Heptyl butyrate, a putative pheromone involved in social communication of Vespula germanica *wasps*

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Insectes Sociaux
International Journal for the Study of Social Arthropods

ISSN 0020-1812

Insect. Soc.
DOI 10.1007/s00040-017-0591-6

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Insectes Sociaux

RESEARCH ARTICLE

Heptyl butyrate, a putative pheromone involved in social communication of *Vespula germanica* wasps

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Received: 16 June 2017 / Revised: 2 October 2017 / Accepted: 4 November 2017

Abstract Greater knowledge on the social communication of invasive *Vespula germanica* wasps is needed to fully understand their foraging behavior. This is particularly valuable considering that poison baiting is currently the only effective way of reducing wasp density. Heptyl butyrate is an attractant for many wasp species, but attempts to determine effects on *V. germanica* have yielded mixed results. We studied the behavior elicited by heptyl butyrate on *V. germanica* wasps in field experiments with foraging wasps. We also analyzed headspace volatiles of live *V. germanica* workers, to determine if heptyl butyrate is emitted. Heptyl butyrate was present in the headspace of live workers. Amounts of heptyl butyrate averaged 1.4 ± 0.2 ng per sample per hour, where each sample included six workers. Wasps approaching filter papers treated with different concentrations of heptyl butyrate hovered over it, but only a small percentage landed on it. Pure heptyl butyrate elicited the greatest response although all the concentrations tested were attractive. When heptyl butyrate was applied to protein baits, a greater number landed on the treated baits than on untreated ones, demonstrating this compound enhances attractiveness of baits. Results from our study suggest that heptyl butyrate is a pheromonal compound involved in attracting conspecifics to food resources, but other cues are needed to trigger landing.

Keywords Attractant · Recruitment · Semiochemical · Social insects · Yellowjackets · Heptyl butanoate

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Introduction

Vespula germanica is an invasive species in many countries of the Southern hemisphere including Argentina, Chile, South Africa and New Zealand (Beggs et al. 2011). This exotic insect has become a serious pest because it can reach high population densities in invaded areas, where it affects human outdoor activities and has a negative impact on native ecosystems and biodiversity (Beggs et al. 1998; Sackmann et al. 2000), as well as fruit and beekeeping industries (Clapperton et al. 1989; Ward et al. 2002). As social insects, *V. germanica* wasps are very successful invaders, show a great degree of phenotypic plasticity and complex behavior and learning capacities which make them very adaptable to different habitats (D'Adamo et al. 2000; D'Adamo and Lozada 2007; Spradbery and Dvorak 2010). These characteristics, coupled with the fact that their venomous sting poses a health hazard, add up to render their management very challenging.

Vespula germanica wasps prey on insects, feed on aphid honeydew and fruit, and scavenge on carrion, garbage and food associated with human outdoor activities (Akre

Published online: 10 November 2017

1982). Previous studies conducted with foraging wasps have reported the occurrence of numerous learning abilities at the individual level while relocating resources. The fact that *V. germanica* is a social species adds further complexity to the analysis of its relocating behavior, as individual learning overlaps with social communication, which greatly improves resource exploitation.

On one hand, odors emitted by wasps are involved in foraging communication at the food source, leading to local enhancement, a resource-based recruitment mechanism consisting in the attraction of foragers by conspecifics at a protein bait in *V. germanica* (D'Adamo et al. 2000; D'Adamo and Lozada 2005). On the other hand, nest recruitment, or recruitment at a distance have also been observed (D'Adamo et al., 2000; Lozada et al., 2016). These mechanisms, which lead conspecifics to a certain site and facilitate efficient exploitation of temporary resources, have been identified in several species of wasps (Wilson-Rankin, 2014) and involve visual as well as olfactory cues (D'Adamo et al. 2000, 2003; Richter 2000). For example, spiroacetals identified in the abdominal extracts of *V. germanica* and *V. vulgaris*, inhibit aggressive behavior in conspecifics (Francke et al. 1979; 1978). Moreover, D'Adamo et al. (2004; 2000) suggest the presence of a pheromone in head extracts of *V. germanica* that attracts conspecifics. The authors propose the occurrence of a pheromonal compound used to recruit conspecifics to a food resource, although the active compounds involved have not been identified yet.

Further knowledge on the social communication of these invasive insects is needed to fully understand their foraging behavior, which is particularly valuable considering that poison baiting is currently the only viable option to reduce invasive wasp density (Harris et al. 1991; Beggs et al. 1998; Hanna et al. 2012). Thus, there is a need to develop a wasp attractant that is more reliable, long lasting, cost effective, and specific, than meat (El-Sayed et al. 2009; Unelius et al. 2016). Several wasp attractants have been identified over the years and some are used in commercial lures. These include isobutanol, acetic acid, heptyl butyrate and combinations of these (Landolt 1998; Landolt et al. 2007; Landolt et al. 1999; Davis et al. 1969). The effect of heptyl butyrate on wasps was found by chance while researching attractants for the little house fly *Fannia canicularis* (L.), (Davis et al. 1967, 1969) and the nature of the biological activity has not been investigated (Landolt and Zhang 2016). Recently, Unelius et al. (2014) found that mussels volatiles which included heptyl butyrate and other similar esters were very attractive to *V. vulgaris* wasps. When they tested individual components, heptyl was the best single attractant. Later, Unelius et al. (2016) also found that lures comprising compounds from animals, plants and fungi, including heptyl butyrate, were very effective in capturing *V. vulgaris* wasps (Unelius et al. 2016). The existence of a pheromone involved in social communication of wasps is supported by several studies (Macdonald et al. 1973; D'Adamo et al. 2000, 2003; Buteler et al. 2016). However, the effect of heptyl butyrate on *V. germanica* has yielded mixed results. Several studies report no attractiveness (Landolt et al. 2007a; Dörre 2015) or only a slight response (Davis et al. 1969; Landolt et al. 2003) of *V. germanica* wasps to heptyl butyrate. Thus far, studies testing attractiveness of lures have been conducted assessing trap captures of baited traps, where trap design (Bacandritsos et al. 2006) as well as relative density of each species at the sites, and competitive interactions with other social wasps at or in traps (Landolt et al. 2003) may be confounding factors.

Therefore, our research investigates the role of heptyl butyrate as a pheromone involved in recruitment in workers of *V. germanica* by means of behavioral bioassays. For this purpose, we studied the behavior elicited in *V. germanica* wasps by heptyl butyrate in field experiments with foraging worker wasps. We also collected and analyzed headspace volatiles of live *V. germanica* workers to determine whether heptyl butyrate is emitted.

Materials and methods

Wasps headspace volatile collection

Bioassays were conducted in and around San Carlos de Bariloche, (41°S, 71°W), Rio Negro, Argentina, according to procedures outlined by (D'Adamo and Lozada 2007). All experiments were carried out under natural conditions along the shores of Gutierrez and Moreno Lakes, in March, 2016 when *V. germanica* wasps are typically most active. The field trials were completed within a 2-week time frame in order to reduce the variation due to increases in density over the nest growing season. Given that free-flying wasps were used, the individuals used could have originated from the same or from different nests.

V. germanica wasps were collected in flight when they approached the lake shore to consume water. This procedure was chosen to avoid any potential confounding odors released by bait in a trap. They were aspirated into a laboratory wash bottle modified as a 'wasp vacuum' (Buteler et al. 2016). An air stream purified by means of a charcoal filter was blown over six living wasps enclosed in the 250-ml glass chambers (43 cm length × 6 cm o.d.) (Bachmann et al. 2015). Volatiles were collected in traps made of 25 mg of HayeSep® Q (Grace, Deerfield, IL, USA). Headspace volatiles were collected for a period of 2 h. The portable volatile collection system used is a modification of the system originally described by Heath Manukian (1992) to collect air in an open system. The system is powered by a 12-V motor/diaphragm vacuum pump system (Model 5002-0408 DC-PM, 3000 rpm, Rietschie Thomas) controlled by an on/

off electrical light switch. This part of the system produces the vacuum required to draw the air from the collecting point. The vacuum is established using Tygon® tubing connections to a pair of flowmeters (Series MR 3000, Model 3A13, Key Instruments) that regulate the airflow rate. The system is complete when two 1.5 m Tygon® tubes (0.95 cm OD × 0.64 cm ID) are attached, each one extending from the flowmeter to the HayeSep® trap (Sigma Scientific Florida). The system described above is assembled inside a plastic container (25 × 25 × 20 cm), containing a smaller metal box (15 × 15 × 7 cm) connected to it by plastic tubing. The smaller box has two mounted flowmeters that control airflow; these are connected to the collecting traps by the Tygon® tubing. The box is also used to store all the Tygon® tubing in the system. The experiment was replicated 6 times. As control, volatiles from empty tubes were also collected 6 times.

After collection, the trapped volatile compounds were eluted with 150 µl of methylene chloride and subsequently identified using an Agilent 7890A gas chromatograph coupled to Agilent 5977 selective mass detector equipped with a HP-5 column (30 m ± 0.32 mm inner diameter ± 0.25 µm film thickness; Agilent Technologies). The initial oven temperature was 35 °C and after 1 min the oven temperature was increased to 100 °C at 5 °C min-1 and from 100 to 230 °C at 12 °C min-1, then held for 10 min. Samples were injected in the splitless mode with the injector purged at 30 s with nitrogen as the carrier gas at 27.6 cm/s flow velocity. The identity of heptyl butyrate emitted by wasps was determined from the comparison to the mass spectra and retention times of an authentic standard. For quantification, dodecane was used as internal standard. The detector response was assumed to be 1. Commercial heptyl butyrate and dodecane were obtained from Sigma–Aldrich (Milwaukee, WI, USA).

Field behavioral experiments

Three different behavioral bioassays were conducted in the same area and dates as detailed above. The first bioassays investigated the response of *V. germanica* workers to heptyl butyrate that was volatilized under ambient conditions. Bioassays consisted on placing a filter paper on the lakeshore where wasps typically foraged. The number of wasps hovering and landing on the filter paper was recorded over a period of 10 min. Treatments consisted of applying 0.1 ml of pure heptyl butyrate or 0.1 ml of heptyl butyrate at varying concentrations in ethanol. The concentrations used were 17.2, 0.172, 0.0172, 0.00172 micrograms/ml. As control, a filter paper treated with 0.1 ml of ethanol was also tested.

The second experiment tested whether wasps preferred meat baits treated with heptyl butyrate or untreated meat baits. The bait consisted of a white plastic dish (diameter = 7 cm) with another smaller container (2.5 cm diameter) holding 15 g of ground fresh bovine meat placed on top. Treated baits consisted of the application of 100 µL of heptyl butyrate onto a filter paper (Whatman No. 1) placed on the white dish of the bait while control baits were placed on untreated filter paper. Treated and control baits were placed 1.5 m from each other. The choice and time of the first approaching wasp as well as the number of wasps landing on each bait were recorded for a period of 10 min. The third experiment was a no-choice bioassay, following the same procedure as outlined above except that the treated and untreated baits were placed in areas of similar abundances but they were not offered simultaneously. In all cases, wasp visits were assigned one response class, either hovering or landing. Hovering occurred when the flying wasp approached the source and remained flying over it. A wasp was considered to have landed if after hovering, it touched the source with all six legs. Each set of experiments was replicated 15 times in areas separated at least 200 m from each other. The number of wasps landing and hovering in choice and no-choice tests were compared between treatments with a Student's t test (SAS 9.3) for paired or independent samples, respectively (SAS Institute, 2011). The time of the first landing for treated or control baits were compared with a Wilcoxon signed rank test. The number of wasps hovering and landing on filter papers treated with different concentrations of heptyl butyrate were compared with ANOVA (PROC MIXED, SAS Institute 2011). The variables were log transformed to better meet Anova assumptions of normality and variance homocedacy. Heptyl butyrate concentration was the fixed effect and replicate was included as a random factor. LsMeans among concentrations were compared with the Tukey adjustment.

Results

Emission of heptyl butyrate by wasps

Analysis of headspace volatiles revealed the presence of heptyl butyrate as determined by retention time and comparison of ion fragmentation patterns to the authentic standard. Amounts of heptyl butyrate averaged 1.4 ± 0.2 ng per sample per hour where each sample included six workers. Other compounds collected were not characterized or quantified, given that they were not part of the scope of the study. Heptyl butyrate was not detected in blank samples containing no wasps.

Heptyl butyrate attracted *V. germanica* wasps when applied to filter paper. Wasps were observed to hover and land on treated filter paper while untreated filter paper did not elicit any response from wasps, and so it was not included in the analysis. There was a significant difference between the total number of wasps landing ($F = 10.27$, d.f.= 4, 55; $P < 0.0001$) and hovering ($F = 18.42$, d.f.= 4, 55; $P < 0.0001$) on the filter papers among heptyl butyrate concentrations (Fig. 1). Filter papers treated with pure heptyl butyrate attracted more wasps than all the other concentrations. No differences in attractiveness were observed among the rest of the concentrations tested (Fig. 1). The mean number of hovering events per experiment (31.5 ± 8.1) for the pure compound was much greater than the number of landings observed (6.5 ± 1.7). The same pattern was observed for all the treatments tested (Fig. 1).

When wasps had a choice between meat baits treated with heptyl butyrate and control meat baits there were also differences in the number of wasps landings between treatments ($t = 0.561$, $df = 14$, $P = 0.0002$). Wasps clearly preferred to land on treated baits (Fig. 2). Moreover, the time it took

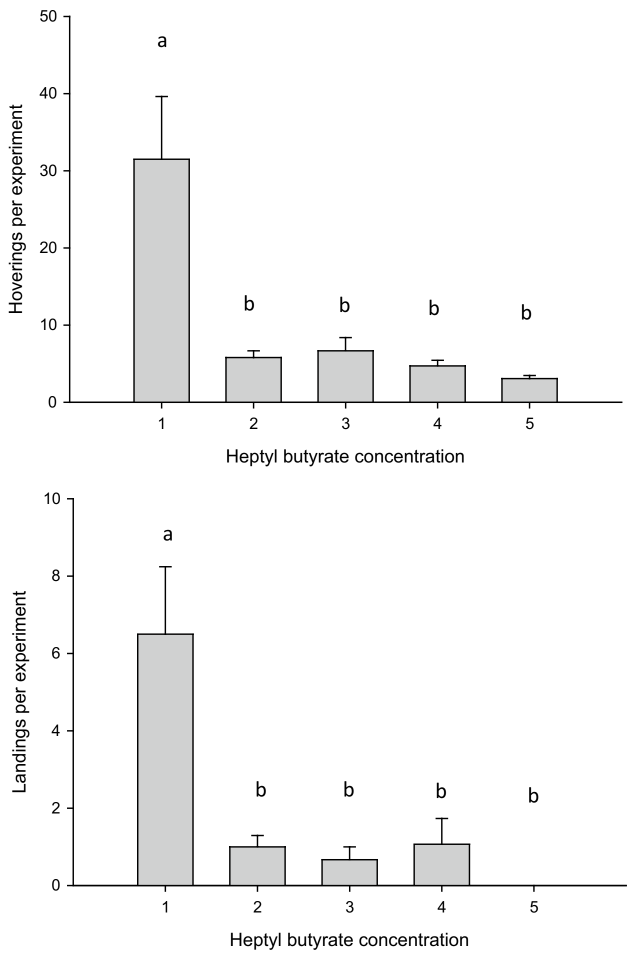

Fig. 1 Mean number of hovering or landing wasps over filter paper treated with 0.1 ml of heptyl butyrate or untreated filter paper in a field setting. *X* axis numbers represent each treatment: *1* pure heptyl butyrate; *2* 17.2 micrograms/ml; *3* 0.172 micrograms/ml; *4* 0.0172 micrograms/ml; *5* 0.00172 micrograms/ml of heptyl butyrate in ethanol. Each bioassay had a duration of 10 min. $N = 15$. Bars with different letters represent significantly different means at $\alpha = 0.05$ ANOVA

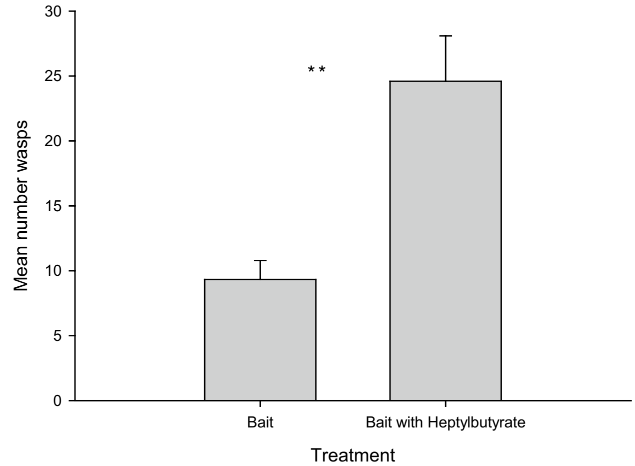

Fig. 2 Mean number of wasps arriving at the baits in a preference bioassay where wasps could choose between ground meat baits treated with 0.1 ml of heptyl butyrate or control baits. $N = 15$. **Represents significant differences at $\alpha = 0.05$ Student's *t* test

the first wasp to land on the bait varied significantly across bait treatment (Wilcoxon $S = -40.5$; $P = 0.018$). The time of the first landing varied considerably across bioassays, but on average it took 87.5 ± 30.1 s to wasps to arrive to a control bait in comparison to an average of 34.33 ± 10.72 s when the bait was treated with heptyl butyrate. Even in no-choice tests, a significantly greater number of wasps were observed in treated baits than in control baits (Fig. 3) (Student's $t = 2.688$; $df = 17$, $P = 0.015$). No other insect species approached the baits or filter paper treated with heptyl butyrate.

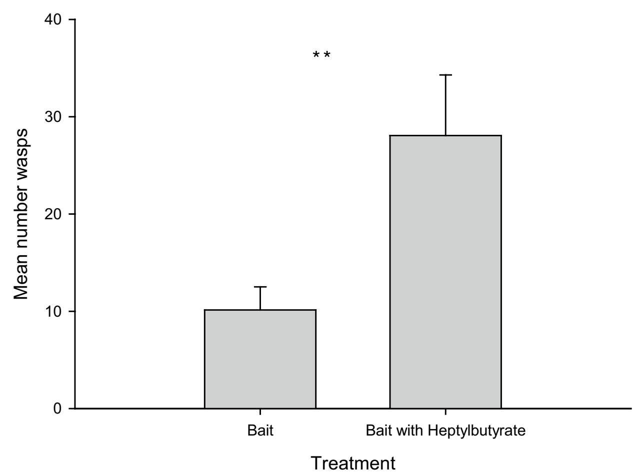

Fig. 3 Mean number of wasps arriving at protein baits, in independent bioassays with a duration of 10 min. Treatments consisted of 15 g of ground meat that were either treated with 0.1 ml of heptyl butyrate or left untreated. $N = 15$ bioassays per treatment. **Represents significant differences at $\alpha = 0.05$ Wilcoxon signed rank test

Discussion

This is the first behavioral study evaluating the response of free-flying *V. germanica* wasps towards heptyl butyrate that volatilized from a treated substrate under ambient conditions. The present study is also the first one to detect and quantify heptyl butyrate in headspace volatiles of live *V. germanica* worker wasps. We propose that heptyl butyrate might be involved in social communication of this species by having a role in attracting conspecifics to a food source. Wasps were more likely to arrive at the bait when they perceived this compound emanating from a treated substrate. These findings support previous studies which showed that foragers are attracted to a protein resource by the odor of conspecifics (D'Adamo et al. 2000, 2003). These authors reported an increased attraction of wasps to meat bait when wasp odors were offered simultaneously. This outcome is comparable to our observation in the current study, with heptyl butyrate added to the meat bait. Given that wasp odor contains heptyl butyrate at similar amounts at which wasps are attracted by it in the field, this study supports that this compound is part of the pheromonal system of foraging *V. germanica*. Overall, this warrants a detailed analysis of volatiles emitted by wasps and the behavior elicited by them to identify other behaviorally active compounds. The next step would be to carry out a gas chromatography coupled to an electroantennogram detector (GCEAD) procedure to determine which other compounds are active at the sensory level and warrant a detailed behavioral characterization and molecular identification. Heptyl butyrate as well as other volatiles emitted by wasps may be one signal in the overall social cognition and foraging behavior in vespids (Macdonald et al. 1973; Lozada et al. 2016). This compound could be involved in recruitment or attraction at the food resource, which occurs through visual and odor cues, allowing these wasps to enhance the exploitation of food resources (Santoro et al. 2015; Lozada et al. 2016).

Currently, ground meat is the bait of choice for toxic baits (Wood et al. 2006; Sackmann and Corley 2007) as well as traps. However, meat has many drawbacks including attraction of non-target organisms, consistency of its contents (Wood et al. 2006) and short duration of attractiveness due to drying out and decomposing (Reid and MacDonald 1986; Spurr 1995). Ground meat used as a bait also experiences changes in palatability with weather (Harris et al. 1991; Spurr 1995). Our results demonstrate that heptyl butyrate is an attractant for *V. germanica* and that it could provide an alternative to meat as a lure that is more specific to wasps and is inexpensive for use in traps. It is already used as food additive. The fact that meat with heptyl butyrate attracted more *V. germanica* wasps than meat alone, suggests that this compound could also be used in conjunction with toxic baits to increase effectiveness of the method, which depends on multiple visits. The fact that many more wasps were attracted to hover over the heptyl butyrate than to land on it in absence of a food resource supports previous studies showing that foraging involves visual as well as odor cues and suggests that pheromones may be one of the cues attracting foragers, but other cues are needed to trigger landing. Moreover, this could explain at least in some cases why traps loaded with heptyl butyrate did not catch many wasps (Landolt et al., 2007b; Dörre, 2015). Wasps may approach traps and hover near them without entering the traps in cases where these involve closed containers and open sticky traps (Bacandritsos et al., 2006; Unelius et al., 2016) may be more efficient in capturing wasps as they hover near the source.

The results from the current study as well as those reported by Hanna et al. (2012) suggest that the use of heptyl butyrate would increase bait attractiveness and removal, improving the efficacy of fipronil to suppress wasp populations. Heptyl butyrate is a food grade compound of low toxicity (EPA, 2008) which does not attract other insects (Davis et al. 1967), and thus, it should also be considered when managing *V. germanica* wasps as lures for traps or toxic baits. Further research should investigate whether addition of heptyl butyrate allows for an earlier deployment of toxic baits, before density of the pest reaches nuisance levels in peak season. Also, by improving efficacy of the baits, heptyl butyrate may reduce the amount of time toxic exposure in the field, reducing the negative impact of the insecticide (Hanna et al. 2012). This is particularly interesting considering that vespids have invaded native forests, National Parks and urban environments, where the impact of control measures on non-target organisms is of great importance. Thus, understanding the foraging behavior and communication in these wasps is essential to develop environmentally friendly management tools. Recent research focusing on the development of lures derived from diverse odor sources (El-Sayed et al. 2009; Brown et al. 2014, 2015; Unelius et al. 2014, 2016) demonstrates the need for novel and enhanced wasp attractants.

The present study adds to the current knowledge on behavior of *V. germanica* as it relates to conspecific odor cues and heptyl butyrate in particular. A recent study identified attraction of *V. vulgaris* to several alkyl butanoates present in mussel headspace, of which heptyl butyrate showed the strongest response (Unelius et al. 2014). Given that mussels are not part of the diet of vespid wasps, which typically prey or scavenge on arthropods, the explanation as to why wasps are attracted to these compounds may be associated to behavioral plasticity and an ability to react to cues from food resources they encounter for the first time (Beggs et al. 2011). The present study provides a plausible ecological explanation of the attractiveness of wasps to mussels and heptyl butyrate by suggesting it is related to an innate behavioral attraction to a pheromone involved in social communication. On the other hand, Unelius et al. (2014) proposed that heptyl butyrate and other attractive compounds present in mussels may originate from microorganisms, as their production continued after the mussels were dead (Unelius et al. 2014). Microbial volatile emissions have also been found to mediate wasps orientation to fermented sugar sources (Brown et al. 2015). Given that *V. germanica* are scavengers, they may be attracted to fungi or microorganisms associated with decomposing matter. It would be interesting to test whether emission of heptyl butyrate occurs in dead *V. germanica* individuals or in those treated with an antibiotic, to provide further understanding on the origin of this compound.

Our findings further support the literature by showing that the response of wasps to heptyl butyrate is widespread across vespids and also suggests that this compound may be involved in social communication, having great potential as a tool to incorporate into invasive wasp management.

Acknowledgements We thank Dr. Rikard Unelius for valuable comments that enriched the manuscript.

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