# Trap Catches of Bark Beetle Predators Unaffected by the *Ips* Pheromone Lanierone in Southeastern United States[1]

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J. Entomol. Sci. 60(2): 000–000 (Month 2024)
DOI: 10.18474/JES24-13

**Abstract** In 2003–2004, a trapping study with multiple-funnel traps was conducted in Florida, Georgia, North Carolina, and Louisiana to evaluate the effects of the bark beetle pheromones ipsenol, ipsdienol, and lanierone on catches of bark beetles and associated species. The results on bark and ambrosia beetles have been reported previously. Herein, we report on the responses of predators in the same study. Ipsenol and/or ipsdienol attracted several species of coleopteran predators: *Enoclerus nigripes* (Say) (Cleridae); *Temnoscheila virescens* (F.) (Trogossitidae); *Lasconotus* species (Zopheridae); *Corticeus* species (Tenebrionidae); and *Platysoma attenuatum* LeConte, *Platysoma cylindricum* (Paykull), and *Platysoma parallelum* (Say) (Histeridae). Lanierone was not attractive alone, nor did it enhance trap catches of any of these predator species. In Georgia, lanierone interrupted attraction of *E. nigripes* to traps baited with ipsenol. We highlight that the use of lanierone appears to be restricted to three *Ips* species in the subgenus *Ips* (*Bonips*). Further research on the general role of lanierone in the chemical ecology of bark beetles and predators should be conducted over a broad geographic range.

**Key Words** lanierone, ipsenol, ipsdienol, predators, bark beetles

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Predators commonly “eavesdrop” on the communication systems used by insects (Peake 2005, Raffa 2001, Zuk and Kolluru 1998). Numerous species of bark beetles (Coleoptera: Curculionidae: Scolytinae) use pheromones to locate mating partners and hosts for larval development (Birch 1984; Borden 1982; Byers 1989, 2007; El-Sayed 2023). Therefore, it is not surprising that predators of bark beetles are attracted by pheromones used by bark beetles (Allison et al. 2013, Erbilgin and Raffa 2001, Grégoire et al. 1992, Kenis et al. 2007, Raffa 2001, Wood 1982). In Europe, the pheromones produced by *Ips typographus* L. (Coleoptera: Curculionidae) attract predators such as *Thanasimus formicarius* (L.) (Coleoptera: Cleridae) (Bakke and Kvamme 1978, 1981; Hansen 1983; Kenis et al. 2007).

In eastern North America, the pheromone frontalin used by *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae) is strongly attractive to the predator *Thanasimus dubius* (F.) (Coleoptera: Cleridae) (Billings and Cameron 1984, Costa and Reeve 2011, Dixon and Payne 1980, Payne et al. 1984, Sullivan and Clarke

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[1] Received 27 January 2024; accepted for publication 9 March 2024.

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2021, Vité and Williamson 1970). Other common bark beetle pheromones such as ipsenol and ipsdienol are also attractive to *Th. dubius*, especially when combined with host volatiles (Billings and Cameron 1984, Costa and Reeve 2011, Herms et al. 1991, Miller and Asaro 2023, Mizell et al. 1984). In general, responding to bark beetle pheromones likely help predators to find adult and larval prey for adult predators and egg and larval prey for larval predators (Dahlsten 1982, Kenis et al. 2007, Wegensteiner et al. 2015).

In the southeastern United States, there are three common species of bark beetles in the genus *Ips* (Coleoptera: Curculionidae) that generally breed in weakened, dying, or downed pine trees: *Ips avulsus* (Eichhoff), *Ips calligraphus* (Germar), and *Ips grandicollis* (Eichhoff) (Coleoptera: Curculionidae) (Atkinson 2023, Birgersson et al. 2012). *Ips grandicollis* uses ipsenol as an aggregation pheromone, whereas *I. calligraphus* uses ipsdienol and *cis*-verbenol (Allison et al. 2012; Birgersson et al. 2012; Hughes 1974; Miller 2023; Miller et al. 2005a; Renwick and Vité 1972; Vité and Renwick 1971; Vité et al. 1972, 1976). Ipsdienol and lanierone are the pheromones for *I. avulsus*; *I. avulsus* is also attracted to ipsenol as a kairomone (Birgersson et al. 1995, 2012; Allison et al. 2012; Hedden et al. 1976; Hughes 1974; Miller 2023; Miller et al. 2003, 2005a; Vité et al. 1972).

Attraction of bark beetle predators to traps baited with ipsenol and ipsdienol has been documented for various species, especially clerids (Allison et al. 2013; Bakke and Kvamme 1978, 1981; Billings and Cameron 1984; Costa and Reeve 2011; Poland and Borden 1997; Raffa 2001). In the southeastern United States, the same is true for predators in other families of Coleoptera, such as Histeridae, Trogossitidae, and Zopheridae (Allison et al. 2013). However, responses by predators to lanierone have not been documented. Previously, we published results on the attraction of bark and woodboring beetles to traps baited with lanierone, ipsenol, and ipsdienol in the southeastern United States (Miller and Asaro 2005, Miller et al. 2005a). This article focuses on trap catches of bark beetle predators captured in the same study.

## Materials and Methods

In 2003–2004, we conducted four trapping experiments in the southeastern United States to determine the responses of bark beetles, and associated species of predators, to the bark beetle pheromones ipsenol, ipsdienol, and lanierone. The experimental protocols and site conditions have been described previously (Miller and Asaro 2005, Miller et al. 2005a). The same trapping study was conducted at each of four locations (Table 1) by using standard 8-unit multiple-funnel traps (Phero Tech Inc., Delta, British Columbia, Canada). A randomized block design was used at each location with four replicate blocks in North Carolina (32 traps) and six replicate blocks at each of the remaining three locations (48 traps at each location). In each block of eight traps, traps were separated by 10–15 m and blocks were separated by 15–500 m. Collection cups contained approximately 150 ml of propylene glycol and water solution (Peak RV & Marine Antifreeze, Old World Industries Inc., Northbrook, IL) to kill and preserve beetles (Miller and Duerr 2008).

Bubble-cap lures of the three pheromones (chemical purities >98%) were obtained from Phero Tech Inc. Release rates of racemic ipsenol, racemic

**Table 1. Location, predominant pine species, and trapping dates for four experiments on flight responses of predators to multiple-funnel traps baited with ipsenol, ipsdienol, and lanierone in the southeastern United States.**

| Experiment | Location | Coordinates | Predominant Pine Species | Trapping Dates |
|---|---|---|---|---|
| 1 | Apalachicola National Forest, FL | 30.400°N, 84.485°W | *Pinus palustris* Miller and *Pinus elliottii* Engelmann | 30 March–16 June 2004 |
| 2 | Oconee National Forest, GA | 33.339°N, 83.475°W | *Pinus taeda* L. | 11 April–8 July 2003 |
| 3 | Kisatchie National Forest, LA | 31.904°N, 92.803°W | *P. palustris* and *P. taeda* | 28 April–22 June 2004 |
| 4 | Coweeta Hydrological Laboratory, NC | 35.069°N, 83.436°W | *Pinus strobus* L. | 12 May–30 July 2003 |

ipsdienol, and lanierone from the devices were approximately 0.2, 0.2, and 0.02 mg/d, respectively, at 22–24°C (determined by manufacturer). The following eight lure treatments were applied randomly to one trap in each block of eight traps: (1) blank control, (2) ipsenol, (3) ipsdienol, (4) lanierone, (5) ipsenol + lanierone, (6) ipsdienol + lanierone, (7) ipsenol + ipsdienol, and (8) ipsenol + ipsdienol + lanierone. Voucher specimens were deposited in the University of Georgia Collection of Arthropods (Athens).

Trap catch data were analyzed with the SYSTAT 13.1 and SigmaStat 3.01 statistical packages (SYSTAT Software Inc., Point Richmond, CA) for species caught in sufficient numbers ($n \geq 60$). Treatments with zero catches at a location were omitted from analyses (Reeve and Strom 2004). Data were transformed by $\ln(y + 1)$ as needed to ensure normality and homoskedasticity (Pepper et al. 1997), verified by the Shapiro–Wilk and equal variance tests, respectively. Mixed-model analysis of variance (ANOVA, three-way) was used to analyze data for species captured in all treatments at a location, specifically *Enoclerus nigripes* (Say) (Cleridae) in Georgia, *Temnoscheila virescens* (F.) (Trogossitidae) in Florida and Louisiana, and *Lasconotus* species (Zopheridae) in Florida. Data for all species caught in sufficient numbers were subjected to one-way mixed-model ANOVA followed by the Holm–Sidak multiple comparison test (Glantz 2005) for species with a significant treatment effect.

## Results

We captured a total of 7,353 bark beetle predators across 9 species and 6 families of Coleoptera (Table 2). Geographic variation in occurrence was noted among most species captured in our study. *Enoclerus nigripes* was caught in Georgia and North Carolina, but not in Louisiana or Florida; *Th. dubius* was only caught in Louisiana and North Carolina. *Platysoma attenuatum* LeConte, *Platysoma cylindricum* (Paykull), and *Platysoma parallelum* (Say) (Histeridae) were caught in three of four states, but differed in the states that they were absent in our collections. *Catogenus rufus* (F.) (Passandridae) was only caught in Georgia and Louisiana, whereas *Te. virescens* was caught in Florida, Georgia, and Louisiana, but not in North Carolina. By contrast, *Lasconotus* species and *Corticeus* species (Tenebrionidae) were caught in all four states.

In Georgia, trap catches of *E. nigripes* were affected by ipsdienol and ipsenol, with significant interactions between both compounds and lanierone (Table 3). Catches in traps baited with ipsenol or ipsenol + ipsdienol (with or without lanierone) were greater than those in traps baited with ipsdienol or ipsenol + lanierone (Fig. 1A). Catches of *E. nigripes* in blank traps or traps baited with lanierone were lower than those in traps baited with the remaining six treatments. Blank traps in North Carolina did not capture any *E. nigripes* (Fig. 1B). There was a significant treatment effect among the remaining seven treatments ($F_{6,18} = 14.54$; $P < 0.001$). As in Georgia, catches of *E. nigripes* in traps baited with ipsenol + ipsdienol (with or without lanierone) in North Carolina were greater than those in traps baited with ipsenol + lanierone (Fig. 1B). The lowest catches were in traps baited with lanierone. There were insufficient numbers of *Th. dubius* caught for statistical analyses (Table 2).

**Table 2. Trap catches of predators (Coleoptera) in four trapping experiments conducted in Florida (FL), Georgia (GA), Louisiana (LA), and North Carolina (NC) in 2003–2004.**

| Family and species | FL | GA | LA | NC | Total |
|---|---|---|---|---|---|
| Cleridae | | | | | |
| *Enoclerus nigripes* | —[a] | 481 | — | 133 | 614 |
| *Thanasimus dubius* | — | — | 39 | 36 | 75 |
| Histeridae | | | | | |
| *Platysoma attenuatum* | 54 | — | 313 | 80 | 447 |
| *Platysoma cylindricum* | — | 905 | 59 | 1,244 | 2,208 |
| *Platysoma parallelum* | 193 | 168 | — | 58 | 419 |
| Passandridae | | | | | |
| *Catogenus rufus* | — | 65 | 10 | — | 75 |
| Tenebrionidae | | | | | |
| *Corticeus* spp. | 3 | 221 | 14 | 30 | 268 |
| Trogossitidae | | | | | |
| *Temnoscheila virescens* | 794 | 684 | 164 | — | 1,642 |
| Zopheridae | | | | | |
| *Lasconotus* spp. | 261 | 1,231 | 75 | 38 | 1,605 |
| Total | 1,305 | 3,755 | 674 | 1,619 | 7,353 |

[a] Dashes indicate that none were captured.

**Table 3. ANOVA *P* values for effects of lanierone (L), ipsdienol (D), and ipsenol (S) on trap catches of predators where species captured in all treatments.**

| Factor | *Enoclerus nigripes* Georgia | *Temnoscheila virescens* Florida | *Temnoscheila virescens* Louisiana | *Lasconotus* spp. Florida |
|---|---|---|---|---|
| L | 0.511 | 0.860 | 0.610 | 0.530 |
| D | $<0.001$ | $<0.001$ | $<0.001$ | 0.035 |
| S | $<0.001$ | $<0.001$ | $<0.001$ | $<0.001$ |
| L × D | 0.014 | 0.646 | 0.020 | 0.210 |
| L × S | 0.013 | 0.406 | 0.036 | 0.548 |
| D × S | 0.064 | $<0.001$ | 0.050 | $<0.001$ |
| L × D × S | 0.775 | 0.784 | 0.446 | 0.972 |

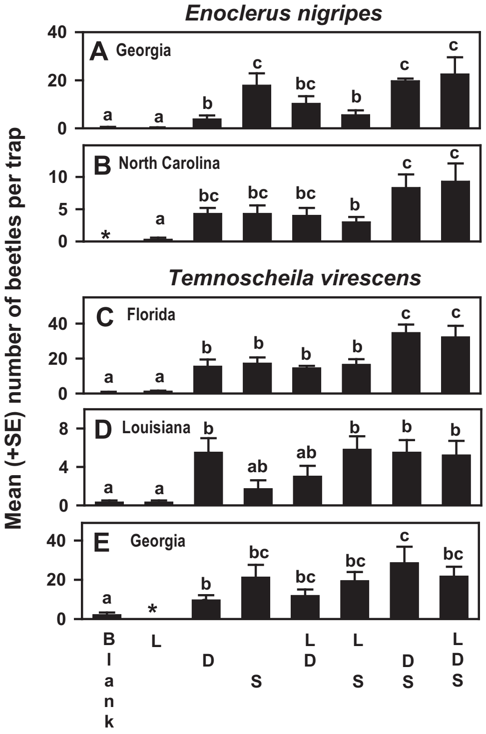

**Fig. 1. Mean (±SE) catches of *Enoclerus nigripes* (Cleridae) and *Temnoscheila virescens* (Trogossitidae) in traps baited with lanierone (L), ipsdienol (D), and ipsenol (S) in the southeastern United States. Means at each location followed by a different letter are significantly different at $P < 0.05$ (Holm–Sidak test). Treatments with an asterisk (*) had zero catches.**

Catches of *Te. virescens* in Florida and Louisiana were affected by ipsenol, ipsdienol, and the interaction between the two compounds (Table 2). There were significant interactions between lanierone and both ipsenol and ipsdienol in Louisiana, but not in Florida. In Florida, catches of *Te. virescens* were greatest in traps baited with ipsenol + ipsdienol (with or without lanierone) and lowest in blank traps and traps baited with lanierone alone (Fig. 1C). In Louisiana, catches were greater in traps baited with ipsdienol, lanierone + ipsenol, and ipsenol + ipsdienol (with or without lanierone) than in blank traps or those baited with lanierone alone (Fig. 1D). Traps baited solely with lanierone did not catch any *Te. virescens* in Georgia (Fig. 1E). There was a significant treatment effect among the remaining seven treatments ($F_{6,30} = 17.86$; $P < 0.001$). Catches of *Te. virescens* in Georgia were greater in traps baited with ipsenol + ipsdienol than in those baited with ipsdienol alone (Fig. 1E). The lowest catches were in blank traps.

In Florida, catches of *Lasconotus* species were affected by ipsenol, ipsdienol, and the interaction between the two compounds (Table 2). Catches in traps baited

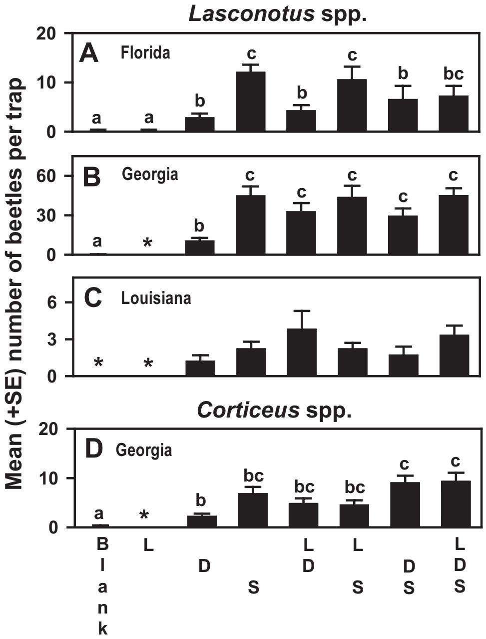

**Fig. 2. Mean (±SE) catches of *Lasconotus* spp. (Zopheridae) and *Corticeus* spp. (Tenebrionidae) in traps baited with lanierone (L), ipsdienol (D), and ipsenol (S) in the southeastern United States. Means at each location followed by a different letter are significantly different at $P <$ 0.05 (Holm–Sidak test). Treatments with an asterisk (*) had zero catches.**

with ipsenol (with or without lanierone) were greater than those in traps baited with ipsenol + ipsdienol and ipsdienol (with or without lanierone) (Fig. 2A). The lowest catches were in blank traps and those baited solely with lanierone (Fig. 2A). In Georgia, traps baited with lanierone alone did not capture any *Lasconotus* species (Fig. 2B). There was a significant treatment effect among the remaining seven treatments ($F_{6,30} = 35.72$; $P < 0.001$). In Georgia, traps baited solely with ipsdienol caught more *Lasconotus* species than blank traps, but less than traps baited with the remaining five lure treatments (Fig. 2B). In Louisiana, blank traps and traps baited with lanierone alone did not capture any *Lasconotus* species (Fig. 2C). There was a significant treatment effect among the remaining six treatments ($F_{5,25} = 2.68$; $P = 0.045$). However, the Holm–Sidak test was unable to separate mean catches of *Lasconotus* species by treatments in Louisiana (Fig. 2C).

*Corticeus* species were not caught in traps baited solely with lanierone in Georgia (Fig. 2D). There was a significant treatment effect among the remaining seven treatments ($F_{6,30} = 7.64$; $P < 0.001$). Catches in traps baited solely with ipsdienol caught less than traps baited with ipsenol + ipsdienol (with or without lanierone) (Fig. 2D). Fewer *Corticeus* species were caught in blank traps than in traps baited with the remaining six treatments.

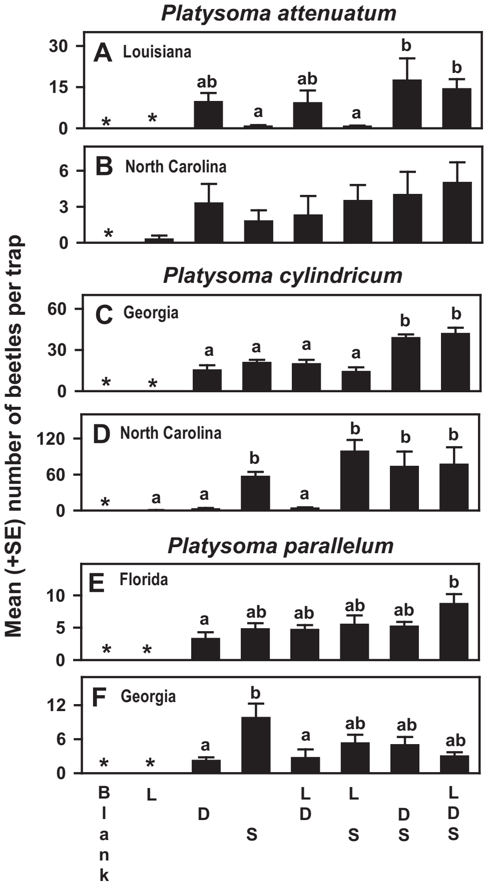

**Fig. 3. Mean (±SE) catches of *Platysoma attenuatum*, *Platysoma cylindricum*, and *Platysoma parallelum* (Histeridae) in traps baited with lanierone (L), ipsdienol (D), and ipsenol (S) in the southeastern United States. Means at each location followed by a different letter are significantly different at $P < 0.05$ (Holm–Sidak test). Treatments with an asterisk (*) had zero catches.**

Sufficient catches of three species of *Platysoma* were caught for analyses at two locations per species (Table 2). None of these species were caught in blank traps at any location (Fig. 3). In addition, traps baited solely with lanierone in Louisiana did not catch any *P. attenuatum* (Fig. 3A). In Louisiana, catches of *P. attenuatum* in traps baited with ipsenol + ipsdienol (with or without lanierone) were significantly greater than those in traps baited with ipsenol or ipsenol + lanierone (Fig. 3A). There was no treatment effect on catches of *P. attenuatum* among the seven nonzero treatments in North Carolina ($F_{6,18} = 0.191$; $P = 0.191$) (Fig. 3B).

Traps baited with lanierone alone did not capture any *P. cylindricum* in Georgia (Fig. 3C). There was a significant treatment effect among the remaining 6 treatments ($F_{5,25} = 15.42$; $P < 0.001$). In Georgia, traps baited with ipsenol + ipsdienol (with or without lanierone) caught more *P. cylindricum* than those baited ipsenol or ipsdienol (with or without lanierone) (Fig. 3C). In North Carolina, there was a significant treatment effect among the seven treatments excluding blank traps ($F_{6,18} = 76.93$; $P < 0.001$). Catches of *P. cylindricum* were greatest in all traps baited with ipsenol (with or without ipsdienol and/or lanierone) (Fig. 3D).

In both Florida and Georgia, traps baited with lanierone alone did not capture any *P. parallelum* (Fig. 3E, F). There were significant treatments among the remaining six treatments on trap catches of *P. parallelum* in Florida ($F_{5,25} = 3.48$; $P = 0.006$) and Georgia ($F_{5,25} = 4.46$; $P = 0.005$). In Florida, traps baited with all three compounds captured more beetles than those baited solely with ipsdienol. By contrast, catches of *P. parallelum* in Georgia were greater in traps baited solely with ipsenol than in traps baited with ipsdienol (with or without lanierone) (Fig. 3F).

## Discussion

In general, we found that the flight responses of predators to traps baited with ipsenol and ipsdienol were consistent with those found in other studies. As in our study, ipsenol and/or ipsdienol were shown to be attractive to *E. nigripes* in Georgia and *Th. virescens*, *Platysoma* species, and *Lasconotus* species in Georgia and Louisiana (Allison et al. 2013, Miller 2023, Miller and Asaro 2023). At some locations, catches of *Corticeus* species in traps baited with ethanol + α-pinene were enhanced by the addition of ipsenol + ipsdienol (Miller and Asaro 2023), consistent with results in our study (Fig. 2D).

The only effect of lanierone on predators in our study was the interruption of *E. nigripes* to traps baited with ipsenol in Georgia (Fig. 1A). Otherwise, we found no effects from the addition of lanierone to trap catches of any other species of predator. Specifically, lanierone did not enhance attraction of *E. nigripes*, *Te. virescens*, *Lasconotus* species, *Corticeus* species, *P. attenuatum*, *P. cylindricum*, and *P. parallelum* (Figs. 1–3). Similarly, in a recent trapping experiment in Georgia, Miller (2022) found that lanierone did not affect catches of *Th. dubius*, *Cortices* species, and *Te. virescens* in traps baited with ethanol, α-pinene, ipsenol, and ipsdienol. However, in the same experiment, catches of *Lasconotus* species were enhanced by the addition of lanierone, whereas catches of *Platysoma* species were enhanced by the addition of *cis*-verbenol + lanierone (Miller 2022). In addition to ipsenol and ipsdienol, Allison et al. (2013) found that *cis*-verbenol (a pheromone used by *I. calligraphus*) enhanced attraction of *P. parallelum*, but interrupted attraction of *P. attenuatum* to traps baited with ipsenol + ipsdienol; there was no effect on catches of *P. cylindricum*.

As with predators, lanierone appears to have little effect on other species associated with bark beetles. In the southeastern United States, woodborers such as *Acanthocinus obsoletus* (Olivier) and *Monochamus titillator* (F.) (Coleoptera: Cerambycidae) are strongly attracted to ipsenol and ipsdienol (Billings and Cameron 1984; Miller and Asaro 2005; Miller et al. 2013, 2015). However, lanierone did not enhance catches of these two species in traps baited with ipsenol and ipsdienol in Georgia (Miller 2022).

Lanierone was first reported as a pheromone for *Ips pini* (Say) (Coleoptera: Curculionidae) in New York (Teale et al. 1991). *Ips pini* is a transcontinental North American species, ranging as far south in the east as the Appalachian Mountains (Atkinson 2023). The enhancement effect of lanierone on trap catches of *I. pini* in traps baited with its principal pheromone ipsdienol varies widely across its range (Miller et al. 1997, Seybold et al. 1992). In addition to *I. avulsus* and *I. pini*, lanierone is attractive to *Ips integer* (Eichhoff) (Coleoptera: Curculionidae), with attraction interrupted by ipsdienol (Miller et al. 1997). The major known compounds produced by *I. integer* are *cis*- and *trans*-verbenol, with ipsdienol as a minor component (Vité et al. 1972). Production of lanierone by *I. integer* has not been determined nor has lanierone been noted as a pheromone for any other species of bark beetles (El-Sayed 2023).

Lanierone enhanced responses of *Enoclerus lecontei* (Wolcott) (Coleoptera: Cleridae) to ipsdienol-baited traps in British Columbia, Canada, and California and Montana (Dahlsten et al. 2004; Miller et al. 1997, 2005b; Seybold et al. 1992). In British Columbia, both *I. pini* and *E. lecontei* exhibited positive dose responses to lanierone in ipsdienol-baited traps (Miller et al. 2005b). In addition to *Th. dubius* in Wisconsin, lanierone had no effect on the predators *Enoclerus sphegeus* (F.) in British Columbia and California, *Thanasimus undatulus* (Say) in British Columbia, and *Enoclerus nigrifrons* (Say) (Coleoptera: Cleridae) in Wisconsin, as well as *Temnoscheila chlorodia* (Mannerheim) (Coleoptera: Trogossitidae) in California (Miller et al. 1997, 2005b; Seybold et al. 1992).

It is unclear why three common pheromones (ipsenol, ipsdienol, and *cis*-verbenol) used by Ipini (Coleoptera: Scolytinae) bark beetles in the southeastern United States are broadly attractive to woodborers and bark beetle predators, whereas lanierone is not attractive to these same species. Lanierone has not been noted for any other species of Ipini (El-Sayed 2023), even though it was first detected $>$30 yr ago in *I. pini* (Teale et al. 1991). It is possible that lanierone may be a recently evolved pheromone among a few closely related species.

The three species attracted by lanierone (*I. avulsus*, *I. integer*, and *I. pini*) are all in the same subgenus, *Ips* (*Bonips*) (Cognato 2015, Cognato and Sperling 2000, Cognato and Vogler 2001). The chemical ecologies of the two other species in this subgenus, *Ips bonanseai* (Hopkins) and *Ips plastographus* (LeConte) (Coleoptera: Curculionidae), have not been studied, particularly with respect to lanierone. Pheromones can be useful in determining or verifying phylogenies (Cognato et al. 1997, dos Santos et al. 2023).

If recently evolved among the three *Ips* (*Bonips*) species, it is possible that there has been limited opportunities and time for widespread responses to evolve among predators and woodborers. Only one predator, *E. lecontei*, sympatric with both *I. pini* and *I. integer* in western North America, is known to be attracted to lanierone (Miller et al. 1997, 2005b; Seybold et al. 1992). Clearly, further studies across a broad geographical range are needed to better evaluate the role of lanierone in the chemical ecology of bark beetles and associated species of predators and woodborers. For example, electroantennogram studies could determine whether various species of predators and woodborers can even detect lanierone.

## Acknowledgments

We thank Chris Crowe, Jim Meeker, and Alex Mangini (USDA Forest Service) for technical assistance and Richard Hoebeke (University of Georgia Collection of Arthropods) for verifications of species identities. The findings and conclusions in this publication are those of the authors and should not be construed to represent any official USDA or U.S. Government determination or policy. The use of trade or firm names in this publication is for reader information and does not imply endorsement by the USDA of any product or service. This research was supported by the USDA Forest Service. The USDA is an equal opportunity provider, employer, and lender.

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