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Enantiospecific response of *Ips avulsus* (Coleoptera: Curculionidae: Scolytinae) to ipsdienol depends on semiochemical context

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Colonization of hosts by bark beetles is generally mediated by aggregation pheromones. Species competing for the same resource can limit interspecific interactions and maintain reproductive isolation by using different pheromones. In the southern United States, 3 sympatric species of *Ips* breed in pine hosts, each with a different pheromone blend. *Ips avulsus* (Eichhoff) uses ipsdienol and lanierone; *Ips calligraphus* (Germar) uses ipsdienol, *cis*-verbenol, and *trans*-verbenol; and *Ips grandicollis* (Eichhoff) uses ipsenol. Different species can also minimize cross-attraction by using different enantiomeric ratios of the same pheromones. Studies on the enantiomeric ratio of ipsdienol used by *I. avulsus* have come to contradictory conclusions in part because of geographic and seasonal variation. There is growing evidence that semiochemical context, in the form of different co-baits used in trapping experiments, may also play a role in the responses of *I. avulsus* to enantiomeric ratios of ipsdienol. We conducted a trapping study at 2 locations with traps baited with (+)-ipsdienol or racemic ipsdienol and co-baited with ipsenol, lanierone, or both ipsenol and lanierone. We found context-dependent effects of both lanierone and ipsenol on the response of *I. avulsus* to ipsdienol. We suggest that responses to different bait and co-bait combinations may have been shaped by different types of interactions such as the absence of conspecifics or a related species, or the presence of beneficial or antagonistic interspecific interactions.

Key words: ipsdienol, ipsenol, lanierone, enantiomeric ratio, bark beetle

Introduction

Engraver beetles (*Ips* spp.) mediate attacks on susceptible host material (phloem tissue of stressed, dying, or recently dead pines) with aggregation pheromones (Vité et al. 1978, Byers 1989). Aggregation pheromones can provide engraver beetles with reproductive isolation from sympatric and synchronic species. For example, trials with infested bolts suggest that species-specific aggregation pheromones limit cross-attraction among the southern *Ips* (*Ips avulsus* (Eichhoff), *Ips calligraphus* (Germar), and *Ips grandicollis* (Eichhoff)) (Vité et al. 1964, Birch et al. 1980, Byers 1989). Chemical analyses have found that *I. avulsus* and *I. calligraphus* produce ipsdienol. Additionally,

field trials have demonstrated that the most attractive blends with the fewest number of pheromone components include ipsdienol for all 3 species (in *I. grandicollis*, blends of ipsenol and *cis*-verbenol or ipsenol and ipsdienol were equally attractive) (Allison et al. 2012). In addition to qualitative and quantitative differences in the pheromone blend, enantiomeric composition of pheromone blends can minimize cross-attraction among species and contribute to reproductive isolation (Meier et al. 2016).

Despite the necessity for reproductive isolation, the southern *Ips* are sometimes found colonizing the same hosts (Birch et al. 1980, Paine et al. 1981). There is evidence that this phenomenon is not

only due to similar responses to host volatiles in the 3 species but can also be facilitated by cross-attraction. The most striking example of this cross-attraction is the response of *I. avulsus* to ipsenol. While ipsenol is produced only by *I. grandicollis*, using ipsenol as a co-bait in traps baited with ipsdienol and lanierone (2 main pheromone compounds of *I. avulsus*) increases the capture of *I. avulsus* beetles (Miller et al. 2005, Allison et al. 2012). Birch et al. (1980) and Paine et al. (1981) highlighted that, because of differential competitive ability among the southern *Ips*, the colonization of a host by multiple species depends on the identity and order of arrival of the species as well as the numbers of responding beetles per species. This phenomenon should theoretically create context-specific responses by beetles to different pheromone baits and co-baits.

The optimal enantiomeric composition of ipsdienol for attracting *I. avulsus* remains unclear (Vité et al. 1978, Smith et al. 1990, Strom et al. 2003, Miller and Allison 2011, Queffélec et al. 2023). For example, while Vité et al. (1978) reported that catches in traps baited with (−)-ipsdienol were greater than those in traps baited with (+)-ipsdienol or racemic ipsdienol, Strom et al. (2003) reported that racemic ipsdienol is more attractive than (−)-ipsdienol. One factor that complicates the interpretation of this literature is the use of different pheromone co-baits among studies. Field trapping studies that manipulated the semiochemical context (i.e., pheromone co-bait) observed that the effect of the enantiomeric composition of ipsdienol on the capture of *I. avulsus* varied among co-baits (Smith et al. 1990, Miller and Allison 2011). Semiochemical context is known to affect trap captures by attractive compounds in *Ips* species and in other wood borers (Sweeney et al. 2010, Miller 2023, Sullivan 2023). However, this phenomenon has been primarily studied in the context of host volatiles being used as co-baits. Rarely have the effects of semiochemicals produced by competitors been studied.

Another factor that confounds the interpretation of this literature is seasonality, as studies have been run at different times of year. Seasonal variability in bark beetle responses to pheromones has been reported, including seasonal variability in the response of *Ips pini* to ipsdienol (Teale and Lanier 1991). In fact, previous field trapping studies that attempted to characterize enantiospecific responses of *I. avulsus* to ipsdienol were unable to discriminate between semiochemical context and seasonal effects as mechanisms explaining variations in response by *I. avulsus* to ipsdienol enantiomers (Miller and Allison 2011).

In this study, we used a field trapping experiment duplicated in Louisiana and Georgia to test for an effect of semiochemical context (i.e., pheromone co-bait) on the response of *I. avulsus* to ipsdienol enantiomers. Specifically, traps were baited with either (+)-ipsdienol or racemic ipsdienol and were co-baited with ipsenol, lanierone, or both ipsenol and lanierone.

Materials and Methods

Two identical field trapping experiments were conducted in Louisiana, USA, and Georgia, USA, to assess interactions between the enantiomeric composition of ipsdienol (racemic or (+)-ipsdienol) and pheromone blend co-baits (i.e., ipsenol, lanierone, and ipsenol + lanierone) on the response of *I. avulsus*. These experiments were analyzed separately. Eight blocks of six (2 × 3) 8-unit multiple-funnel traps were established in linear arrays of traps spaced ca. 15 m apart within and between blocks. Traps were suspended from ropes between trees, with the collection cup of each trap ca. 0.5 m above ground. To increase retention of captured beetles, traps were equipped with wet cups that contained 150–200 ml of propylene glycol (Peak RV and Marine Antifreeze, Old World Industries Inc.,

Northbrook, IL, USA) as the killing fluid (Miller and Duerr 2008, Allison et al. 2014, Allison and Redak 2017).

In both experiments, each block contained the following 6 randomly distributed treatments: (i) racemic ipsdienol and racemic ipsenol; (ii) racemic ipsdienol and lanierone; (iii) racemic ipsdienol, racemic ipsenol, and lanierone; (iv) (+)-ipsdienol and racemic ipsenol; (v) (+)-ipsdienol and lanierone; and (vi) (+)-ipsdienol, racemic ipsenol, and lanierone. Traps were emptied, and trap captures were recorded 4 times at 2-wk intervals. On top of the *I. avulsus* beetles targeted and captured during these experiments, *I. calligraphus* and *I. grandicollis* beetles were also caught in the traps. *Ips avulsus* beetles were counted and identified at the species level using the morphology of the elytral armature (Wood 1982). Experiments in Louisiana and Georgia were conducted in predominately loblolly pine (*Pinus taeda* L.) stands that had experienced a prescribed burn 1–2 yr prior. In Louisiana, the experiment was conducted in the Catahoula Ranger District, Kisatchie National Forest from 9 September 2010 until 3 November 2010. Temperatures ranged from 1.7 to 36 °C with an average temperature of 22.2 °C and average precipitation of 1.1 ± 3.9 mm/day (mean ± SD). The trees within the stands were planted in 1958. In Georgia, the experiment was conducted in a naturally regenerated stand within the Oconee National Forest from 15 September 2010 until 10 November 2010. Temperatures ranged from −1 to 35 °C with an average temperature of 17.8 °C and average precipitation of 2.1 ± 6.5 mm/day. Bubble cap lures of racemic ipsdienol, (+)-ipsdienol, racemic ipsenol, and lanierone (chemical purities, >98%) were purchased from Contech Enterprises Inc. (Victoria, BC, Canada). The enantiomeric ratio of (+)-ipsdienol was 97:3 (+):(−). The release rates of the ipsenol, ipsdienol, and lanierone bubble cap lures were approximately 0.2, 0.2, and 0.02 mg/day, respectively, at 22–24 °C (determined by Contech Enterprises Inc.).

During the experiment conducted in Louisiana, some traps fell to the ground. The entire 2-wk interval during which a trap was on the ground was discarded. Consequently, for that experiment, trap capture was calculated as the total number of beetles captured divided by the number of trapping days (i.e., the number of days the trap was not found on the ground). The response variable, trap capture, was log-transformed to correct for overdispersion and predicted using a linear mixed-effects model with the lme function from the nlmer package (Bates et al. 2015) in R (R Core Team 2022). Block number was set as a random effect, and bait, co-bait, and their interaction were set as fixed effects. Model selection was done through a stepwise backward selection process using *P*-values until a minimum adequate model was identified (Zuur et al. 2009, Chapter 5).

In Georgia, there were no fallen traps; therefore, trap captures were not corrected according to trapping days. Consequently, trap capture was a count variable and was predicted using a generalized linear mixed-effects model with a Poisson distribution and a log-link function and corrected for overdispersion using a negative binomial distribution. The glmmTMB function in the glmmTMB package (Brooks et al. 2017) in R (R Core Team 2022) was used to perform the analysis. Five models using block number as a random effect and using the following fixed effects were compared: (i) null model (no fixed effect), (ii) bait, (iii) co-bait, (iv) bait and co-bait, and (v) bait, co-bait, and their interaction (Table 2). The Akaike weight (*w*) of each model was calculated and used to identify the models that fell within a 95% confidence interval (Zuur et al. 2009, Chapter 21).

Results

In Louisiana, mean corrected captures ranged from 6.3 ± 11.2 ((+)-ipsdienol and ipsenol) to 501.4 ± 357.0 (racemic ipsdienol,

ipsenol, and lanierone) for *I. avulsus* beetles (Fig. 1). In Georgia, mean total captures ranged from 60.9 ± 29.7 ((+)-ipsdienol and ipsenol) to 7,893.8 ± 3,029.7 (racemic ipsdienol, ipsenol, and lanierone) for beetles (Fig. 2).

Model selection showed that, in Louisiana, bait, co-bait, and their interaction had a significant effect on trap captures (*P*-values < 0.05; Table 1). When predicting trap captures in Georgia, we found that model v had the lowest Akaike's information criteria (AIC) compared with the other models (AIC_v = 755.3; Table 2). Furthermore, model v had an Akaike weight greater than 0.95 (w_v = 0.999), indicating that model v was the only model within the 95% confidence interval. Model v includes bait, co-bait, and their interaction as fixed effects, indicating that, in Georgia, bait, co-bait, and their interaction had a significant effect on trap captures.

Regardless of co-bait, the traps baited with racemic ipsdienol captured more beetles than traps baited with (+)-ipsdienol in both

Louisiana and Georgia (Figs. 1 and 2). Regardless of bait, traps co-baited with both ipsenol and lanierone captured more beetles than traps co-baited with ipsenol alone or lanierone alone in both Louisiana and Georgia (Figs. 1 and 2).

In Figs. 1 and 2, we used trap captures by traps baited with both ipsenol and lanierone as a baseline to quantify the decrease in trap captures when either lanierone or ipsenol were omitted. In Louisiana, in traps baited with racemic ipsdienol, trap captures decreased by 91% in traps co-baited with lanierone alone compared with traps co-baited with both ipsenol and lanierone (Fig. 1). Trap captures decreased by 79% in traps co-baited with ipsenol alone compared with traps co-baited with both ipsenol and lanierone. In traps baited with (+)-ipsdienol, trap captures decreased by 77% in traps co-baited with lanierone alone compared with traps co-baited with both ipsenol and lanierone (Fig. 1). Trap captures decreased by 93% in traps co-baited with ipsenol alone compared with traps co-baited with
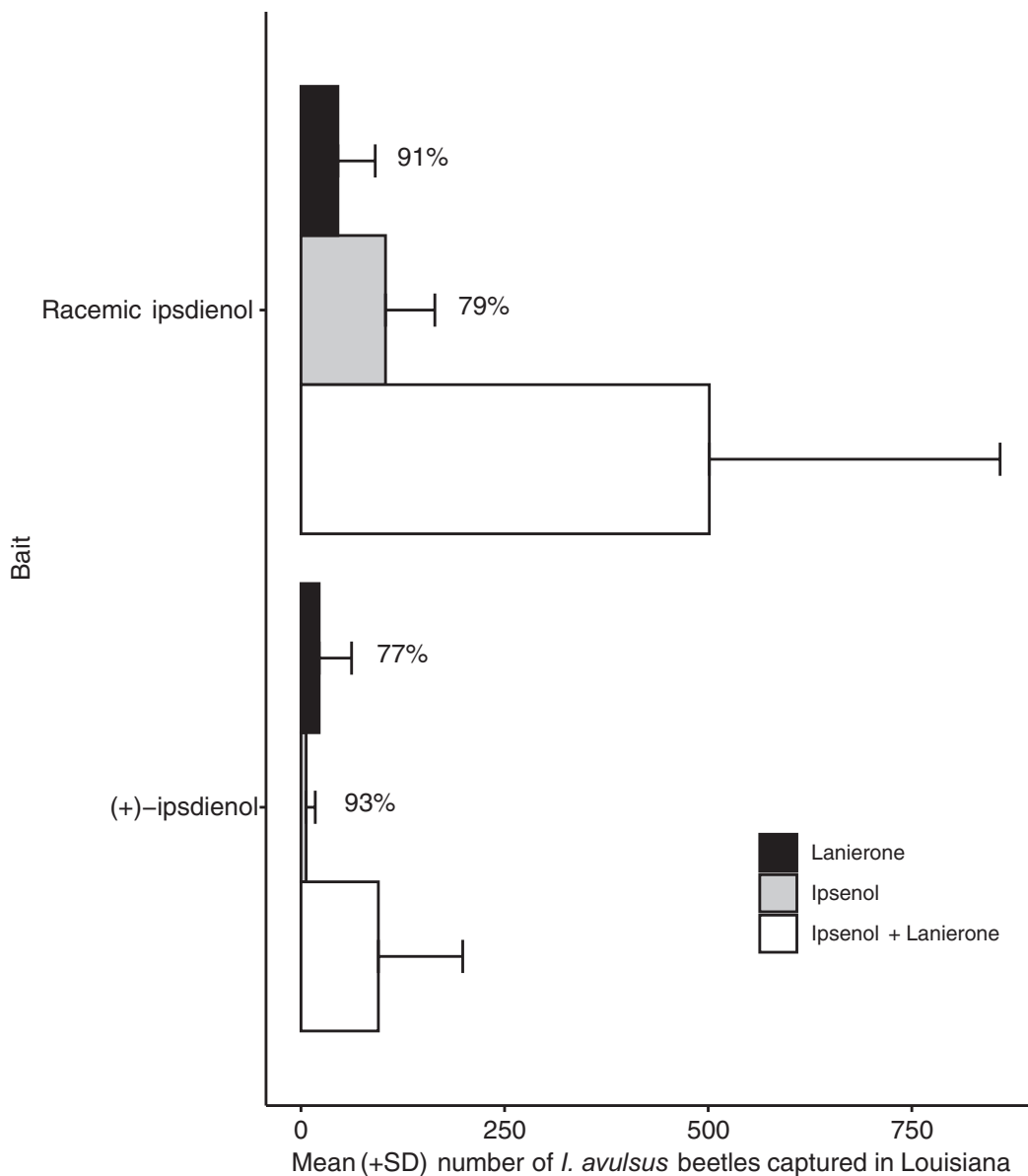

Fig. 1. Mean number of *Ips avulsus* individuals captured per trapping treatment in Louisiana. The percentages indicate the decrease in trap captures when compared with traps co-baited with both ipsenol and lanierone. Only traps baited with the same enantiomeric ratio of ipsdienol are compared.
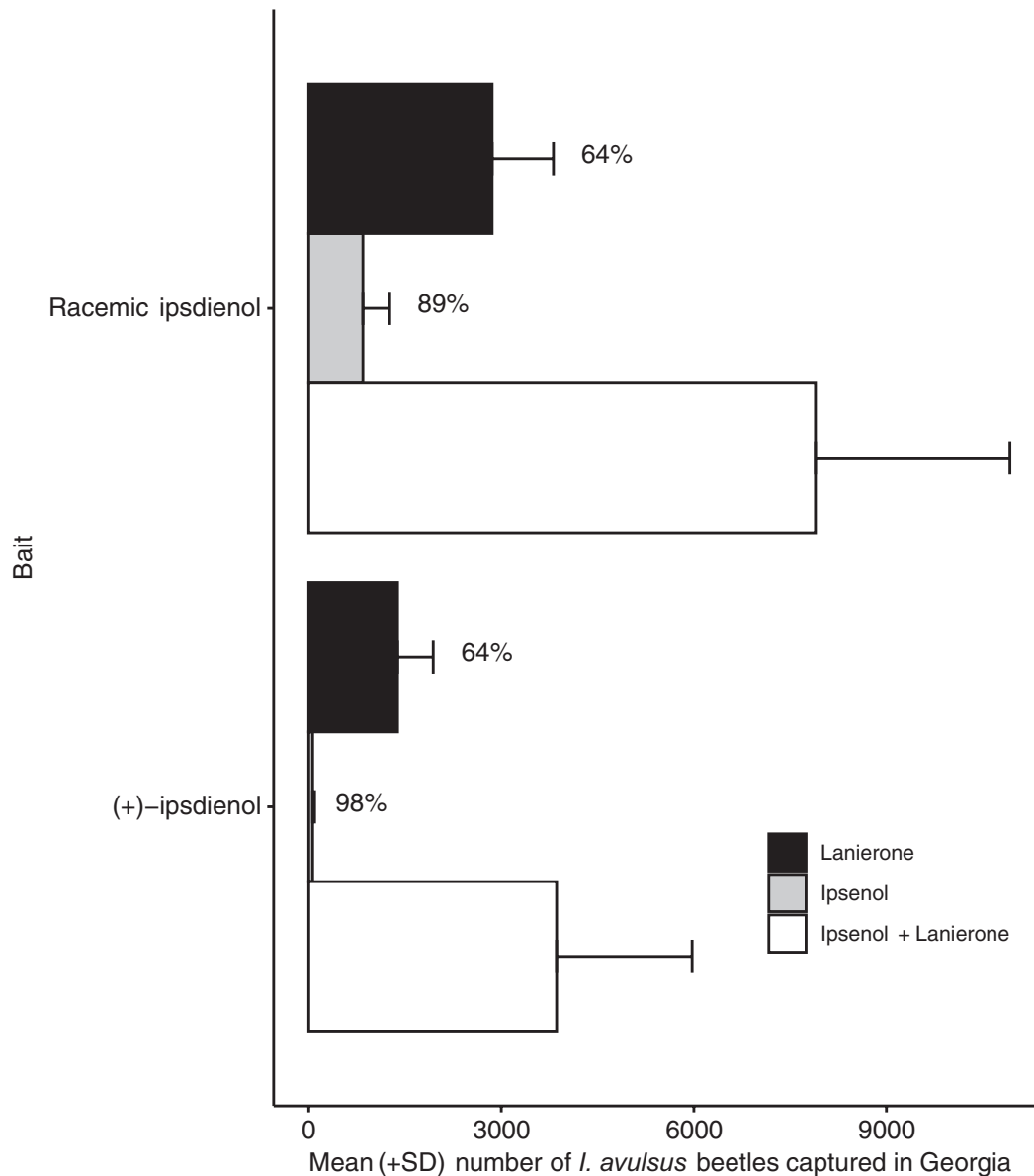
Fig. 2. Mean number of *Ips avulsus* individuals captured per trapping treatment in Georgia. The percentages indicate the decrease in trap captures when compared with traps co-baited with both ipsenol and lanierone. Only traps baited with the same enantiomeric ratio of ipsdienol are compared.

Table 1. Minimum adequate model predicting the number of captures by each trapping treatment in Louisiana

Variable	Estimate	Standard error	*P*-value
Intercept	0.676	0.437	0.131
Bait racemic ipsdienol	3.828	0.594	<0.001
Co-baits ipsenol + lanierone	3.427	0.594	<0.001
Co-bait lanierone	1.1444	0.594	0.020
Bait racemic ipsdienol: co-baits ipsenol + lanierone	−2.031	0.840	0.021
Bait racemic ipsdienol: co-bait lanierone	−2.845	0.840	0.002

both ipsenol and lanierone in Louisiana. In Georgia, in traps baited with racemic ipsdienol, trap captures decreased by 64% and 89% in traps co-baited with lanierone alone and ipsenol alone, respectively, compared with traps co-baited with both ipsenol and lanierone (Fig. 2). In traps baited with (+)-ipsdienol, trap captures decreased by 64% and 98% in traps co-baited with lanierone alone and ipsenol alone,

respectively, compared with traps co-baited with both ipsenol and lanierone (Fig. 2).

Discussion

Previous studies have focused on the enantiospecific response of *I. avulsus* to ipsdienol (Smith et al. 1990, Strom et al. 2003, Miller and

Table 2. AICs and Akaike weights of the 5 generalized linear mixed-effects models compared for model selection when predicting trap captures in Georgia

Model	Bait	Co-bait	Bait × co-bait	AIC	*w*
i				861	<0.0001
ii	x			857.6	<0.0001
iii		x		820	<0.0001
iv	x	x		787.5	<0.0001
v	x	x	x	755.3	0.999

x, model terms used.

Table 3. Minimum adequate model (model v) predicting the number of captures by each trapping treatment in Georgia

Variable	Estimate	Standard error
Intercept	4.107	0.165
Bait racemic ipsdienol	2.607	0.222
Co-baits ipsenol + lanierone	4.126	0.222
Co-bait lanierone	3.110	0.220
Bait racemic ipsdienol: co-baits ipsenol + lanierone	–1.870	0.312
Bait racemic ipsdienol: co-bait lanierone	–1.868	0.311

Allison 2011, Queffelec et al. 2023). However, these studies have reported contradictory results. When co-baited with ipsenol (Vité et al. 1978) or *trans*-verbenol and *cis*-verbenol (Smith et al. 1990), (–)-ipsdienol was found to be more attractive to *I. avulsus* than racemic and (+)-ipsdienol in Texas. However, when co-baited with ipsenol and *cis*-verbenol, racemic ipsdienol was 100–1,000 times more attractive to *I. avulsus* (Smith et al. 1990). When co-baited with lanierone (Strom et al. 2003), ipsenol, or lanierone and α-pinene (Miller and Allison 2011), racemic ipsdienol was most attractive in Louisiana, Texas, Florida, and Georgia. Finally, when co-baited with ipsenol, lanierone, and α-pinene, (+)-ipsdienol was as attractive as racemic ipsdienol in Georgia (Miller and Allison 2011). While these variations could be attributed to population specificity (Lanier et al. 1972, 1980, Seybold et al. 1995, Miller et al. 1996, 1997, Song et al. 2011) and seasonal preferences (Teale and Lanier 1991), our study also demonstrates that co-baits interact differently with different enantiomeric ratios of ipsdienol, creating a context-dependent response by *I. avulsus* (Tables 1 and 3).

Overall, traps baited with racemic ipsdienol performed better than traps baited with (+)-ipsdienol (Figs. 1 and 2). This enantiospecific response has been widely hypothesized to allow for the avoidance of hybridization and interspecific competition between related species that also use ipsdienol for pheromone communication (Seybold 1993). In Louisiana and Georgia, *I. calligraphus* occurs in sympatry with *I. avulsus* and attacks the same hosts (Schoeller and Allison 2013). *Ips calligraphus* also uses ipsdienol for pheromone communication but likely uses a different enantiomeric ratio of this compound (Kohnle et al. 1994).

In both Louisiana and Georgia, when comparing the decrease in trap captures in traps baited with racemic ipsdienol and ipsenol (Louisiana: 79% decrease; Georgia: 89% decrease; Figs. 1 and 2) to the decrease in trap captures in traps baited with (+)-ipsdienol and ipsenol (Louisiana: 93% decrease; Georgia: 98% decrease; Figs. 1 and 2), we observed a greater decrease of trap captures in traps baited with (+)-ipsdienol compared with traps baited with racemic

ipsdienol. This indicates a context-dependent effect of lanierone. Lanierone is produced by *I. avulsus*, but not by *I. calligraphus* (Vité et al. 1972). Because of interindividual variation in the enantiomeric ratio produced within a species (Queffelec et al. 2023), the enantiomeric ratio of ipsdienol provides an ambiguous message about the identity of the signaler. The presence of lanierone clarifies this message for *I. avulsus* in case the signaler is producing a ratio uncommon to *I. avulsus*. Consequently, while traps baited with racemic ipsdienol and ipsenol contain the appropriate enantiomeric ratio for *I. avulsus* and would signal the potential presence of *I. avulsus*, traps baited with (+)-ipsdienol and ipsenol signal the absence of *I. avulsus* because they contain the wrong enantiomer and no lanierone. This would lead to a greater decrease in trap captures in traps baited with (+)-ipsdienol when omitting lanierone.

In Georgia, there was no difference in the decrease in trap captures between the traps baited with racemic ipsdienol and lanierone (64% decrease; Fig. 2) and traps baited with (+)-ipsdienol and lanierone (64% decrease; Fig. 2). However, in Louisiana, there was a greater decrease in trap captures in traps baited with racemic ipsdienol and lanierone (91% decrease; Fig. 1) compared with traps baited with (+)-ipsdienol and lanierone (77% decrease; Fig. 1). This indicates that, at least in Louisiana, there is a context-dependent effect of ipsenol. Furthermore, Miller and Allison (2011) recorded a similar phenomenon in Georgia where trap captures by traps baited with (+)-ipsdienol, lanierone, and α-pinene decreased more significantly when compared with traps baited with racemic ipsdienol, lanierone, and α-pinene than trap captures by traps baited with (+)-ipsdienol, ipsenol, lanierone, and α-pinene when compared with traps baited with racemic ipsdienol, ipsenol, lanierone, and α-pinene.

Ipsenol is not produced by *I. avulsus* (Birgersson et al. 2012) but is produced by *I. grandicollis* (Vité et al. 1972), a related species of bark beetle that occurs in sympatry with *I. avulsus* and that exploits the same hosts (Paine et al. 1981). Hence, the presence of ipsenol signals the presence of *I. grandicollis* to *I. avulsus*. Our observation that traps baited with racemic ipsdienol, ipsenol, and lanierone capture more beetles than traps baited with racemic ipsdienol and lanierone corroborates past observations (Allison et al. 2012) and would indicate that *I. avulsus* prefers a tree that contains both *I. avulsus* and *I. grandicollis* to a tree that only contains *I. avulsus*. It is possible that the presence of *I. grandicollis* provides interspecies facilitation through predator avoidance or by helping to overcome host defenses. Additionally, Paine et al. (1981) demonstrated that *I. grandicollis* has weak competitive ability compared with *I. avulsus*. They showed that *I. grandicollis* colonized a smaller surface of the host tree in the presence of *I. avulsus*, while *I. avulsus* was not affected by the presence of *I. grandicollis*. Birch et al. (1980) also suggested that due to the size difference between the 2 species, *I. avulsus* might be able to exploit parts of the phloem that stay unexploited by *I. grandicollis*. While the traps baited with (+)-ipsdienol, ipsenol, and lanierone could also signal the presence of *I. grandicollis*, the presence of (+)-ipsdienol could also signal the potential presence of *I. calligraphus* on the host. However, *I. calligraphus* has greater competitive ability compared with *I. avulsus* and *I. grandicollis* (Paine et al. 1981). Perhaps in the context of a potential tripartite interaction, the presence of *I. grandicollis* becomes less attractive to *I. avulsus*.

In this study, we showed that the response of *I. avulsus* to different enantiomeric ratios of ipsdienol depends on co-bait. We hypothesize that these co-baits signal the type of interspecific interactions that *I. avulsus* would encounter on a host. Some combinations of baits and co-baits might signal the absence of conspecifics or a related species, while others might signal beneficial or antagonistic interspecific interactions. Pheromone signals are fine-tuned communication

systems. This work suggests that both intraspecific interactions (Queffelec et al. 2023) and interspecific interactions generate selection acting on them. While we are confident that semiochemical context can influence response, additional tests are needed to investigate how consistent this phenomenon is in space and time.

Acknowledgments

Conflict of Interest

The authors of this manuscript have no relevant financial or non-financial interests to disclose.

Author Contributions

Joséphine Queffelec (Data curation [Supporting], Formal analysis [Lead], Methodology [Supporting], Validation [Equal], Visualization [Lead], Writing – original draft [Equal], Writing – review & editing [Equal]), Justin M. Gaudon (Formal analysis [Supporting], Methodology [Supporting], Validation [Equal], Writing – review & editing [Equal]), Daniel Miller (Conceptualization [Equal], Data curation [Equal], Investigation [Equal], Methodology [Equal], Resources [Equal], Writing – review & editing [Equal]), Jessica L. McKenney (Data curation [Equal], Investigation [Equal], Methodology [Equal], Writing – review & editing [Equal]), and Jeremy D. Allison (Conceptualization [Lead], Data curation [Equal], Funding acquisition [Lead], Investigation [Lead], Methodology [Lead], Project administration [Lead], Resources [Lead], Supervision [Lead], Validation [Equal], Writing – original draft [Equal], Writing – review & editing [Equal])

Data Availability

The data underlying the results of this study are openly available on the Open Government Canada portal at https://doi.org/10.23687/197171a9-9d38-42bf-8a98-891f35f6f539.

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