Diurnality in the defensive behaviour of African honeybees *Apis mellifera adansonii* and implications for their potential efficacy in beehive fences

Isaac Blaise Djoko, Robert Bertrand Weladji and Patrick Paré

Abstract Across the range of African elephants *Loxodonta* spp., negative interactions with people are prevalent, and the impact of the resulting economic losses on farmers calls for solutions. The use of beehive fences, a mitigation method with ecological and socio-economic benefits, is gaining momentum in African savannah landscapes. We assessed the diurnal and nocturnal defensive behaviours of African honeybees *Apis mellifera adansonii* in response to visual and physical disturbances in the Campo–Ma'an conservation area, Cameroon. We examined six bee colonies, assessing their activity level, aggressive behaviour and ability to defend themselves when disturbed at different times of day. We found that activity levels varied between colonies and that colonies were more active during the day and inactive at night. The defensive perimeter around the hives also varied between the colonies and was generally greater during morning and evening periods. Bee colonies did not defend their hives around midday and at night. In response to a threat, bees were more likely to fly out from the hive during daytime than at night, with variation amongst colonies. Overall, as elephant intrusions occur mostly at night, beehive fences alone may not be an adequate mitigation method against crop damage caused by forest elephants *Loxodonta cyclotis*. We suggest combining beehive fences with other mitigation methods to improve crop protection.

Keywords Aggressive behaviour, *Apis mellifera adansonii*, beehive fence, defensive perimeter, forest elephant, *Loxodonta cyclotis*, mitigation, simulation

Supplementary material for this article is available at doi.org/10.1017/S0030605321001721

Introduction

Crop farming can be challenging within the range of African elephants *Loxodonta* spp., and ongoing land-use change exacerbates encroachment of agriculture into elephant habitats (Mmbaga et al., 2017; Puyravaud et al., 2019). Elephants enter farmlands and feed on crops mostly at night (Gunn et al., 2013; Ngama et al., 2016), often leading to negative human–elephant interactions. Several strategies have been developed to promote coexistence, including biological methods (Vollrath & Douglas-Hamilton, 2002; Nelson et al., 2003; King, 2010; King et al., 2017). However, often these strategies are only effective temporarily or do not meet people's expectations in terms of their ability to prevent crop damage by elephants (Nelson et al., 2003; King et al., 2017; Dror et al., 2020).

Honeybees *Apis mellifera* are increasingly being used to protect crops from elephants (Vollrath & Douglas-Hamilton, 2002; Soltis et al., 2014; Ngama et al., 2016; Cook et al., 2017; King et al., 2017). *Apis mellifera adansonii* in West and Central Africa and *Apis mellifera scutellata* in East and Southern Africa (Fletcher, 1978; Engel, 1999) have a reputation of particularly aggressive behaviour, and their stings can kill animals (e.g. humans: Fletcher, 1978; Soumana et al., 2016; waterbuck *Kobus ellipsiprymnus*: Barnes et al., 2005; goats *Capra* spp.: Karidozo & Osborn, 2005). They repel intruders crossing their defensive perimeters (Lecomte, 1961) by spreading pheromones (Wright et al., 2018), buzzing or stinging (Soltis et al., 2014; King & Raja, 2016; King et al., 2018). The effect of pheromone release on savannah elephants *Loxodonta africana* has been demonstrated in Greater Kruger National Park, South Africa (Wright et al., 2018). In Kenya, farms protected by beehive fences were more productive than unprotected farms as elephants succeeded only in 20% of their attempts at breaking such fences (King et al., 2017). Similarly, in Gabon empty hives and hives with low bee activity ($<$ 40 bee movements per minute; a bee movement being defined as a bee exiting or entering the hive) did not deter elephants, whereas active hives (40–60 bee movements per minute) did (Ngama et al., 2016).

Bees are predominantly diurnal insects and only a few species fly at night (Theobald et al., 2006). For example, *A. m. adansonii* can take advantage of moonlight to forage at night (Fletcher, 1978; Theobald et al., 2006), and when disturbed, *A. m. scutellata* have been observed to swarm from beehives to repel elephants during the night as well as during the day (King, 2013). Farmers are often reluctant

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Received 3 August 2021. Revision requested 18 October 2021. Accepted 19 November 2021. First published online 11 July 2022.

to adopt honeybees as elephant deterrents (King, 2010; Noga et al., 2015; King et al., 2017), and in Thailand it was reported that *A. mellifera* and *Apis cerana* were not aggressive towards Asian elephants *Elephas maximus* when disturbed during the day or at night (Dror et al., 2020). These geographical and temporal variations in the behaviour of bees call for site-specific research to validate the efficacy of honeybees as potential elephant deterrents. This should be done before investment in beehive fences is promoted.

Encroachment of agricultural areas into elephant habitat around Campo–Ma'an National Park (Cameroon) has intensified in recent years, increasing competition between people and elephants over space and resources (MINFOF, 2014). We experimentally assessed the aggressiveness of disturbed *A. m. adansonii* at different times of day to determine whether they could be used to deter intruding elephants. In the first study of this kind in this area, we artificially disturbed and recorded the behavioural responses of *A. m. adansonii* during daytime and night-time periods to assess their potential efficacy for use in beehive fences to protect crops. We evaluated three indicators of honeybee efficacy in protecting crops from simulated elephant visits: (1) the activity level of colonies (measured as the frequency of bee movements at the hive entrance), (2) the level of aggressive behaviour of the colonies (measured as the mean distance from hives at which honeybees showed defensive behaviour), and (3) the bees' response in the form of a defensive flight when disturbed by an intruder.

Study area

We conducted our field experiments in Mabiogo (Fig. 1), one of 162 villages in the Campo–Ma'an conservation area in southern Cameroon, which includes Campo–Ma'an National Park (264,064 ha). Approximately 111,000 people of various socio-cultural backgrounds live in the conservation area, all of which rely on agriculture and forest products, including wild honey, for their livelihoods (Tiani et al., 2005; MINFOF, 2014). Staple food crops are grown during the two annual rainy seasons, and farmers experience interactions with wildlife from the Park, including an estimated population of 544 (range: 425–695) free-ranging forest elephants *Loxodonta cyclotis* (MINFOF, 2014). The Park is unfenced and beekeeping is unusual in the area. However, interactions between elephants and wild honeybee colonies are expected to occur in the forest. The mean annual precipitation is c. 2,500 mm, the mean annual temperature is 22–28 °C, and the area maintains high humidity throughout the year. Many rivers and swamps are present in the area and the vegetation consists of trees and herbaceous flowering plants (Tchouto, 2004).

Methods

Data collection

We collected data during 24 June–10 August 2019. In 2017, we had constructed a total of 22 Kenyan top bar hives (Supplementary Plate 1) following a previous conceptual model (King, 2014), and had distributed these to two farmers to start apiculture. We numbered the hives H_1–H_{22} and placed them at the edges of the farms. We set the distance between neighbouring hives at 10 m (King, 2014). Two years after we set up the hives, only six hives, colonized at different time periods, had active colonies (H_1, H_6, H_{12} and H_{14} from

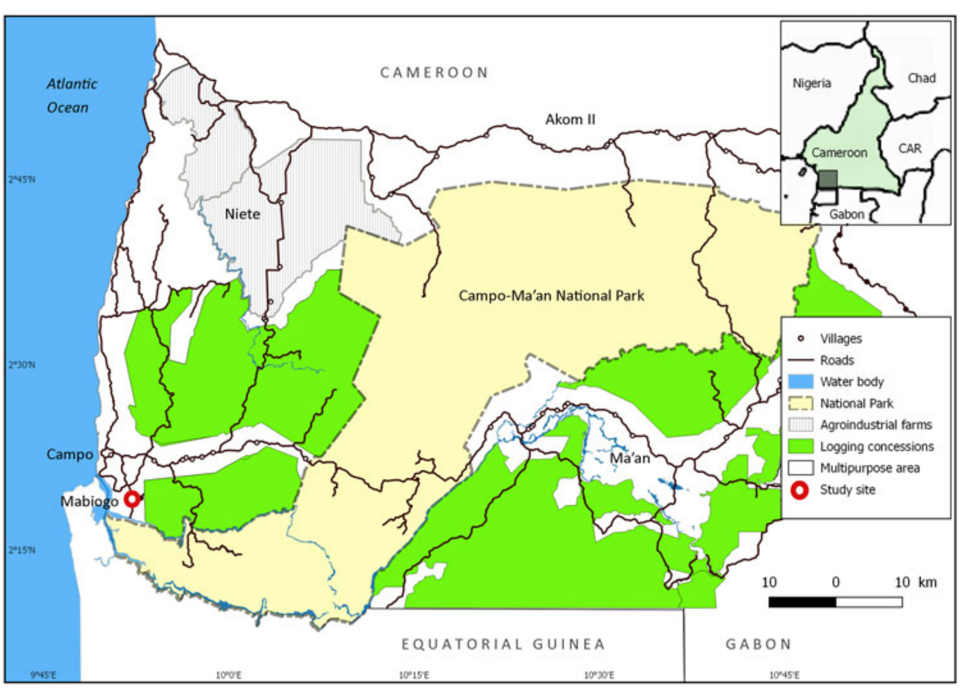

FIG. 1 Location of Mabiogo, the study site in the Campo–Ma'an conservation area, Cameroon.

one farmer H_8 and H_{17} from the other farmer) and we treated each colony as an experimental unit. For safety reasons we wore beekeeper suits, gloves and rubber boots when assessing bee activity (Nouvian et al., 2016). At each farm we collected data regarding both visual and physical disturbances at different times during the day (morning: 05.00–12.00, noon: 12.00–14.00, afternoon: 14.00–18.00) and at night (evening: 18.00–21.00, night: 21.00–00.00).

Activity level of the colonies

To assess whether the activity level of the colonies (a measure of defensive behaviour) would affect their ability to deter elephants, we recorded 5-minute videos of bees entering and leaving each beehive (Woyke, 1992; Ngama et al., 2016) using a high-resolution infrared camera (Sony HDR-SR12, Sony, Tokyo, Japan) that enabled us to record at night, for a total of six recordings per hive. We only included videos from which we were able to obtain counts of bees. We calculated the activity level using the following formula (Ngama et al., 2016):

$$\text{Number of bee movements/minute} = (\text{Number}_{leaving} + \text{Number}_{entering})/5$$

Defensive reaction of honeybees to an approaching observer

Hives are guarded by soldier bees who control the flow of bees in and out of the hive, ward off impending threats and alert the colony in the event of approaching threats (Breed et al., 2004; Nouvian et al., 2016). To assess the ability of *A. m. adansonii* to repel encroaching intruders (using vision or scent), we walked at a constant pace from random positions towards the hive entrance and stopped when an attack occurred. We measured the distance between the hive and the position of the observer to determine the defensive perimeter of the hives. We considered an attack to be the circular movement of bees around the person approaching the hive. Bee movements were passive (inoffensive) or active, potentially resulting in a bee sting (Lecomte, 1961; Nouvian et al., 2016).

Response of honeybees to a physical threat

Physical disturbance triggers the defensive behaviour of honeybees (Fletcher, 1978; Breed et al., 2004; King, 2010). When elephants walk through a beehive fence they cause multiple hives to swing, leading to the bees releasing an alert pheromone, flying out or targeting and repelling intruders (King et al., 2007; King, 2010). To assess the bees' defensive response to a simulated disturbance, we used a stick to mimic an elephant entering the farm and noted whether at least one bee flew out of the hive beyond a distance of 1 m. We coded the responses in a binary fashion according to whether bees flew > 1 m away from their hive or not (i.e. flying ≤ 1 m from their hive).

We waved the stick near the entrance of the hive for 1 minute, and then gently touched the guard bees sitting at the entrance of the hive, without introducing the stick into the hive. We noted the start time of each disturbance to account for the effects of weather parameters on the bees' activity (Lecomte, 1961; Breed et al., 2004). To control for the possible influence of temperature on bee activity, we measured the ambient temperature and that within the hives, the latter using a thermal probe placed inside the hive prior to the physical disturbance of the colony and removed after data collection (Burrill & Dietz, 1981). We used a mini weather station to record air humidity.

We performed two successive disturbances at every visit for each hive, separated by a 5-minute break. Each sequence of data collection at a hive lasted c. 13 minutes, therefore totalling c. 31 minutes per hive per visit. At the end of the second sequence we recorded the internal temperature of the hive before extracting the probe. During the disturbance, a field assistant recorded the time, air humidity and whether or not bees flew from the hive, whilst remaining at least 4 m away from the hive, which corresponds to the minimum distance between hives when constructing beehive fences (King, 2010). To allow the colonies to calm down during the 5-minute break, we moved 10 m away from the hives. When bees from the disturbed colony remained agitated beyond the 5-minute break, we chased them away using a smoker before initiating the next sequence of data collection. We took precautions to avoid modifying the behaviour of the colonies with smoke (Woyke, 1992).

Data analysis

We used repeated ANOVAs to assess the differences in activity level between colonies and between times of day, followed by a Tukey honestly significant difference test for post hoc analysis to compare colonies. In the analysis of the defensive perimeter before the physical disturbance we considered all values equal to 0 m to be the dormant state of the hives and omitted them from the analysis to avoid minimizing the mean defensive zone of the colonies, which could be misinterpreted by farmers. To assess the temporal variation of the defensive perimeter, we used the linear mixed-effect function of the *lme4* package in *R 3.6.3* (Bates et al., 2015; R Core Team, 2020) fitted by restricted maximum likelihood. We considered the response variable to be the distance at which the defensive reaction was observed, and included the day (i.e. date) of the observation as a random term because we took repeated measures on the same day. For the explanatory variables we used the time of day (categorical variable with five values: morning, noon, afternoon, evening and night), the colonies (categorical variable with six values, representing the individual hives) and the order of the test (first or second approach). When we found a significant effect of time of day or colony, we performed a Tukey honestly significant difference test to compare the mean distance at which defensive behaviour was observed between different times of day and between colonies.

We used χ^2 tests to assess the dependency between disturbances and the occurrence of honeybees flying > 1 m away from the hive. We used the *lme4* package in *R* (Bates et al., 2015) fitted by maximum likelihood (Laplace approximation) with a binomial distribution and a logit link to assess the effects of the colony, temperature in the hives (a continuous variable) and time of day on whether or not bees flew > 1 m away from the hive. We used likelihood ratio tests to assess the significance of the effects of time of day and colony. We included the day (date) as a random term because we took repeated measures on the same day, and considered colony, time of day and temperature inside the hive to be fixed variables in the model. We used Tukey honestly significant difference tests when we observed differences between different times of day or between colonies. We performed statistical analyses with the significance level set at 0.05.

Results

Activity level of the colonies

The activity of bees prior to physical disturbance differed significantly between diurnal and nocturnal periods ($F_{(1,154)} = 565$, $P < 0.001$) and between colonies ($F_{(5,72)} = 7.45$, $P < 0.001$). Colonies were active during the day with a mean of 49 bee movements per minute (range: 35.69 ± SD 11–69.55 ± SD 16.53) and were inactive during the night. Colony H_{14} was significantly more active than colonies H_1, H_8, H_{12} and H_{17} (Tukey honestly significant difference test at 95% CI, all adjusted $P < 0.05$), and colony H_6 was significantly more active than colony H_{17} (Tukey honestly significant difference test at 95% CI, adjusted $P = 0.043$). All other pairs were not significantly different in terms of bee activity (Tukey honestly significant difference test at 95% CI, all adjusted $P > 0.05$; Fig. 2).

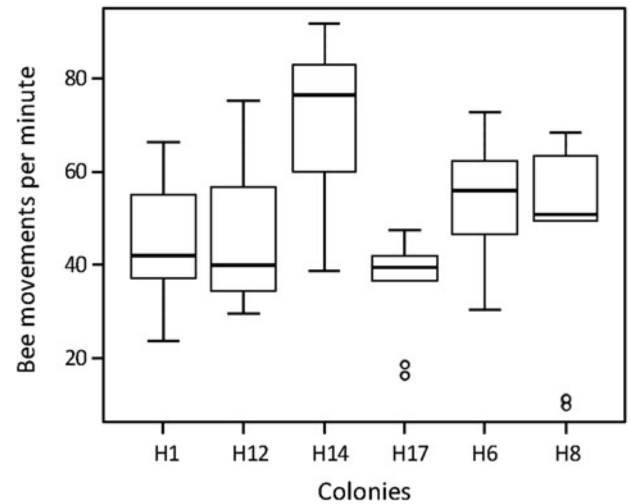

Fig. 2 Distribution of the number of African honeybee *Apis mellifera adansonii* movements per minute (entering and exiting) at the entrance of each hive during daytime periods. The horizontal lines within the boxes represent the median, and the boxes the interquartile range (between the 25 and 75 percentiles). The upper and lower whiskers represent the maximum and minimum values, respectively, that are within 1.5 times the interquartile range. The circles denote outliers.

Defensive reaction of honeybees to an approaching observer

We performed 276 approaches, of which 20% yielded a defensive response and 80% did not. Of the 134 nocturnal approaches (48.5% of all approaches), 95% yielded no reaction, and we recorded a defensive response rate of 5% in the evening. Of the 142 diurnal approaches (51.5% of all approaches), 65.5% yielded no reaction and 34.5% yielded a reaction. The mean defensive perimeter across different times of day and colonies was 4.05 ± SD 2.5 m. The distance from which bees responded to an approaching observer differed significantly between times of day ($F_{(4,25)} = 4.716$, $P = 0.006$; Table 1), with a larger defensive perimeter in the evening than at other times (Table 1). The mean defensive perimeter also differed significantly between colonies ($F_{(5,25)} = 8.692$, $P < 0.001$; Table 1), with colony H_1 having the largest defensive perimeter (7.0 ± SD 2.8 m). There was no difference in defensive perimeter ($F_{(1,54)} = 1.55$, $P = 0.219$) between the first (mean 3.58 ± SD 2.58 m) and second approach (4.40 ± SD 2.34 m).

Response of honeybees to a physical threat

Of the 276 disturbances, 51% (n = 142) were diurnal, and 49% (n = 134) were nocturnal. The majority (63.4%, n = 175) of the disturbances resulted in a defensive flight of honeybees ($\chi^2 = 19.841$, df = 1, $P < 0.001$), with 67% (n = 117) occurring during the day and 33% (n = 58) at night. When assessing whether bees responded to a threat, we found a significant difference between times of day ($\chi^2 = 20.2$, df = 1, $P < 0.001$; Fig. 3a) and colonies ($\chi^2 = 120$, df = 1, $P < 0.001$; Fig. 3b). The results from our mixed model showed that on average, compared to at night, bees flew more during the morning (3.842 ± SE 0.872, $P < 0.001$), noon (4.732 ± SE 1.039, $P < 0.001$) and afternoon (4.279 ± SE 1.053, $P < 0.001$). Response to a threat did not differ between morning, noon and afternoon (all pairwise comparisons $P > 0.05$). Similarly, compared to colony H_1, bees from colonies H_{17} (−4.897 ± SE 0.930, $P < 0.001$) and colony H_8 (−2.708 ± SE 0.783, $P = 0.005$) responded less

TABLE 1 Mean defensive perimeters (m) of African honeybee *Apis mellifera adansonii* colonies at different times of day in response to an approaching observer, and corresponding Tukey honestly significant difference (HSD) tests. All tests performed at P = 0.05, and a, b, c and d refer to the result of the test between colonies: hives with the same letters were not significantly different from each other.

	Diurnal periods			Nocturnal periods			
Colony	05.00–12.00	12.00–14.00	14.00–18.00	18.00–21.00	21.00–00.00	Mean ± SD	Tukey HSD test
H_1	7.00	9.50	4.00	6.60	0.00	7.00 ± 2.80	a
H_6	4.86	2.67	4.80	0.00	1.00	4.19 ± 1.87	b
H_8	1.00	0.00	0.00	5.00	0.00	3.00 ± 2.83	b,c
H_{12}	2.50	1.50	3.00	0.00	0.00	1.89 ± 1.40	c,d
H_{14}	5.00	3.36	3.50	0.00	0.00	3.60 ± 1.12	b,d
H_{17}	0.00	1.00	2.50	0.00	0.00	2.00 ± 1.73	b,c
Mean ± SD	4.73 ± 2.22	3.22 ± 2.45	3.91 ± 1.58	6.33 ± 2.94	1.00	4.05 ± 2.50	

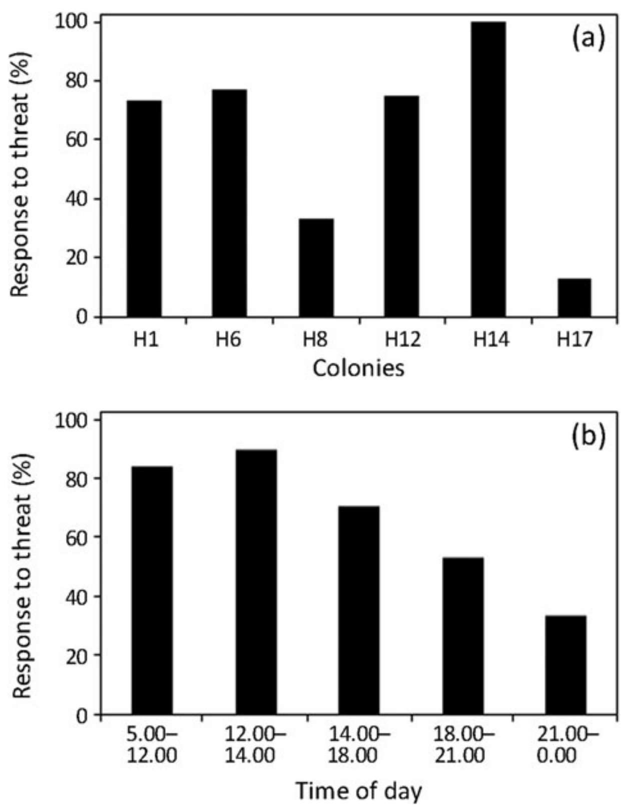

FIG. 3 Per cent response (defined as flying > 1 m away from the hive) of African honeybees to physical disturbances (a) for different colonies and (b) for different times of day.

frequently with a defensive flight when threatened. Bees from colony H_{12} showed a defensive flight more often than those from colonies H_{17} (5.547 ± SE 1.115, $P < 0.001$) and H_8 (3.359 ± SE 1.069, $P = 0.015$), and bees from colony H_6 responded more than those from colonies H_8 (2.642 ± SE 0.787, $P = 0.007$) and H_{17} (4.830 ± SE 0.956, $P < 0.001$). All other pairwise comparisons were non-significant (all $P > 0.05$).

Discussion

We found that honeybee colonies differed in their activity level and defensive behaviour when disturbed. In addition, honeybee colonies were only active during the day and their defensive perimeters were greater in the morning and evening when the bees appeared to be more sensitive to disturbance. These findings suggest that beehive fences may be less effective at deterring intruders at night.

Activity level of the colonies

We assessed the activity level of *A. m. adansonii* as an indicator of aggressive behaviour and found that the activity levels of most colonies were above the requirements for use as beehive fences. Four colonies exhibited daytime activity of 40–60 bee movements per minute, levels that have been found to be effective for deterring forest elephants in Gabon (Ngama et al., 2016). However, activity levels of two colonies were below the required range for an effective deterrent. This suggests that when setting up beehive fences, colonies should be selected for inclusion based on their activity levels (Ngama et al., 2016).

At night all colonies were clustered at the entrances of their hives and visibly inactive because of decreasing temperature (Burrill & Dietz, 1981) and increasing humidity (Supplementary Fig. 1). We observed no bees flying prior to us disturbing the colonies at night. This corroborates findings from a study in Thailand using *A. m. scutellata* and *A. cerana* (Dror et al., 2020). However, it contradicts observations of *A. m. adansonii* foraging at dusk, under low light intensity. Had the bees been more active at night, it would have increased their potential use in beehive fences, as most elephant intrusions into agricultural areas occur at night (King, 2010; Ngama et al., 2016).

Defensive reaction of honeybees to an approaching intruder

In response to an approaching intruder, bees were mostly inactive, except in the morning and twilight periods when they were more likely to fly and attack intruders. Similar patterns of aggressive behaviour in *A. mellifera* have been reported previously (Lecomte, 1961; Woyke, 1992). This finding is not surprising because most foraging bees exit the hive in the morning and return in the evening (King, 2010). Hives are guarded by mature foragers who are more experienced and produce more pheromones than younger individuals (Nouvian et al., 2016). We argue that beehive fences would be more effective during the morning and dusk than during other times of day because mature foragers help defend the hives during these periods. These two periods have also been reported as the times when elephants frequently enter or leave plantations (King, 2009; Gunn et al., 2013; Ngama et al., 2016). Active colonies could thus potentially repel elephants approaching during the evening because, if disturbed, the bees would probably fly out and attack the elephants (it is not completely dark until 19.00 in this area).

Response of honeybees to a physical threat

Our results showed that disturbed bees were more likely to fly out from the hive and repel intruders during the day than at night. All colonies reacted vigorously to physical disturbance during the daytime, with bees flying in all directions to identify and sting the intruder. Similar responses of bees to physical threats during the daytime and at twilight have been reported previously (Woyke, 1992; Ngama et al., 2016; King et al., 2017). However, their decreased level of defensive behaviour after dusk reduces their effectiveness in repelling animals with a high cognitive capacity such as elephants (Dror et al., 2020). At night, physical disturbances resulted in bees falling to the ground because they were unable to fly; they had to walk towards the support of the hive to climb up and return to it. The bees buzzed loudly in response to such night-time disturbances, except during periods of bright moonlight, when no buzzing occurred. Although forest elephants in Gabon avoided colonies with high levels of activity (Ngama et al., 2016), our results suggest that the inactivity of bees at night could be noticed and exploited by forest elephants through breaches in the fences at night, particularly if the elephants are exposed repeatedly to such bee behaviour (Dror et al., 2020).

Towards the end of the study we noted that bees from the smallest colonies (H_8, H_{12} and H_{17}) flew inside their hives when disturbed rather than away from the hive and towards the source of disturbance, even during the daytime. This was unexpected as bees are usually aggressive during the daytime. We argue that repeated disturbances could reduce the aggressiveness of colonies, especially the smallest ones, because of the loss of mature guards, leaving the hives inadequately protected by less experienced guards (Nouvian et al., 2016). In contrast, larger colonies such as H_1, H_6 and H_{14} (Supplementary Plate 2b) were more reactive and never inactive during the day. Colony size thus affects the bees' response to a threat, although hives can become less reactive especially when the queen bee is not in the hive (Lecomte, 1961; Woyke, 1992; Supplementary Plate 2a).

In summary, our findings highlight the need to combine other mitigation methods with beehive fences to improve their effectiveness (Nelson et al., 2003; King, 2010). Although we observed low levels of defensive flights around noon and at night, bees may still be able to deter elephants at these times as buzzing and pheromones could be part of their defensive mechanism and may have a deterrent effect on elephants. More research into these aspects of bee behaviour is required to improve our understanding of the efficacy of beehive fences.

The predictive capacity of our study is limited because our experimental design did not involve beehives being disturbed by actual elephants. Nevertheless, it provides valuable insights into the potential effectiveness and limitations of beehive fences to deter forest elephants and reduce crop losses that affect people living near protected areas. Our findings on the threat response of *A. m. adansonii* thus have the potential to facilitate informed decision-making regarding the use of beehive fences to address crop damage by elephants.

Acknowledgements We thank the Zoo de Granby, MITACS Accelerate, Quebec Centre for Biodiversity Sciences and Concordia University for financial support; Valerie Michel of Zoo de Granby for helping with data collection and data entry; Alexander Boucher and Alys Granados for editing the manuscript; and the Ministry of Forestry and Wildlife of Cameroon, particularly Benjamin Sock, former Conservator of the Campo–Ma'an National Park, for enabling the work to take place.

Author contributions Conception and design: IBD, RBW; data collection: IBD; data analysis: IBD, RBW; writing: IBD; revision: all authors.

Conflicts of interest None.

Ethical standards Data collection and safe handling of animals were conducted in accordance with the Animal Research Ethics certificate provided by Concordia University (Protocol number 30003983). The research protocol was reviewed and approved by the Ministry of Forestry and Wildlife of Cameroon prior to carrying out the experiment. The research otherwise abided by the *Oryx* guidelines on ethical standards.

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