A novel interference behaviour: invasive wasps remove ants from resources and drop them from a height

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This study reports a novel form of interference behaviour between the invasive wasp Vespa vulgaris and the New Zealand native ant Prolasius advenus. By videotaping interactions at bait stations, we found that wasps commonly remove ant competitors from food resources by picking up the workers in their mandibles, flying backward and dropping them unharmed some distance from the food. Both the frequency and the efficiency of the wasp behaviour significantly increased with the abundance of ant competitors. Ant removals were the most common interference events initiated by wasps when ants were numerous, while intraspecific conflicts among wasps were prominent when few ants were present. The ‘ant-dropping’ behaviour emphasizes how asymmetry in body sizes between competitors can lead to a pronounced form of interference, related to asymmetric locomotion modes.

Keywords: ants; asymmetric competition; interference behaviour; invasive wasps

1. INTRODUCTION
Competition may occur indirectly when two species exploit a common but limiting resource, or directly when one species interferes with the capacity of the other species to utilize resources. Although both mechanisms have long been recognized as common in nature, the evolutionary and ecological importance of heterospecific interference has yet to receive the same attention as the role of exploitative competition [1].

Interference interactions between species are common in social insects, and examples are particularly abundant among ants or wasps [2,3]. However, interactions between members of these two groups have seldom been documented. While ant avoidance has been reported with wasps caching prey [4], very few interference behaviours have been studied. Cleptobiosis (wasps robbing food from ants) was reported for the first time only recently [5], and there are a few observations of wasps guarding mutualists against ants [6,7]. Overall, direct interactions and their underlying behavioural mechanisms are still relatively unknown in competitive contexts. Importantly, such interactions could be of crucial importance for our understanding of biological invasions involving the two social insect groups. For example, antagonistic interactions at food between native ants and invasive wasps have been advanced as a potential explanation for the relatively low success of Vespa vulgaris in Argentina [8].

The social wasp Vespa vulgaris (Vespidae) is native to temperate regions of the Northern Hemisphere. It is a major invasive species in New Zealand, especially in beech (Nothofagus spp.) forests [9]. In this habitat, native scale insects produce a large amount of carbohydrate-rich honeydew, which is consumed by V. vulgaris, and a variety of native animals including ants. Protein is therefore hypothesized to be the most limiting resource for native and introduced predators. Accordingly, wasps and the native ant Prolasius advenus (Formicinae) have been observed scavenging on the same prey (e.g. dead cicadas; J. Grangier 2010, personal observation). To investigate potential interference between the two species, we filmed interactions at protein-based baits. Preliminary observations revealed that wasps occasionally pick ant workers up in their mandibles to drop them some distance away. Here, we present an extensive survey aimed at determining the prevalence of this unknown behaviour among the full range of interactions between foraging ants and wasps. Under the assumption that it represents an interference behaviour, we hypothesized that dropped ants should be effectively removed from the disputed resource, over a distance and at a frequency increasing with the ant abundance. We also examined how this behaviour was expressed in relation to the abundance of wasp competitors and the occurrence of intraspecific conflicts among them.

2. MATERIAL AND METHODS
Experiments were conducted from February to May 2010 (austral summer–autumn), in beech forests of the South Island of New Zealand. In four different sites, a total of 48 bait stations were randomly installed on the leaf litter, each of them consisting of a white circular plastic area of 200 cm² in the middle of which we placed approximately 4 g of canned tuna fish. Bait stations were filmed using tripod-mounted cameras (see the electronic supplementary material for details).

Ants and wasps co-occurred on 45 of the 48 bait stations (total video time = 51 h; with 41 ± 2 min, mean ± s.e. video duration per station). Nearly all ants were P. advenus. We counted ants visiting baits every 10 min on videos, and wasps every 2 min because the latter are much more mobile. These values were averaged in order to calculate a mean frequency for each bait station. The total number of wasp–wasp aggressive interactions per video was also counted and time-averaged. Each interaction between foraging ants and wasps was inspected frame-by-frame, each frame providing a 1/30 second snapshot of behaviour. Interactions were scored as one out of 12 behavioural categories (see the electronic supplementary material for details). Particular attention was paid when a wasp removed an ant by flying backward and dropping it away from the resource. These ‘ant-dropping’ events were carefully analysed in order to note: (i) the behaviour of the targeted ant just before the removal by the wasp, which was eating, walking around the food or attacking the wasp; (ii) the dropping distance, which was measured by using a reference grid on the surface of the plastic area used as the bait station; (iii) whether the dropped ant was successfully removed from the food (i.e. if the distance between the ant and the food after the removal was bigger than the initial distance); (iv) whether the wasp and the dropped ant returned to the food after the interaction, and if so, which one arrived first when both returned; and (v) whether the dropped ants presented any obvious signs of wounds, based on their posture and the way they moved. For each parameter, we excluded the few cases in which evaluation was
made difficult by the positions of insects, which is why sample sizes shown in the results vary according to each parameter under consideration.

3. RESULTS

A total of 1295 ant–wasp interactions were identified on 45 bait stations (mean number of contacts ± s.e. per bait station = 28.8 ± 5.3; figure 1a). Most of these interactions (63.7%) were only brief, non-aggressive contacts when ant and wasp trajectories crossed. However, ants were aggressive towards the wasps following 26.3 per cent of the contacts, rushing at them, biting or spraying acid. Wasps, which on average weigh 212 times more than individual ants (data not shown), most often responded by moving away. However, even at baits with high ant abundances, wasps were able to maintain a presence throughout all the video recording time. Wasps obviously tried to limit the contact with ants, but they also occasionally initiated interactions. In 62 cases (4.8% of interactions) from 20 bait stations in three sites, the wasp picked up an ant, flew off several centimetres and dropped it (figure 1b and the electronic supplementary material, movies S1 and S2). Just before the dropping behaviour, most of the targeted ants were feeding or walking around the food (59.0 and 36.1%, respectively). They were aggressive towards the wasp in only 4.9 per cent (3 out of 61) of cases. Following the interaction, 89.8 per cent of dropped ants showed no obvious signs of damage. The wasp was never seen leaving the arena with the ant. Ant workers were successfully moved away from the food in 83.9 per cent of the cases, and wasps most often came back to the food within seconds after ant removal (52 out of 62 for both parameters). By contrast, 47.3 per cent (26 out of 55) of dropped ants did not return to the food and left the bait station, suggesting that their activities were strongly disturbed by such interactions. Even when both the ant and the wasp returned to the food after a dropping event (n = 20), the wasp preceded the ant in 75 per cent of cases.

As predicted, both the frequency of this ant-removal behaviour (percentage of total number of interactions) and the dropping distance were positively correlated with the mean number of ants at baits (figure 2a, b). The frequency of these events, as well as the ant
they were more numerous (figure 2). Thus, wasp–wasp aggressive interactions replaced the ant-dropping events as the most frequent form of interference when ant abundance was low, as indicated by the negative correlation between the frequencies of the two types of interactions (figure 2e). Finally, we also observed the ant-dropping behaviour under natural conditions between a wasp and a group of ants foraging in leaf litter (n = 2), and when using both larval and adult mealworms as more realistic prey items (n = 4) (see the electronic supplementary material, movie S3).

4. DISCUSSION

We observed native ants clearly competing with invasive wasps. Intraspecific conflict among wasps was prominent when few ants were present, but interference behaviours with ants were predominant when ants were abundant. In this context, a widespread behaviour of wasps was to fly off with an ant and drop it away from the food. Our results ruled out failed predation attempts, as wasps were never seen leaving the bait station with an ant and as most of removed ants were not injured. It is also unlikely to be a defensive response, as in most cases targeted ants were not behaving aggressively towards wasps. This, along with the fact that both the frequency and the efficiency of ant removals increased with the ant abundance, instead supports our initial hypothesis of a competitive strategy. Our study thus clearly suggests that wasps were attempting to facilitate their access to the food by removing the competing ants.

To the best of our knowledge, this represents a new form of interference behaviour. Some tropical polistine wasps have been reported to use a similar behaviour but only in a defensive context, avoiding predatory attacks by ants to their colony by dropping scout workers away from their nest [10,11]. As a competitive strategy, this behaviour appears efficient at the individual level, with most of dropped ants successfully removed from the food baits and seriously disturbed from their foraging activities. That most of the targeted ants were unharmed after these events is surprising given the marked size difference between competitors. The absence of ant killing by wasps may be related to the chemical weaponry commonly used by P. adelaeus workers, which was clearly repellent for the wasps (figure 1a).

Social wasps lack nest-based food recruitment mechanisms, and individual workers adopt a largely independent and opportunistic strategy. As a consequence, they are known to prefer quick and early exploitation of resources rather than defending resources from competing ants that can recruit massively [12]. Our finding partially supports this view, in the sense that the ant-dropping behaviour brings only short-term advantages to wasps. It can thus be hypothesized to be most efficient if focused on the first scout ants discovering a natural, defensible prey, by possibly
disturbing and delaying ant recruitment. However, our results suggest that wasps increased their competitive efforts when ants were more numerous. They dropped their competitors away even when bait stations were frequented by several tens of ants. This is in sharp contrast, for example, with tropical Polybia sericea (Vespidae), which was reported to never reclaim caterpillar prey where more than one ant was present [4]. Our findings therefore extend the range of known competitive strategies of social wasps by demonstrating that V. vulgaris can engage in pronounced interference interactions even when competing with aggressive, recruiting ants.

It is usually thought that larger animals tend to be superior to smaller ones in interference competition [13]. With one competitor literally hurled away by the other, our study shows that this trend is very marked when asymmetry in body size is coupled with asymmetry in locomotion type.

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