RESEARCH NOTE

Interspecific competition between ants and African honeybees (*Apis mellifera scutellata*) may undermine the effectiveness of elephant beehive–deterrents in Africa

Reece Thornley[1,2] | Robin Cook[3,4] | Matthew Spencer[5] |
Catherine L. Parr[5,6,7] | Michelle Henley[3,8,9]

[1]Centre for Biodiversity Dynamics in a Changing World, Department of Biology, Aarhus University, Aarhus C, Denmark

[2]Ecoinformatics and Biodiversity, Department of Biology, Aarhus University, Aarhus C, Denmark

[3]Elephants Alive, Hoedspruit, South Africa

[4]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

[5]School of Environmental Sciences, University of Liverpool, Liverpool, UK

[6]Centre for African Ecology, School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

[7]Department of Zoology & Entomology, University of Pretoria, Pretoria, South Africa

[8]Applied Behavioural Ecology and Ecosystem Research Unit, School of Environmental Sciences, University of South Africa, Florida, South Africa

[9]Department of Philosophy, Faculty of Humanities, University of Johannesburg, Auckland Park, South Africa

Correspondence
Catherine L. Parr, School of Environmental Sciences, University of Liverpool, Liverpool, UK.
Email: kate.parr@liverpool.ac.uk

Reece Thornley, Centre for Biodiversity Dynamics in a Changing World, Department of Biology, Aarhus University, Aarhus C, Denmark.
Email: reecethornley@hotmail.com

Abstract

Beehive deterrents are commonly used to mitigate human–elephant conflict and protect woody vegetation. To ensure hive activity, reduce abscondment risks, and maintain deterrent effectiveness, resident bee colonies require supplementary feeding during periods of low resource availability. However, our study found that ants frequently consume the supplementary feed in open feeders intended for bees. *Anoplolepis custodiens* was the most numerically dominant species that excluded bees from the feeders, followed by *Camponotus* and *Crematogaster* spp. With higher ant abundance, the predicted probability of zero bees being present at feeders increased up to 82%. This competition may undermine the efficacy of beehive deterrents as a conflict mitigation tool. We developed a simple and effective ant exclusion method that raised the overall predicted probability of bees' presence at supplementary feeding stations from 32% to 68%. Our findings suggest that innovative solutions to exclude ants from supplementary feed may improve the implementation and success of this conflict mitigation method across Africa.

1 | INTRODUCTION

Conservation stakeholders in South Africa are concerned that high African elephant populations (*Loxodonta africana*) lead to the expiration of large/iconic trees and, subsequently, the homogenization of savanna woody structure and diversity (O'Connor et al., 2007). Likewise, crop raiding by elephants across Africa severely undermines conservation efforts, causing human–wildlife conflict, and compromising people's livelihoods (Vogel et al., 2020). To overcome these challenges, hives of African honeybees (*Apis mellifera scutellata*; hereafter, bees) have been lauded as an effective and ethical way of mitigating these tensions. Bees have been shown to be an effective elephant deterrent, reducing damage to large and iconic trees [e.g., Marula trees (*Sclerocarya birrea*)] and significantly reducing elephant crop raiding (−80%) in East Africa (Cook et al., 2018; King et al., 2017). This has led to the widespread adoption of this conservation tool across Africa over the last 8 years, and ensuring this elephant deterrent is effective is of significant interest to conservation practitioners, protected area authorities, and local communities (King, 2020).

While beehives have been shown to be an effective elephant deterrent, Cook et al. (2018) raised the point that supplementary feeding (a mixture of sugar water and nectar/pollen substitute) must be provided in the dry seasons or during drought periods to maintain beehive occupation and activity when key resources (e.g., water, nectar, and pollen) are scarce (Caron, 2021). Supplementary feeding mitigates the physiological constraints, such as temperature extremes and food/water scarcity, that reduce hive activity by increasing the risk of desiccation, starvation, and heat stress for bees (Abou-Shaara et al., 2017; Tan et al., 2012). Beehive activity during the dry season is crucial as elephant impact on woody vegetation and human–wildlife conflict is at its highest (Greyling, 2004; Loarie et al., 2009). Supplementary feeding is one of the essential tools used to maintain hive activity and mitigate elephant impact on woody vegetation and human–elephant conflict. However, observations of open feeding stations (e.g., feeding not directly in the hive) have revealed potentially concerning competition between ants and bees for the supplementary feed (R. Cook, *personal observation*, and K. Bunney, *unpublished data*).

Interspecific competition through behavioral aggression (e.g., biting, swarming, etc.) for resources, territory, and defense, is a cornerstone of ant, and bee (though to a lesser extent) ecology in African savannas (Hölldobler & Wilson, 1990; Parr, 2008; Rudolph & Palmer, 2013). Niche partitioning, distinct foraging behavior, and space requirements usually reduce interspecific competition between these two taxa under normal conditions, reducing the risk of interspecific interactions (Barônio & Del-Claro, 2018). However, the provision of sugar and nectar during the dry season may result in the artificial modification of species niche spaces and may therefore result in direct competition between ants and bees for supplementary feed during a resource-limited period. Consequently, it is necessary to understand whether interspecific competition for supplementary feed could reduce bee access to supplementary feed and undermine their conservation value.

The extent to which interspecific competition with ants and temperature may undermine the ability of the bees to access supplementary feed during the dry season is currently unknown. Accordingly, we aimed to investigate: (1) what level of ant abundance would reduce the probability of bee abundance at the feeders, (2) whether excluding ants from the bee feeders would increase the probability of bee abundance at the feeders, (3) if air temperature influenced bee abundance. We predicted that (1) interspecific competition between ants and bees will result in reduced bee abundance at the feeding stations due to the bees' naturally less aggressive behavior compared with ants, (2) excluding ants from the feeders will substantially increase the probability of bee abundance at the feeders, and (3) lower air temperatures will limit bee abundance at the feeders.

2 | METHODS

2.1 | Study site

Data were collected at Ndabushi Bushveld Retreat (hereafter referred to as Ndabushi), a small (14 hectare) property located in the lower bushveld of the Greater Kruger National Park, Limpopo Province, South Africa (24°20′26.4″ S, 31°09′18.3″ E). Ndabushi has a hot and semi-arid climate, with a dry (18.8°C on average, April–September) and wet season (24.1°C, average, October–March). The mean annual rainfall is 500 mm per annum. Ndabushi falls within the Granite Lowveld vegetation unit (SVl 3) in the Savanna biome (Mucina & Rutherford, 2006). The site has a limited number of meso-herbivores (e.g., Nyala, *Tragelaphus angasii*), but no mega-herbivores are present.

2.2 | Supplementary feeding and beehive placement

All data were collected in a one-hectare site dominated by knobthorn [Senegalia (Acacia) nigrescens] savanna woodland. We suspended four active hives from knobthorn trees at a height of 1.5–2 m from the ground (Cook et al., 2018), after ensuring all hives were healthy and active. Feeders were attached to four different knobthorn trees that were >5 m apart, and within 15 m of trees containing active beehives. The supplementary feed is a mixture of sugar, nectar, and water, following the described methods by Cook et al. (2018). Feeders consisted of 2–3 metal containers, filled with the sugar solution, attached to a wooden plank, covered in wire-mesh [to prevent mammals such as primates (etc.) from accessing the feed], and secured to a tree trunk. These feeders are "open feeders" for example, not directly placed within the hive, and so are accessible to most invertebrates in the system. The containers were filled with sticks to prevent the bees from drowning. The feeders were re-filled every 2–3 days (depending on logistical constraints) from June 7 to 30, 2019. There was a gap of 2 days between the first feeding and the start of data collection to allow both bees and ants adequate time to locate this new resource. Bees are known to travel up to 9.5 km from their hive in search of food and water (Beekman & Ratnieks, 2000), and so we assumed that all hives had equal access to all feeders.

2.3 | Ant species

Ant ground abundance and genus were recorded using six pitfall traps filled with 80% ethanol solution, 1 m from the base of each tree containing a supplementary feeding station (24 in total). Pitfall traps were in place for 5 days, both before supplementary feeding was started and for 5 days before ants were excluded from the feeders (Parr et al., 2004). These specimens were then counted and identified to the morpho species level.

2.4 | Ant–bee abundance

Data were collected for three observation periods per day between 07 h 30 min and 17 h 30 min. Ants and bees were observed on the feeders in the trees and on the ground directly below the feeder, where supplementary sugar feed dripped into small puddles [roughly 30 cm^2, referred to collectively as the feeder, except when discussing Ant Exclusion (see below)]. Bee abundance was categorized as the number of bees that were present at the feeders (0, 1–20, and >20 individuals). Ant abundance was recorded as the percentage of the feeder surface area that was covered by ants from 0%, 1%–25%, 25%–50% to 51%–100%. We used percent cover as a proxy for abundance, as ants were too numerous to be counted individually. As temperature is known to influence ant and bee activity (Abou-Shaara et al., 2017; Hölldobler & Wilson, 1990), we recorded air temperature using a hand-held Kestrel® weather station (Kestrel Meters, Boothwyn, PA).

2.5 | Ant exclusion

From June 29, 2019 to July 02, 2019, ants were excluded from the four trees containing feeders to determine bee access to supplementary feed in the absence of ants. Prior to the exclusion, ants were flushed from the tree trunk and feeders using warm water. Once each tree and feeder were free of ants, we applied a 7-cm wide layer of engine grease to the entire circumference of the tree trunk, 30 cm above the base of each tree, to prevent ants from gaining access to the feeders. Ants still had access to supplementary feed that dripped on the ground, and so these observations were recorded separately. We then recorded ant–bee abundance at the feeders in the same manner as described above to record the effect that the exclusion of ants had on bee abundance at the feeders.

2.6 | Statistical analysis

2.6.1 | Ant–bee abundance

To determine which factors influenced the predicted probability of varying bee abundances at the feeders, we used a multinomial logistic regression (Qian et al., 2012), implemented in the package *nnet* in *R* 3.5.2 (R Foundation for Statistical Computing, 2021; Venables & Ripley, 2002, section 7.3). See Agresti (2002, section 7.1), Burnham and Anderson (2002), and Thornley et al. (2020) for more detailed descriptions of this modeling approach. Our model attempted to estimate the predicted probability of bee abundance at the feeding stations, as a function of ant abundance, air temperature, squared air temperature, whether observations were in trees or on the ground, and if observation were recorded during our exclusion treatment or not. We included the interaction between ant exclusion and ground/tree observation to address the caveat that ants could not be excluded from supplementary feed on the ground during our exclusion experiment. By including this interaction term, we account for changes in bee abundance based on the manipulation of ant abundance (or lack of) that result from ant exclusion, and where bees and ants were recorded feeding during the exclusion experiment.

We both air temperature and squared temperature as an explanatory variables to allow for the possibility of a quadratic relationship, i.e., an optimum temperature within our temperature range. The ground temperature and temperature of the feeder was not included in the model, as it was co-linear with air temperature ($r(490) = 0.71$; Dormann et al., 2013), and air temperature more likely to directly drive bee abundance (Abou-Shaara et al., 2017). We fitted a saturated model including all the outlined predictors and used the *dredge* function in the *MuMIn* package (Bartoń, 2022) to select the best-fitting model based on the models AICc, and extracted the predicted probability of ant abundance from our best-fitting model. Figures were created using the *ggplot* package using the predicted probabilities extracted from our model outputs produced using the *nnet* package (Wickham, 2022).

3 | RESULTS

3.1 | Best fitting model for bee abundance

Bee abundance at the feeders was influenced by ant abundance, squared air temperature, and ant exclusion, with an interaction between ant abundance being recorded on the ground or in the tree (during the exclusion part of the experiment only). No other model was considered as the delta value >2 (Symonds & Moussalli, 2011; Table A1).

3.2 | Ant species

During our study, *Anoplolepis* spp. ants were the most numerically dominant species, which increases substantially in numbers once feeding was commenced. On the feeders, we noted that arboreal ants from the genus *Camponotus* and *Crematogaster* were also consistently recorded, but due to their arboreal ecology, they were not recorded in the ground feeders in significant numbers (Table A2).

3.3 | Ant abundance

Ant abundance substantially reduced bee abundance at the feeders (Figure 1). The most adverse effect on bees was at 51%–100% ant abundance, where bees had an 82% probability of being entirely absent from the feeders and only a 1% probability of high abundance (>20 bees; Figure 1). Low levels of ant abundance (1%–25%) were sufficient to decrease the probability of high bee abundance from 36% to 27%, but low ant abundance did not adversely affect the probability of low bee abundances (e.g., 1–20 bees,

Figure 1). High bee abundance decreased consistently in probability when ant abundance ≥26% (Figure 1).

3.4 | Ant exclusion

Our method of ant exclusion was effective at preventing ants access to feed placed in trees, which facilitated consistently higher bee abundances (Figure 2). When ants were excluded from tree feeders, the probability of high bee abundance (>20 bees) increased from 6% to 16% and low bee abundance (1–20) from 25% to 77% (Figure 2). The probability of zero bees declined dramatically from 68% to 8% when ants were excluded from tree feeders (Figure 2).

The exclusion of ants from tree feeders did not inhibit ants from accessing the supplementary feed that drips onto the ground, where high ant abundances continued to dominate the supplementary feed, excluding bees in the process (probability of zero bees on the ground during the exclusion trial increased from 72% to 85%, and the predicted probability of >20 bees was only 0.1%; Figure 2).

3.5 | Bee abundance and temperature

Air temperature affected bee abundance independently of our other predictor variables (e.g., the effect of
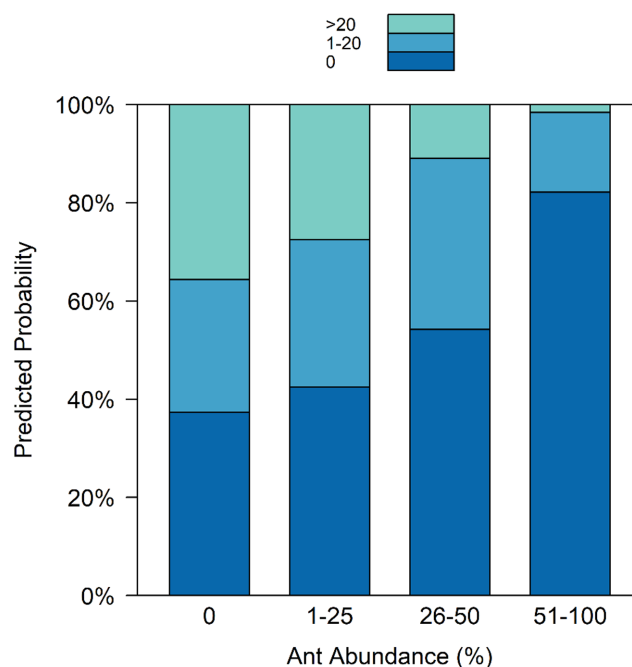

FIGURE 1 Predicted probability (%) of our three bee abundance categories (0, 1–20, and >20) occurring at the feeders with increasing ant abundance (increasing percentage of the feeders covered in ants).
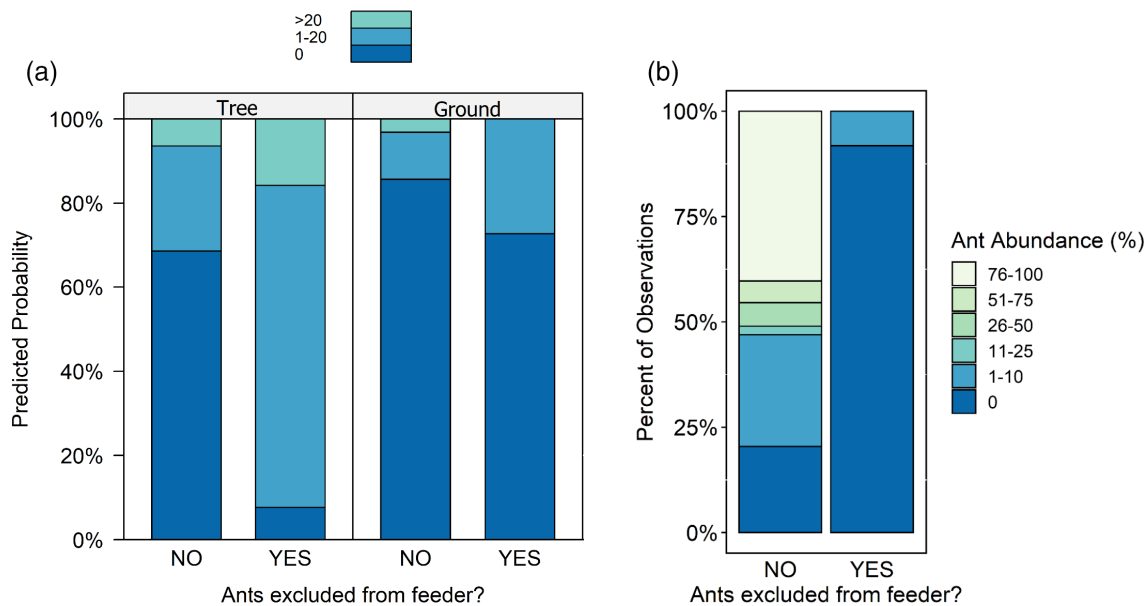
FIGURE 2 (a) Predicted probability (%) of our 3 bee abundance categories (0, 1–20, and >20) relative to whether ants were excluded from tree feeders, or the ground (where interspecific competition with ants was still present) during the exclusion experiment. (b) The percent of ant abundance categories recorded at the feeders, in the trees, before ($n = 190$) and during ($n = 49$) during ant exclusion.

temperature was not influenced by ant abundance). Air temperatures between 17 and 24°C predicted the greatest probability of high bee abundance (6%–8%, respectively), lower bee abundance was most probable at 24°C (25%), and temperature extremes (e.g., <10°C and >37°C) were the most likely to result in zero bees at the feeders. Ground temperature did not affect bee or ant abundance.

4 | DISCUSSION

Our study demonstrated that ants can have a substantial impact on bee abundance through the competitive exclusion of bees from open supplementary feeding stations. Ants, therefore, may have a significant effect on the effectiveness of beehives as elephant deterrents during the dry season. Ant presence alone does not prevent bees' access to supplementary feed; however, ants leverage numerical dominance and behavioral aggression to exclude bees from supplementary feed severely reducing the probability of bees utilizing this resource. Our study demonstrates an easy-to-use method of ant exclusion, that is effective at inhibiting ant access, and facilitating high bee abundance, at the feeders during resource-limited periods.

Behavioral aggression by ants is common in African savanna systems, where the defense of spatially and temporally limited resources is necessary to ensure colony fitness, growth, and reproduction (Parr, 2008; Parr et al., 2005). Supplementary feeding provides a highly nutritious resource during a severely resource-limited time of year.

Consequently, the utilization and robust defense of such a resource by ants should be expected, as it removes resource scarcity as a limiting factor of ant colony fitness, growth, and expansion (Bishop et al., 2014). However, the spatial and temporal limitations constraining colonies of ants during the dry season also apply to bee colonies (Klein et al., 2019). Supplementary feed is provided to mitigate the possibility of bees absconding from their hives, as well as to maximize the effectiveness of the beehive deterrent action during the dry season when elephant impact on Marula trees, and crop raiding elsewhere, is at its highest (Cook et al., 2018; Cook & Henley, 2019). High levels of ant utilization of supplementary feed may seriously undermine the effectiveness of supplementary feed by causing resource scarcity to persist as a limiting factor of bee abundance and beehive activity in the dry season (Kuboja et al., 2020). This may reduce hive activity, increasing the risk of beehive abscondment, and the habituation of elephants to empty or low-activity hives—further undermining the deterrent's effectiveness. To improve our understanding of inter-specific competition and its implications, further research is needed that assesses the exact size, and population structure of beehives to understand exactly how hive health and activity is affected by interspecific competition, and the abundance threshold where bee activity becomes an ineffective deterrent. Currently, it is unclear what proportion of the bees diet is made up of supplementary feed in comparison to wild food alternatives (e.g., pollen from flowers), although both should be quite low considering

the time of year. However, this should be investigated to ascertain the importance of supplementary feed for bees at this time of year. Furthermore, the provisioning of supplementary feed may give domesticated bees a competitive advantage by increasing their fitness and ability to compete with their wild counterparts and other pollinators. This is because domesticated bees could increase disease exchange where individuals interact at supplementary feeders or on flowers, competition for resources in the wet season (e.g., floral resources), and indirect effects through changes in the plant community could all reduce wild pollinator fitness and success (Mallinger et al., 2017). Where these beehive deterrents and supplementary feeders are broadly used across the landscape, biodiversity trade-offs (e.g., mitigating elephant tree damage vs. effects on wild pollinators) of using this method should be investigated further.

During our study, *Anoplolepis custodiens* was overwhelmingly the most common ant species (Table A2). *Anoplolepis custodiens* is notoriously aggressive, and specializes in the consumption and exploitation of sugar-based carbohydrates, making the supplementary feed an ideal resource (Mothapo & Wossler, 2017; Wittman et al., 2018). Other ants, particularly the arboreal *Crematogaster* spp., were also observed competing with bees for access to the supplementary feed but did not recruit conspecifics to feeders in substantial numbers, like *Anoplolepis* ants. However, these species still exhibited significant behavioral aggression (e.g., biting and charging toward bees) that inhibited bee access to supplementary feed (*personal observation*). The intense numerical dominance and interspecific aggression by *Anoplolepis* and other ant species resulted in a high level of competitive exclusion of bees (42%–82%, Figure 1) throughout the first phase of our study. However, we did not collect the data needed to analyze ant species effects separately—which would be advisable for future research. Furthermore, ant community composition and structure change along rainfall, temperature, vegetation, and topographic gradients (Parr et al., 2004), and so interspecific competition and aggression between bees and ants may vary in intensity depending on the location. Invertebrate surveys (e.g., pitfall traps) would thus be advisable before employing the beehive deterrent to gauge the potential for interspecific competition. This being said, highly aggressive and competitive ant species are present throughout southern, eastern, and central Africa (Fisher & Bolton, 2019), and so ant–bee competition may be a persistent challenge to the effectiveness of the beehive deterrents without sufficient intervention. However, due to the limited sample size in our experiment (one field site), further research would be required to ascertain the scale of this issue beyond the specific ecological context (e.g., a greater range of rainfall, temperatures, etc.) of our experiment and personal observations.

We have demonstrated a method of ant exclusion from open feeding stations that is simple, economical, and dramatically increases bee abundance at feeders by eliminating interspecific competition between bees and ants within trees. The effective exclusion of ants from tree feeders facilitated substantially greater access for bees to the supplementary feed. For example, the probability of no bees at the tree feeders decreased from 52% to 7% when ants were excluded from the trees. However, extreme aggression and the competitive exclusion of bees by ants persisted on the ground, where ant exclusion was not possible. Therefore, the redesign of the feeders, in addition to the exclusion of ants, would be advisable to ensure the most effective and economical delivery of supplementary feed to bees. Cook et al. (2018) originally estimated a minimum running cost of $900 per year to provide supplementary feed to 50 occupied beehives during the South African dry season (March–August). To put our results into context, we assume the same cost of beehive maintenance and feeding given by Cook et al. (2018) and if ant/bee abundance correlates to the amount of food consumed by each species. An 82% predicted probability of 51%–100% ant abundance at the feeders throughout the dry season could result in $738 per year being wasted on supplementary feed being consumed by ants across 50 beehives. Furthermore, beehive deterrents could potentially have an added cost of $27.75 per beehive to replace bee colonies that abscond because of resource scarcity caused by the usurpation of supplementary feed. The potential for beehive abscondment directly because of interspecific competition with ants, however, warrants further investigation.

We have shown that interspecific competition for supplementary feed can be prevented through the application of engine grease to tree trunks, which substantially increased bee access to the supplementary feeding stations while costing as little as $2–$6 per tree, per year, to apply and maintain an 8–10 cm layer of engine grease or Plantex® (the minimum required to be effective). However, it would be advisable to investigate the feasibility of feeding the beehive colonies directly (e.g., through feeding ramps situated at the entrance of each beehive) to further reduce the potential for interspecific competition and reduce project costs. The use of engine grease was purely for our experimental assay, and due to environmental concerns related to the toxicity of engine grease, we strongly recommend against its wider use to deter ants. As a direct substitute, organic alternatives, such as Plantex® glue or mint, chalk, vinegar solutions, should be used because they are less environmentally hazardous. However, these alternatives were not available at the

time of our experiment. During our experiment, small nontarget animals such as those from Diptera and Hymenoptera were caught in the grease, but these instances were minimal (R. Thornley, *personal observation*). To reduce the risk feeders could also be attached to wooden or metal poles that can be removed when not in use, reducing the long-term exposure of the environment and nontarget animals to any glue or other deterrents used. With the addition of Plantex® glue or other substances on the ropes of each individual beehive to prevent ant invasions (Cook et al., 2018), feeding stations will hopefully remain isolated from ant invasions, increasing the availability and effectiveness of open supplementary feeding for bees.

Lastly, ambient air temperature is an important predictor of bee abundance at the feeders. High abundances of bees (>20) were most likely around 18–26°C, which is consistent with the honeybees' optimum temperature range (e.g., temperature with maximum activity with minimal water loss) of 20°C (e.g., Abou-Shaara et al., 2017; Tan et al., 2012). Fewer bees are likely to be present at the feeders during low or high temperatures, as bees remain at their hives to maintain beehive temperature to an optimum of 36–37°C (e.g., through fanning; Peters et al., 2019). Ensuring that beehives and supplementary feeders are placed in a location with adequate shade to prevent exposure to extreme heat and desiccation will help facilitate higher bee activity and greater use of supplementary feed.

Our findings suggest that ant–bee competition may be a major threat to the sustainability of the beehive mitigation method for tree protection and human–elephant conflict. Innovative methods that exclude ant competition from supplementary feed are required to ensure that beehive occupancy levels remain high when resources are limited and elephant impact increases.

AUTHOR CONTRIBUTIONS

Conceptualization: Reece Thornley, Catherine L. Parr, Michelle Henley, Robin Cook. **Data collection:** Reece Thornley, Robin Cook. **Data analysis:** Reece Thornley, Matthew Spencer, Catherine L. Parr. **Writing and reviewing of manuscript:** Reece Thornley, Robin Cook, Matthew Spencer, Catherine L. Parr, Michelle Henley.

ACKNOWLEDGMENTS

FUNDING INFORMATION

CONFLICT OF INTEREST STATEMENT

DATA AVAILABILITY STATEMENT
Please contact the corresponding author for data access requests.

ORCID
Reece Thornley https://orcid.org/0000-0002-0625-519X

REFERENCES

Abou-Shaara, H. F., Owayss, A. A., Ibrahim, Y. Y., & Basuny, N. K. (2017). A review of impacts of temperature and relative humidity on various activities of honey bees. *Insectes Sociaux*, *64*(4), 455–463. https://doi.org/10.1007/s00040-017-0573-8

Agresti, A. (2002). *Categorical data analysis* (2nd ed.). John Wiley & Sons.

Barônio, G. J., & Del-Claro, K. (2018). Increase in ant density promotes dual effects on bee behaviour and plant reproductive performance. *Arthropod-plant interactions*, *12*, 201–213.

Bartoń, K. (2022). Package "MuMIn": Multi-Model Inference. 1, Version 1.47.1.

Beekman, M., & Ratnieks, F. L. (2000). Long-range foraging by the honey-bee, *Apis mellifera* L. *Functional Ecology*, *14*(4), 490–496. https://doi.org/10.1046/j.1365-2435.2000.00443.x

Bishop, T. R., Robertson, M. P., van Rensburg, B. J., & Parr, C. L. (2014). Elevation-diversity patterns through space and time: Ant communities of the Maloti-Drakensberg Mountains of southern Africa. *Journal of Biogeography*, *41*(12), 2256–2268. https://doi.org/10.1111/jbi.12368

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach* (2nd ed.). Springer-Verlag.

Caron, D. M. (2021). Necropsy of a hive. In T. R. Kane & C. M. Faux (Eds.), *Honey bee medicine for the veterinary practitioner* (pp. 339–350). John Wiley & Sons, Ltd. https://doi.org/10.1002/9781119583417.ch27

Cook, R. M., & Henley, M. D. (2019). Complexities associated with elephant impact on *Sclerocarya birrea* subsp. *caffra* in the greater Kruger National Park. *South African Journal of Botany*, *121*, 543–548. https://doi.org/10.1016/j.sajb.2019.01.016

Cook, R. M., Parrini, F., King, L. E., Witkowski, E. T. F., & Henley, M. D. (2018). African honeybees as a mitigation method for elephant impact on trees. *Biological Conservation*, *217*, 329–336. https://doi.org/10.1016/j.biocon.2017.11.024

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., Mcclean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Fisher, B. L., & Bolton, B. (2019). *Ants of Africa and Madagascar*. University of California Press. https://doi.org/10.1525/9780520962996

Greyling, M. D. (2004). *Sex and age related distinctions in the feeding ecology of the African elephant* [Faculty of Science, University of the Witwatersrand]. http://hdl.handle.net/10539/7489

Hölldobler, B., & Wilson, E. O. (1990). _The ants._ Harvard University Press/Springer.

King, L. E. (2020). Elephants and bees using beehive fences to increase human—Elephant coexistence for small-scale farmers in Kenya, Elephants and Bees in Kenya. In B. Frank & J. A. Glikman (Eds.), _Human–wildlife interactions: Turning conflict into coexistence_ (pp. 216–241). Cambridge University Press.

King, L. E., Lala, F., Nzumu, H., Mwambingu, E., & Douglas-Hamilton, I. (2017). Beehive fences as a multidimensional conflict-mitigation tool for farmers coexisting with elephants. _Conservation Biology_, _31_(4), 743–752. https://doi.org/10.1111/cobi.12898

Klein, S., Pasquaretta, C., He, X. J., Perry, C., Søvik, E., Devaud, J. M., Barron, A. B., & Lihoreau, M. (2019). Honey bees increase their foraging performance and frequency of pollen trips through experience. _Scientific Reports_, _9_(1), 1–10. https://doi.org/10.1038/s41598-019-42677-x

Kuboja, N. M., Road, S., & Kikuu, C. (2020). Absconding of Honeybee Colonies from Beehives: Underlying Factors and its Financial Implications for Beekeepers in Tanzania. _International Journal of Agricultural Science, Research and Technology in Extension and Education Systems_, _10_(4), 185–193.

Loarie, S. R., van Aarde, R. J., & Pimm, S. L. (2009). Elephant seasonal vegetation preferences across dry and wet savannas. _Biological Conservation_, _142_(12), 3099–3107. https://doi.org/10.1016/j.biocon.2009.08.021

Mallinger, R. E., Gaines-Day, H. R., & Gratton, C. (2017). Do managed bees have negative effects on wild bees?: A systematic review of the literature. _PLoS One_, _12_(12), e189268. https://doi.org/10.1371/journal.pone.0189268

Mothapo, N. P., & Wossler, T. C. (2017). Patterns of floral resource use by two dominant ant species in a biodiversity hotspot. _Biological Invasions_, _19_(3), 955–969. https://doi.org/10.1007/s10530-016-1336-6

Mucina, L. & Rutherford, M.C. (Eds). (2006). _The Vegetation of South Africa, Lesotho and Swaziland._ Strelitzia 19, South African National Biodiversity Institute, Pretoria.

O'Connor, T. G., Goodman, P. S., & Clegg, B. (2007). A functional hypothesis of the threat of local extirpation of woody plant species by elephant in Africa. _Biological Conservation_, _136_(3), 329–345. https://doi.org/10.1016/j.biocon.2006.12.014

Parr, C. L. (2008). Dominant ants can control assemblage species richness in a South African savanna. _Journal of Animal Ecology_, _77_(6), 1191–1198. https://doi.org/10.1111/j.1365-2656.2008.01450.x

Parr, C. L., Robertson, H. G., Biggs, H. C., & Chown, S. L. (2004). Response of African savanna ants to long-term fire regimes. _Journal of Applied Ecology_, _41_(4), 630–642. https://doi.org/10.1111/j.0021-8901.2004.00920.x

Parr, C. L., Sinclair, B. J., Andersen, A. N., Gaston, K. J., & Chown, S. L. (2005). Constraint and competition in assemblages: A cross-continental and modeling approach for ants.

The American Naturalist, _165_(4), 481–494. https://doi.org/10.1086/428292

Peters, J. M., Peleg, O., & Mahadevan, L. (2019). Collective ventilation in honeybee nests. _Journal of the Royal Society, Interface_, _16_(150), 20180561.

Qian, S. S., Cuffney, T. F., & McMahon, G. (2012). Multinomial regression for analyzing macroinvertebrate assemblage composition data. _Freshwater Science_, _31_(3), 681–694. https://doi.org/10.1899/11-026.1

R Foundation for Statistical Computing. (2021). R: A language and environment for statistical computing, Version 4.0.3.

Rudolph, K. P., & Palmer, T. M. (2013). Carbohydrate as fuel for foraging, resource defense and colony growth—A long-term experiment with the plant-ant _Crematogaster nigriceps_. _Biotropica_, _45_(5), 620–627. https://doi.org/10.1111/btp.12040

Symonds, M. R. E., & Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. _Behavioral Ecology and Sociobiology_, _65_(1), 13–21. https://doi.org/10.1007/s00265-010-1037-6

Tan, K., Yang, S., Wang, Z. W., Radloff, S. E., & Oldroyd, B. P. (2012). Differences in foraging and brood nest temperature in the honey bees _Apis cerana_ and _A. mellifera_. _Apidologie_, _43_(6), 618–623. https://doi.org/10.1007/s13592-012-0136-y

Thornley, R., Spencer, M., Zitzer, H. R., & Parr, C. L. (2020). Woody vegetation damage by the African elephant during severe drought at Pongola Game Reserve, South Africa. _African Journal of Ecology_, _58_(4), 658–673. https://doi.org/10.1111/aje.12736

Venables, W. N., & Ripley, B. D. (2002). _Modern applied statistics with S-plus_ (4th ed., p. 495). Springer. https://doi.org/10.2307/2685660

Vogel, S. M., Lambert, B., Songhurst, A. C., McCulloch, G. P., Stronza, A. L., & Coulson, T. (2020). Exploring movement decisions: Can Bayesian movement-state models explain crop consumption behaviour in elephants (_Loxodonta africana_)? _Journal of Animal Ecology_, _89_, 1055–1068. https://doi.org/10.1111/1365-2656.13177

Wickham, H. (2022). Package 'ggplot2'.

Wittman, S. E., O'Dowd, D. J., & Green, P. T. (2018). Carbohydrate supply drives colony size, aggression, and impacts of an invasive ant. _Ecosphere_, _9_(9), e2403. https://doi.org/10.1002/ecs2.2403

APPENDIX

TABLE A1 Model output for a multinomial logistic regression models.

(Intercept)	Air temperature	Ant abundance	Exclusion treatment: ground or feed	df	logLik	AICc	Delta	Weight
+	+	+	+	16	−282.928	599.0011	0	0.793532
+	−	+	+	14	−286.407	601.6938	2.692692	0.206468
+	+	−	+	10	−309.448	639.3527	40.35156	1.37E−09
+	+	+	−	10	−311.295	643.0476	44.04651	2.16E−10
+	−	−	+	8	−316.846	649.9899	50.98882	6.72E−12
+	−	+	−	8	−319.756	655.8091	56.80804	3.66E−13
+	+	−	−	4	−369.325	746.732	147.7309	6.61E−33
+	−	−	−	2	−377.571	759.1656	160.1645	1.32E−35

Note: + indicates where the model term was included, and − indicates where model term was excluded from the model selection process.

TABLE A2 Ant genus abundance in relation to feeder number and treatment.

During/before	Feeder (tree)	Genus name	Abundance
Before	Control	Anoplolepis	36
Before	Control	Crematogaster	1
Before	Control	Monomorium	2
Before	Control	Pheidole	1
Before	Control	**Total**	**40**
Before	Feeder 1	Anoplolepis	32
Before	Feeder 1	Crematograster	2
Before	Feeder 1	Monomorium	1
Before	Feeder 1	Pheidole	2
Before	Feeder 1	Tetraponera	1
Before	Feeder 1	**Total**	**38**
Before	Feeder 2	Anoplolepis	12
Before	Feeder 2	Monomorium	13
Before	Feeder 2	Ocymyrmex	3
Before	Feeder 2	Pheidole	6
Before	Feeder 2	Technomyrmex	2
Before	Feeder 2	Tetramorium	2
Before	Feeder 2	**Total**	**37**
Before	Feeder 3	Anoplolepis	578
Before	Feeder 3	Crematogaster	1
Before	Feeder 3	Monomorium	29
Before	Feeder 3	Ocymyrmex	1
Before	Feeder 3	Pheidole	13
Before	Feeder 3	Polyrhachis	2
Before	Feeder 3	Technomyrmex	1
Before	Feeder 3	Tetramorium	19
Before	Feeder 3	**Total**	**644**

TABLE A2 (Continued)

During/before	Feeder (tree)	Genus name	Abundance
Before	Feeder 4	*Anoplolepis*	7
Before	Feeder 4	*Camponotus*	3
Before	Feeder 4	*Crematogaster*	1
Before	Feeder 4	*Monomorium*	1
Before	Feeder 4	*Pheidole*	4
Before	Feeder 4	*Tetramorium*	5
Before	Feeder 4	**Total**	**21**
During	Control	*Crematograster*	3
During	Control	*Monomorium*	9
During	Control	*Ocymyrmex*	1
During	Control	*Pheidole*	3
During	Control	*Technomyrmex*	2
During	Control	**Total**	**18**
During	Feeder 1	*Anoplolepis*	40
During	Feeder 1	*Camponotus*	2
During	Feeder 1	*Crematograster*	1
During	Feeder 1	*Monomorium*	32
During	Feeder 1	*Pheidole*	28
During	Feeder 1	*Polyrhachis*	1
During	Feeder 1	*Tapinoma*	2
During	Feeder 1	*Technomyrmex*	38
During	Feeder 1	*Tetramorium*	28
During	Feeder 1	**Total**	**172**
During	Feeder 2	*Anoplolepis*	16
During	Feeder 2	*Bothroponera*	4
During	Feeder 2	*Camponotus*	2
During	Feeder 2	*Monomorium*	10
During	Feeder 2	*Myrmicaria*	1
During	Feeder 2	*Ocymyrmex*	13
During	Feeder 2	*Opthalmopone*	4
During	Feeder 2	*Pheidole*	30
During	Feeder 2	*Polyrhachis*	2
During	Feeder 2	*Technomyrmex*	13
During	Feeder 2	*Tetramorium*	5
During	Feeder 2	**Total**	**100**
During	Feeder 3	*Anoplolepis*	4837
During	Feeder 3	**Total**	**4837**
During	Feeder 4	*Anoplolepis*	9903
During	Feeder 4	**Total**	**9903**

Note: Ants were recorded using six pitfall traps filled with 80% ethanol solution, 1 m from the base of each tree containing a supplementary feeding station. Pitfall traps were in place for 5 days, both before supplementary feeding was started and during.