

An undescribed relationship between the knobthorn tree (*Senegalia nigrescens*), ants, and a lac scale insect in South Africa

Yuki Haba  | Ryan Herbert | Luojun Yang

Department of Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey

Correspondence

Yuki Haba, Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544-2016.
 Email: yhaba@princeton.edu

Funding information

Princeton University

1 | INTRODUCTION

Ecological relationships between ants and trees of the tribe *Acacieae* have been well-documented, sometimes involving scale insects as a third member of the interaction (Beattie & Andrew, 1985; Young, Stubblefield, & Isbell, 1997). While scale insects can be harmful to plants (Becerra & Venable, 1989; Miller & Davidson, 2005), the association of ants with scale insects may provide the tree with a defence against herbivory (Campos & Camacho, 2014; Prior & Palmer, 2018). Specifically, ants forage for the honeydew that scale insects produce from tree sap, and, consequently, they may defend either the scale insect or the tree tissue from potential herbivores.

To our knowledge, aggressive defence by ants and co-occurrence with scale insects have never been reported in the knobthorn tree, *Senegalia nigrescens* (previously known as *Acacia nigrescens*; see Kyalangalilwa, Boatwright, Daru, Maurin, & Bank, 2013), which is a common savannah species that ranges from Tanzania to the southern parts of South Africa. *S. nigrescens* is commonly targeted by herbivores ranging from insects to elephants (Belsky, 1994; Fleming, Hofmeyr, & Nicolson, 2007; Moncrieff, Kruger, & Midgley, 2008).

Here, we report on the lac scale insect *Tachardina africana*, which we found tended by two different ant species on trees of *S. nigrescens* in Kruger National Park, South Africa. We examined the presence of scale insects and ants in trees with and without large herbivores. We also tested how ants on the trees reacted to a perceived threat in order to learn whether or not the ants may defend the scale insects.

All the authors contributed equally

2 | METHODS

We conducted this study within the Skukuza region of Kruger National Park, South Africa, during January 2018. Study sites included an herbivore enclosure treatment (24.99°S, 31.77°E) which has excluded herbivores larger than hares for >15 years (see O'Keefe & Alard, 2002 for more details), an adjacent exposed plot, and a fire-excluded plot 34 km away (25.10°S, 31.45°E) (see Biggs, Biggs, Dunne, Govender, & Potgieter, 2003 for details).

To investigate the potential role of herbivory, we searched for ants and scale insects in *S. nigrescens* trees among the herbivore enclosure versus the adjacent exposed plots. Plots were thoroughly surveyed for all adult *S. nigrescens* (3–20 m in height) present within a randomly chosen, approximately 5-acre area for each treatment. Ants and scale insects were carefully searched for on every *S. nigrescens* tree found (Appendix S1). Ants or scales were counted as present if at least one individual was found.

We then focused on one *S. nigrescens* in the fire-excluded plot for its ample availability of scale insects and ants. We collected specimens and morphologically identified them as *Tachardina africana* (Hall, 1935) through the South African Agricultural Research Council: Biosystematics Division. On the focal *S. nigrescens*, we thoroughly surveyed the number of *T. africana* and their locations on the primary, secondary and tertiary branches.

We identified the genus of ants tending to *T. africana* by morphology (Appendix S1). To test ants for defensive potential, we studied the behaviour of the most prevalent species, *Polyrhachis* sp. (Figure 1, left) on the focal *S. nigrescens* tree. First, we measured time budgets and transitions for *Polyrhachis* behaviour for five individuals for 5 min each based on an ethogram (Figure 2a). Afterwards, we quantified aggressiveness to investigate whether the ants defend scale insects and/or trees (Appendix S1).



FIGURE 1 Ants and *Tachardina africana* interact on *Senegalia nigrescens* trees. (left) Tending by *Polyrhachis* ants, (right) tending by *Crematogaster* ants on a densely clustered *T. africana* colony [Colour figure can be viewed at wileyonlinelibrary.com]

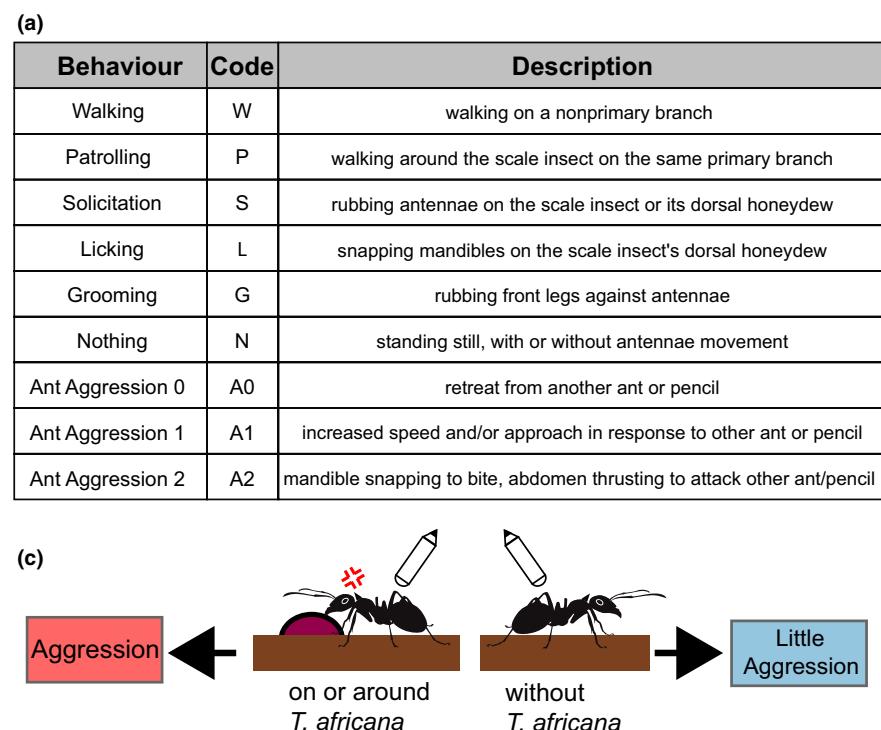


FIGURE 2 Behavioural observations of *Polyrhachis* ants on the *Senegalia nigrescens* tree. (a) Comprehensive Ethogram. Aggression levels were used for both the time budgets and the separate aggression tests. Unless "walking," all ants were tested on primary branches (see Figure 3a). (b) An illustration of the time budget and behavioural transitions of *Polyrhachis* ants near *Tachardina africana* individuals. The size of circles corresponds to the relative time spent on each behaviour, and the size of arrows is proportional to the frequency of the behavioural transitions. P: patrolling, S: solicitation, L: licking, Agg: aggressive behaviours, Others: all other than the aforementioned behaviours. (c) Diagram of *Polyrhachis* ants, which were aggressive almost exclusively if they were on or around *T. africana* [Colour figure can be viewed at wileyonlinelibrary.com]

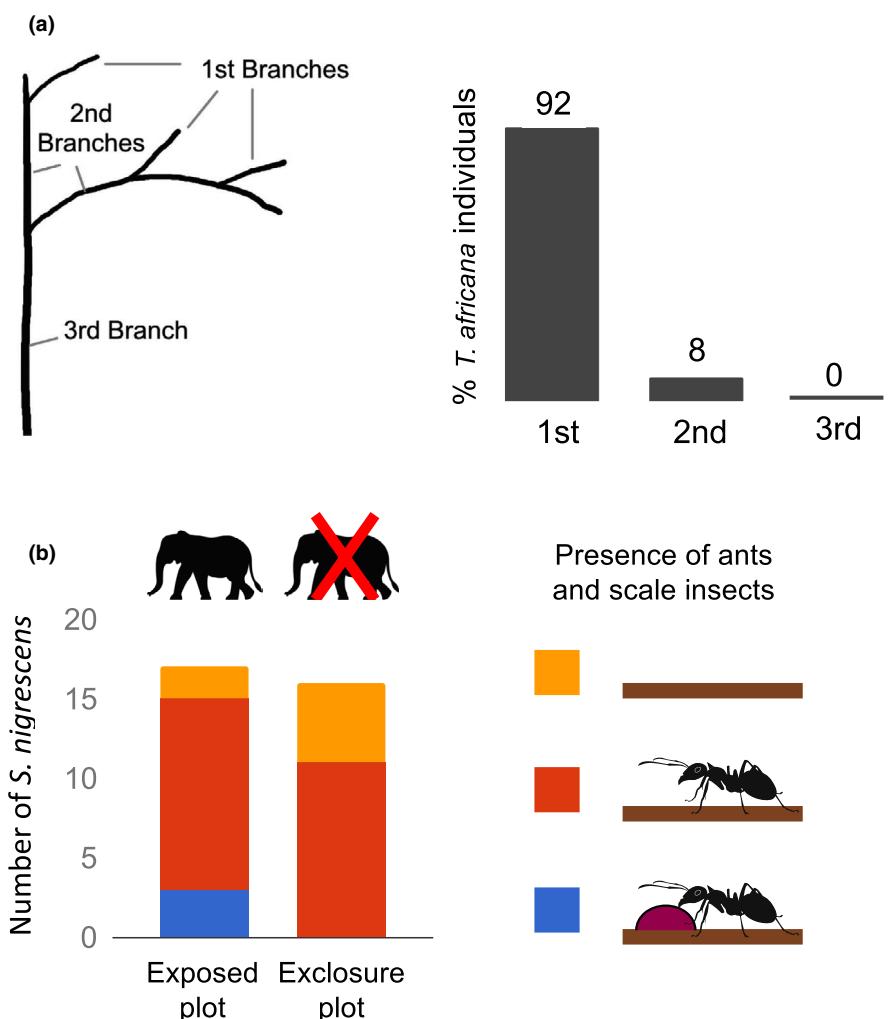
We did not conduct any statistical test due to small sample sizes. The main aim of the current study was to report an undescribed ant-scale-tree association of potential ecological importance and to spark interest for further research.

3 | RESULTS AND DISCUSSION

Our survey of *S. nigrescens* trees across the herbivore exclusion treatment and exposed plots revealed the presence of ants, most

of which were *Polyrhachis* sp., in both unprotected and herbivore-protected trees (Figure 3b). Interestingly, we only found *T. africana* in trees unprotected from herbivores and only in trees where ants were present (Figure 3b). Among the 16 herbivore-protected trees, 11 had ants, but none of the trees had *T. africana*. Fifteen out of the 17 herbivore-unprotected trees had ants, and 4 had *T. Africana*. Overall, *T. africana* was rare, but all four trees with *T. africana* also had ants. Since the scale insect was only found in trees unprotected from herbivores, this suggests there may be a complex relationship between the plant, the ants, the scale insect, and herbivores.

FIGURE 3 Observed patterns of *Tachardina africana* and ant distribution. (a) (left) An illustration of branch order definition used in this study. Primary (1st) branches are terminal, and order increases when same-order branches meet. When different-order branches meet, the higher order is maintained. (right) Distribution of *T. africana* based on branch order ($n = 50$). (b) Prevalence of ants and *T. africana* on *Senegalia nigrescens* surveyed in the exposed and herbivore exclusion plots. Different bar colours correspond to the presence of ants and scale insects on *S. nigrescens* surveyed: orange—no ants nor scale insects present; red—only ants present; blue—both ants and scales insects present [Colour figure can be viewed at wileyonlinelibrary.com]



To quantify the distribution of *T. africana* on a tree, we counted a total of 50 individuals of the *T. africana* scale insect on one focal tree of *S. nigrescens* in a thorough survey. The majority (92%) of scale insects were attached to the primary branches, with only 4 (8%) found on secondary branches (Figure 3a, right). *Tachardina africana* was entirely absent from the tertiary or higher order branches. This pattern may indicate that *S. nigrescens* is most vulnerable to *T. africana* on its distal branches, where sap could be more accessible due to softer and thinner bark and cortex.

The behaviour of *Polyrhachis* ants, when found near individuals of *T. africana*, was dominated by attention to scale insects. The ants spent most of their time either patrolling (39.3%), soliciting (38.5%) or licking *T. africana* (12.9%) (Figure 2b). Furthermore, we found that the level of ant aggression (Figure 2a) was closely associated with the presence of *T. africana*. Ants were most aggressive where *T. africana* was present (average aggression level = 2, $n = 6$), whereas they displayed little aggression where *T. africana* was absent (average aggression level = 0.1, $n = 21$) (Figure 2c). Curiously, aggression was also discovered in *Crematogaster* ants tending to *T. africana* on one *S. nigrescens* (Figure 1, right; Appendix S1). These protective behaviours might confer an indirect benefit to *S. nigrescens* against herbivory. However, its effectiveness on a whole-plant level might

be limited given the sparse distribution of *T. africana* and ants on any single tree.

Further research on the broadscale distribution of *T. africana*, as well as manipulative studies on its interactions with ants and *S. nigrescens*, will be necessary to fully understand the complex relationship between ants, *T. africana*, and *S. nigrescens* trees.

ACKNOWLEDGEMENTS

This work was conducted at the Skukuza Science Leadership Initiative Field Station in Skukuza, South Africa. We thank Karen Vickers and the Nsasni Trust for making the field and laboratory work possible. We thank Lars Hedin, Andy Dobson and Mingzhen Lu for help throughout our fieldwork. We are grateful to Ian Millar at the South African Agricultural Research Council: Biosystematics Division for his pictures and identifications of scale insects. We also thank the 2017 Princeton EEB graduate students for productive discussions.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Yuki Haba  <https://orcid.org/0000-0003-2767-5457>

REFERENCES

- Beattie, A. J., & Andrew, J. (1985). *The evolutionary ecology of ant-plant mutualisms*. Cambridge: Cambridge University Press.
- Becerra, J. X., & Venable, D. L. (1989). Extrafloral nectaries: A defense against ant-Homoptera mutualisms? *Oikos*, 57(2), 276–280. <https://doi.org/10.2307/3565432>
- Belsky, A. J. (1994). Influences of trees on savanna productivity: Tests of shade, nutrients, and tree-grass competition. *Ecology*, 75(4), 922–932. <https://doi.org/10.2307/1939416>
- Biggs, R., Biggs, H. C., Dunne, T. T., Govender, N., & Potgieter, A. L. F. (2003). Experimental burn plot trial in the Kruger National Park: History, experimental design and suggestions for data analysis. *Koedoe*, 46(1), 1–15. <https://doi.org/10.4102/koedoe.v46i1.35>
- Campos, R. I., & Camacho, G. P. (2014). Ant-plant interactions: The importance of extrafloral nectaries versus hemipteran honeydew on plant defense against herbivores. *Arthropod-Plant Interactions*, 8(6), 507–512. <https://doi.org/10.1007/s11829-014-9338-8>
- Fleming, P. A., Hofmeyr, S. D., & Nicolson, S. W. (2007). Role of insects in the pollination of *Acacia nigrescens* (Fabaceae). *South African Journal of Botany*, 73(1), 49–55. <https://doi.org/10.1016/j.sajb.2006.06.010>
- Hall, W. J. (1935). The genus *Tachardina* (Lacciferidae, Coccidae) in Southern Africa. *Bulletin of Entomological Research*, 26(4), 475–486. <https://doi.org/10.1017/S0007485300036816>
- Kyalangalilwa, B., Boatwright, J. S., Daru, B. H., Maurin, O., & Van Der Bank, M. (2013). Phylogenetic position and revised classification of *Acacia* s.l. (Fabaceae: Mimosoideae) in Africa, including new combinations in *Vachellia* and *Senegalia*. *Botanical Journal of the Linnean Society*, 172(4), 500–523. <https://doi.org/10.1111/boj.12047>
- Miller, D., & Davidson, J. (2005). *Armored scale insects pests of trees and shrubs (Hemiptera: Diaspididae)*. Ithaca, NY: Cornell University Press.
- Moncrieff, G. R., Kruger, L. M., & Midgley, J. J. (2008). Stem mortality of *Acacia nigrescens* induced by the synergistic effects of elephants and fire in Kruger National Park, South Africa. *Journal of Tropical Ecology*, 24(6), 655–662. <https://doi.org/10.1017/S0266467408005476>
- O'Keefe, T., & Alard, G. (2002). *Effects of herbivores and fire on riparian and upland savanna ecosystems*. Field operations manual for herbivore and fire exclosures on the Sabie and Letaba Rivers in the Kruger National Park. Unpublished.
- Prior, K. M., & Palmer, T. M. (2018). Economy of scale: Third partner strengthens a keystone ant-plant mutualism. *Ecology*, 99(2), 335–346. <https://doi.org/10.1002/ecy.2104>
- Young, T., Stubblefield, C. H., & Isbell, L. A. (1997). Ants on swollen-thorn acacias: Species coexistence in a simple system. *Oecologia*, 109(1), 98–107. <https://doi.org/10.1007/s004420050063>

SUPPORTING INFORMATION

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

How to cite this article: Haba Y, Herbert R, Yang L. An undescribed relationship between the knobthorn tree (*Senegalia nigrescens*), ants and a lac scale insect in South Africa. *Afr J Ecol*. 2019;57:595–598. <https://doi.org/10.1111/aje.12627>