pests. International Journal of Pest Management, 49, 281–285.
- Evans, H.E. & Eberhard, M.J.W. (1970) *The Wasps*. University of Michigan Press, Ann Arbor, Michigan.
- Gaston, K.J. & Lawton, J.H. (1988) Patterns in the distribution and abundance of insect populations. *Nature*, 331, 709–712.
- Grimaldi, D. & Engel, M.S. (2005) Evolution of the Insects. Cambridge University Press, Cambridge, U.K.
- Grissell, E. (2010) Bees, Wasps, and Ants: The Indispensable Role of Hymenoptera in Gardens. Bees, Wasps, and Ants. Timber Press, Portland, Oregon.
- Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H. *et al.* (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One*, **12**, e0185809.
- Hanley, N., Breeze, T.D., Ellis, C. & Goulson, D. (2015) Measuring the economic value of pollination services: principles, evidence and knowledge gaps. *Ecosystem Services*, 14, 124–132.
- Harris, R.J. (1991) Diet of the wasps Vespula vulgaris and V. germanica in honeydew beech forest of the South Island, New Zealand. New Zealand Journal of Zoology, 18, 159–169.
- Harris, R.J. & Oliver, E.H. (1993) Prey diets and population densities of the wasps Vespula vulgaris and V. germanica in scrubland-pasture. New Zealand Journal of Ecology, 17, 5–12.
- Hochkirch, A. (2016) The insect crisis we can't ignore. *Nature*, **539**, 141–141.
- Isaac, N.J.B., August, T. & Powney, G. (2013) Trends in the Distribution of UK native species 1970–2010 Preliminary report to JNCC. JNCC Report No. 488.
- Kasper, M.L., Reeson, A.F., Cooper, S.J.B., Perry, K.D. & Austin, A.D. (2004) Assessment of prey overlap between a native (*Polistes humilis*) and an introduced (*Vespula germanica*) social wasp using morphology

and phylogenetic analyses of 16S rDNA. *Molecular Ecology*, **13**, 2037–2048.

- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C. *et al.* (2007) Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 66, 95–96, 191.
- Lester, P.J. (2018) *The Vulgar Wasp: The Story of a Ruthless Invader and Ingenious Predator*. Victoria University Press, Wellington, New Zealand.
- Lewandowski, E.J. & Oberhauser, K.S. (2017) Butterfly citizen scientists in the United States increase their engagement in conservation. *Biological Conservation*, 208, 106–112.
- Livingstone, S.W., Cadotte, M.W. & Isaac, M.E. (2018) Ecological engagement determines ecosystem service valuation: a case study from Rouge National Urban Park in Toronto, Canada. *Ecosystem Services*, **30**, 86–97.
- Lockwood, J. (2013) *The Infested Mind: Why Humans Fear, Loathe and Love Insects.* Oxford University Press, New York, New York.
- Losey, J.E. & Vaughan, M. (2012) The economic value of ecological services provided by insects. *Bioscience*, 56, 311–323.
- Loyau, A. & Schmeller, D.S. (2017) Positive sentiment and knowledge increase tolerance towards conservation actions. *Biodiversity and Conservation*, 26, 461–478.
- Lynd, R. (1921) The Pleasure of Ignorance. Scribner, Fairfield, Iowa.
- Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Biodiversity Synthesis.* Washington, District of Columbia.
- Narendran, T.C. (2001) Parasitic hymenoptera and biological control. *Biocontrol Potential and Its Exploitation in Sustainable Agriculture*, pp. 1–12. Springer, Boston, Massachusetts.
- Noriega, J.A., Hortal, J., Azcárate, F.M., Berg, M.P., Bonada, N., Briones, M.J.I. *et al.* (2017) Research trends in ecosystem services provided by insects. *Basic and Applied Ecology.*, 23, 8–23.
- Novacek, M.J. (2008) Engaging the public in biodiversity issues. Proceedings of the National Academy of Sciences, 105, 11571–11578.
- Oliver, T.H., Heard, M.S., Isaac, N.J.B., Roy, D.B., Procter, D., Eigenbrod, F. *et al.* (2015) Biodiversity and resilience of ecosystem functions. *Trends in Ecology & Evolution*, **30**, 673–684.
- Ollerton, J., Erenler, H., Edwards, M. & Crockett, R. (2014) Extinction of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science*, **346**, 1360–1362.
- Picanço, M.C., Bacci, L., Queiroz, R.B., Silva, G.A., Miranda, M.M.M., Leite, G.L.D. *et al.* (2011) Social wasp predators of *Tuta absoluta*. *Sociobiology*, **58**, 621–633.
- Prather, C.M. & Laws, A.N. (2017) Insects as a piece of the puzzle to mitigate global problems: an opportunity for ecologists. *Basic and Applied Ecology*, 26, 71–81.
- Prather, C.M., Pelini, S.L., Laws, A., Rivest, E., Woltz, M., Bloch, C.P. et al. (2013) Invertebrates, ecosystem services and climate change. *Biological Reviews*, 88, 327–348.

- Rabb, R.L. & Lawson, F.R. (1957) Some factors influencing the predation of *Polistes* wasps on the tobacco Hornworm. *Journal of Economic Entomology*, **50**, 778–784.
- Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R. *et al.* (2016) Non-bee insects are important contributors to global crop pollination. *Proceedings of the National Academy* of Sciences, **113**, 146–151.
- Ross, K.G. & Matthews, R.W. (1991) *The Social Biology of Wasps*. Cornell University Press, Ithaca, New York.
- Schmidt, J.O. (2016) *The Sting of the Wild*. John Hopkins University Press, Baltimore.
- Schowalter, T.D., Noriega, J.A. & Tscharntke, T. (2018) Insect effects on ecosystem services–introduction. *Basic and Applied Ecology*, 26, 1–7.
- Senapathi, D., Carvalheiro, L.G., Biesmeijer, J.C., Dodson, C.-A., Evans, R.L., McKerchar, M. *et al.* (2015) The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. *Proceedings of the Royal Society B: Biological Sciences*, 282, 8.
- Sharp, R.L., Larson, L.R. & Green, G.T. (2011) Factors influencing public preferences for invasive alien species management. *Biological Conservation*, 144, 2097–2104.
- Soga, M. & Gaston, K.J. (2016) Extinction of experience: the loss of human-nature interactions. *Frontiers in Ecology and the Environment*, 14, 94–101.
- Spradbery, J.P. (1973) Wasps. An Account of the Biology and Natural History of Solitary and Social Wasps. Sidgwick & Jackson Ltd., Washington, District of Colombia.
- Sumner, S. & Brock, R. (2016) In defense of wasps: why squashing them comes with a sting in the tale. *The Conversation*.
- Sumner, S., Bevan, P., Hart, A.G. & Isaac, N.J.B. Big Wasp Survey. *submitted*.
- Thomson, D.M. (2018) Effects of long-term variation in pollinator abundance and diversity on reproduction of a generalist plant. *Journal* of *Ecology*, in press.
- Vanbergen, A. J. & the Insect Pollinators Initiative (2013) Threats to an ecosystem service: pressures on pollinators. *Frontiers in Ecology and* the Environment, **11**, 251–259.
- Ward, D.F. & Ramón-Laca, A. (2013) Molecular identification of the prey range of the invasive Asian paper wasp. *Ecology and Evolution*, 3, 4408–4414.
- Woodcock, B.A., Isaac, N.J.B., Bullock, J.M., Roy, D.B., Garthwaite, D.G., Crowe, A. *et al.* (2016) Impacts of neonicotinoid use on long-term population changes in wild bees in England. *Nature Communications*, 7, 12459.

Accepted 13 August 2018 First published online 19 September 2018 Associate Editor: Adam Hart