The sensory ecology of fear: African elephants show aversion to olfactory predator signals

Kim Valenta1 | Melissa H. Schmitt2,3 | Manfred Ayasse4 | Omer Nevo4,5,6

1Department of Anthropology, University of Florida, Gainesville, Florida
2Department of Ecology Evolution and Marine Biology, University of California Santa Barbara, Santa Barbara, California
3South African Environmental Observation Network, Ndlovu Node, Phalaborwa, South Africa
4Ulm University, Institute of Evolutionary Ecology and Conservation Genomics, Ulm, Germany
5German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany
6Friedrich Schiller University Jena, Institute of Biodiversity, Jena, Germany

Correspondence
Omer Nevo, Ulm University, Institute of Evolutionary Ecology and Conservation Genomics, Ulm, Germany; German Center for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany; Friedrich Schiller University Jena, Institute of Biodiversity, Jena, Germany. omer.nevo@evolutionary-ecology.de

Funding information
National Research Foundation of South Africa, Grant/Award Number: 120670; Deutsche Forschungsgemeinschaft, Grant/Award Number: NE2156/1-1; University of Florida

Abstract
Human–elephant conflict is a persistent problem across elephant home ranges, that results in economic damage to commercial and subsistence farmers, and physical harm and death to humans and elephants. This problem is likely to intensify with increased development, dwindling of natural habitats, and climate change-driven environmental shifts. Various methods to mitigate human–elephant conflict have been employed, but to date these have been hampered by financial and logistical considerations. Based on the fact that African elephants are predated by lions and possess a remarkable sense of smell, we hypothesize that elephants are strongly averse to olfactory signals of lion presence, and that this can be utilized to create invisible barriers which elephants will not cross. We conducted a series of tests that show that lion dung is an effective deterrent of elephants. We conducted chemical analyses of lion dung and identified the main compounds. We then used synthetic mixtures containing these compounds, and show that they successfully elicit the deterrence effect, even in miniscule concentrations. These results indicate that elephants can be deterred using simple and low-concentration mixtures based on available commercial products, that can be developed into products that offer a safe, sustainable, and cost-effective method to mitigate human–elephant conflict.

KEYWORDS
applied conservation, biological fencing, chemical ecology, elephant deterrence, human–elephant conflict, predator avoidance

INTRODUCTION

Human–elephant conflict occurs everywhere these taxa co-exist, and is a significant problem for both (Sitati, Walpole, Smith, & Leader-Williams, 2003). While difficult to quantify globally, regional analyses have documented that elephants are responsible for an average of 30% of large-mammal caused human injury and fatalities (Acharya, Paudel, Neupane, & Köhl, 2016), with fatalities often followed by retaliatory elephant killings (Riddle,
Schulte, Desai, & van der Meer, 2010). Additional to direct mortality, elephants cause massive damage to human livelihoods and food security, primarily via crop raiding and trampling (Naughton-Treves, 1998). While crop raiding occurs frequently in commercial plantations, subsistence agriculturalists are also affected, with devastating outcomes for financially vulnerable, food-insecure subsistence agriculturalists (Mackenzie & Ahabyona, 2012). In subsistence agricultural regions surrounding protected areas, communities frequently cite elephants as a critical factor in their lack of support for conservation, and non-compliance with conservation efforts (Woodroffe, Thirgood, & Rabinowitz, 2005).

Several schemes have been deployed throughout Africa and Asia to mitigate human–elephant conflict, through creative and diverse means. Beehive fences and the playing of bee sounds have shown some success in deterring elephants from crops (King, Lawrence, Douglas-Hamilton, & Vollrath, 2009), fencing and trenching have been useful in some contexts (Hoare, 2012), and scare shooting, or other loud noises during crop raiding events can also be locally effective (Taylor, 1999). Unfortunately, the vast majority of deterrent methods are expensive to implement, particularly for small-hold farmers, and require intensive maintenance (Sarkar, Chapman, Kagoro, & Sengupta, 2016). Most importantly, they frequently lose effectiveness over time as elephants habituate to them (Enukwa, 2017).

Given that elephants are olfactorily-oriented animals (Nevo, Schmitt, Ayasse, & Valenta, 2020), with the highest number of intact olfactory receptor genes of any known animal (Nimura & Nei, 2007), the key to elephant deterrence probably lies in the nose. Multiple elephant-deterrent endeavors have focused on deterrent odors, from motor oil to chili peppers to bee pheromones (Wright et al., 2018). Most olfactory schemes have focused on compounds that are present as naturally occurring deterrent secondary compounds in foods that are unpalatable to elephants—particularly capsaicinoids, the compound class that results in the human perception of the “hotness” of chillis (Lawless, Rozin, & Shenker, 1985). However, while olfactory signals of unpalatable secondary compounds in plants may deter elephants from actively consuming items broadcasting that signal (McArthur, Finnerty, Schmitt, Shuttleworth, & Shrader, 2019; Schmitt, Shuttleworth, Shrader, & Ward, 2020), the ubiquity of olfactory plant deterrents in an elephant’s landscape are unlikely to result in deterrence from a particular area: elephants may not eat something that smells like a chili, but will probably not avoid an area, or consuming adjacent plants, simply because chillis are present. While a great deal of research has focused on plant-based olfactory deterrence of elephants (Ernest & Robertson, 2019; Hedges & Gunaryadi, 2010; Schmitt, Shuttleworth, Ward, & Shrader, 2018), there has been a dearth of research on predator-based odors. This is despite the fact that fear of predation is a universal and ancient mammalian motivator (Parsons et al., 2018), and scent strongly modulates memory and emotion (Takahashi, 2014). Moreover, fear of predators and their cues is continuously reinforced wherever predators are present.

Predators can impact prey both directly via a predation event that ultimately removes the prey individual from the environment, as well as indirectly (Creel & Christianson, 2008; Lima, 1998). The indirect or non-lethal effects of predation can have a large impact on the behaviors and habitat use of prey species (Creel & Christianson, 2008; Lima, 1998). Many studies have found that the non-lethal effects of predation are long-lasting and have far-reaching consequences for the behavior, habitat use, and demography of prey species (Brown, 1988; Creel & Christianson, 2008; Lima, 1998). For example, many prey species will avoid areas where they perceive the risk of predation to be high (Brown, 1988), even when there is a larger food opportunity available in riskier areas compared to less risky areas, thus demonstrating that the fear of predation can override the temptation of food (Stears & Shrader, 2015). In the case of African and Asian elephants, despite their size, both species are at risk of predation by wild apex predators in their systems: lions (Panthera leo) in Africa, and tigers (Panthera tigris) in Asia. Although it is site- and season-specific, African elephants can make up a significant portion of lion diets (Creel et al., 2018; Davidson, Valeix, Kesteren, Loveridge, & Hunt, 2013; Loveridge, Hunt, Murindagomo, & Macdonald, 2006; Power & Shem Compion, 2009; Wittemeyer, Daballen, Rasmussen, Kahindi, & Douglas-Hamilton, 2005). In fact, in some areas—such as Botswana—lion prides specialize in hunting elephants, with the majority of hunting success occurring when lions focused on elephants aged between 4 and 15 years old (Joubert, 2006; Power & Compion, 2009). Adult elephants are still often targeted by lions, though the attacks are not as successful as those on younger individuals (Joubert, 2006). In other parts of Africa, though the rate that lions successfully hunt elephants is lower than it is in Botswana, there is still a chance that elephants could be attacked by lions. Thus, while the removal of individual elephants from the system due to predation is unlikely to dramatically alter elephant population sizes, the long-lasting indirect effects (i.e., the fear of being attacked) of lions will likely have dramatic impacts to elephant behavior, regardless of age.
Thus it is not surprising that both African and Asian ele-
phants respond to environmental cues that suggest lions
or tigers are present; previous research has found that
both African and Asian elephants exhibit aversive behav-
ioral responses to playbacks of predator sounds
(McComb et al., 2011; Thuppi & Coss, 2013). Some pred-
ator scents cause animals to substantially modify their
range use and activity patterns (Parsons et al., 2018), and
in some cases prey animals become more responsive to
predator signals over time (Cox, Murray, Hall, & Li, 2012).
Given elephant reliance on olfaction (Miller et al., 2015; Plotnik et al., 2019; Plotnik, Shaw, Brubaker,
Tiller, & Clayton, 2014; von Dürckheim et al., 2018), and
the importance of predator avoidance, it is possible that
predator odors can be used as effective elephant
deterrents.

Here, we report an experiment in applied evolution-
ary ecology that utilizes elephant predator avoidance
instincts to mitigate human–elephant conflict. We
hypothesize that given the superior elephant sense of
smell, elephants perceive predation risk from scents asso-
ciated with their main predators, and that this can be
applied to create “molecular barriers” which elephants
will not cross. We tested whether African elephants
(Loxodonta africana) show aversion to predator-related
odors (carcasses, cheetah feces, dog feces, African lion
feces), odorless controls (water), and control stimuli (her-
bivore feces), and confirmed elephant aversion to lion
fecal odor. We then conducted chemical analyses of lion
fecal material and identified its main constituents.
Finally, we show that application of a mixture of two of
the main chemical compounds in lion feces reproduces
the aversion effect. This approach may yield a safe and
cost-effective method to mitigate human–elephant
conflict.

2 | METHODS

2.1 | Chemical analysis

Because we hypothesized that elephants show aversion to
predator-related odors, we first completed odorant sam-
pling and analysis of fresh lion feces to qualify their odor-
ant compounds. We collected four fresh (within 24 hr)
fecal samples from a mated pair of lions fed raw meat at
the Carson Springs Wildlife Conservation Foundation,
Gainesville, Florida, USA, in November, 2019. We pooled
feces together, placed ~0.5 kg of feces in inert sampling
bags (Reynolds), and left them to incubate for 20 min.
Air within each bag was then pulled through self-
produced odorant traps at a rate of 0.3 L/min for 10 min,
until complete bag deflation, using a lab pump (GilAir
Plus, Sensidyne). Odorant traps were made of 3 cm qua-
artz tubes with three adsorbent media (Tenax TA 60–80
mesh; Carbrop B 20–40 mesh; Carbosieve S-III 60–80
mesh, Sigma; 1.5 mg each), trapped between layers of
glass wool. We collected eight replicas of the ~0.5 kg
cecal samples to ensure identification of all components,
and five blank control samples.

We analyzed samples on an Agilent 7890B gas chro-
matograph with an Agilent DB-Wax polar capillary col-
umn (30 m, 0.25 mm diameter), using thermal desorption and a cold injection system, and an Agilent
5977A mass spectrometer in EI mode. Samples were
introduced to the thermal desorption unit (TDU) at split
mode (95:5) at 30°C. After 1 min, the TDU began heating
at 100°C/min until it reached 310°C, where it was held
for 8 min. The liner was kept at ~100°C. Following
desorption, the liner heated up at 12°C/s until 250°C,
and held for 8 min. Initial oven temperature was 30°C.
After 1 min, the oven began heating at 10°C/min until it
reached 240°C, and held for 30 min. MSD transfer line
was set to 250°C, MS source to 230°C, and MS quad
to 150°C.

Samples were analyzed using Amdis 2.71. Compo-
nents were identified based on their retention indices
(using a ladder of n-alkane standards) and mass spectra
using NIST11. We identified likely contaminants by com-
paring the runs to blank control samples that were taken
in identical conditions but using an empty sampling bag.
We also excluded known contaminants like siloxanes.

2.2 | Behavioral trials

To understand how African elephants perceive odors in
their system, and determine whether these odors act as
deterrents, we conducted behavioral experiments in
March 2019 and January 2020 at the Adventures with
Elephants facility, Limpopo Province, South Africa. Ini-
tially, we used five semi-tame, adult elephants ranging
between 15 and 20 years old (three females, two males).
Semi-tame African elephants are extremely uncommon
and, given the nature of our experiment, this is an excep-
tionally high sample size for such a study. After a trial
with lion odors, one individual male chose to no longer
participate, thus our full experiment included four indi-
viduals. The herd of elephants currently live in a 500 ha
game reserve that has leopards (Panthera pardus) and
spotted hyena (Crocuta crocuta), but no lions or cheetah
(Acinonyx jubatus), however, the elephants previously
lived in an area that included a wide range of large preda-
tors (African lion, cheetah, spotted and brown hyena
[Hyaena brunnea]) for ~10 years. Thus, although there is
no current predation risk to the elephants from lions, the
elephants are familiar with the threats and odors associated with these different predators. All research was approved by the Duke Institutional Animal Care and Use Committee (IACUC #A248-18-10), and adhered to the laws of South Africa where the behavioral trials took place.

We conducted two experiments. The first experiment was conducted to determine whether predator-related odors acted as deterrents relative to controls. Predator related odors included (a) indirect predator cues (rotting impala meat); (b) predator dung of animals not known to prey on elephants (domestic dog, cheetah); and (c) African lion (Leon panthera) feces. We additionally tested several controls: (a) odorless control (water), and (b) herbivore dung (giraffe, wildebeest), to examine the possibility that elephants dislike feces of any source. Feces and carcasses were collected in the field.

The second experiment was conducted to test if the effect of lion dung can be replicated using mixtures of the main chemical compounds found in lion feces. We tried three combinations: (a) indole; (b) phenol; (c) phenol and indole, all at 1 ppm (molar). These two chemicals were identified in our and previous studies as major lion dung volatiles, and important constituents of other obligate carnivore feces (Frank, Brückner, Blüthgen, & Schmitt, 2018; Mansourian et al., 2016).

The sampling for the two experiments was split between 2019 and 2020. For both experiments and sampling periods, to present the odors to the elephants, we soaked 2 mm cotton twine in each of the 10 odorants. For the 5 mammal species-related odorants for behavioral trials, we collected fresh dung from each species from surrounding farms. We added ~200 mL water to each dung sample to make it slightly runny and soaked the cotton twine in the dung mixture. For synthetic mixtures, we mixed 1 ppm solutions of phenol and indole in water. To absorb the odor of rotting meat (carcass), we soaked the cotton twine in the liquid from the carcass of a recently-killed impala. In 2019, we presented the elephants with the odors on the cotton twine (treatments: string control, wildebeest dung, lion dung, and carcass odors), which was suspended just above the ground (<3 cm) across a 3.5 m wide dirt road path between two hedges. However, for the 2020 trials (treatments: control string, giraffe, dung, indole and phenol, phenol, indole, and cheetah), we threaded the twine through a 4 m long 25 mm diameter PVC pipe to limit the elephant’s ability to handle the cotton twine saturated with the odorants. Each pipe had ~300, 1.5 cm holes drilled into them to allow odors to pass through. The pipe was laid across the same 3.5 m wide dirt road flanked by hedges, limiting the ability of the elephants to bypass the pipe by walking around it (Figure S1). For each trial, each elephant was instructed by a handler to walk down the road while the herd foraged ~100 m away. We measured how long it took for each elephant to walk from 5 m away from the string or pipe until they stepped over the string or pipe with both front feet. Additionally, if elephants tried to divert their route or refused to step over the string or pipe with verbal commands alone, we offered oranges—a reward highly favored by the elephants. A single orange was tossed ~5 m on the opposite side of the string or pipe—just outside the reach of an African elephant’s trunk. Oranges were offered when an elephant would refuse to continue or would begin to turn away to avoid the area, or retreat. We increased the number of oranges incrementally (either when an elephant showed signs of retreating or every ~10 s) until elephants were willing to cross the string or pipe, or until the trial ended. Each trial took ~60 s on average, however the maximum time was ~180 s and the minimum was <30 s if the elephants were unphased by the odorant provided. Importantly, the herd of semi-tame elephants are very well-trained and respond to handler instructions closely, and they have been trained to respond to over 80 verbal commands. Thus, any hesitation in crossing through the odor wall after instruction suggests a clear deterrent response. Moreover, we quantified the number of verbal commands given to the elephants for all treatments. The order in which we presented the odors was random, but consistent across all individuals (see Table S1 for the order of treatments). Due to technical limitations in the field with respect to allowing any potential residual odors to clear the area between trials, we could not make the order in which we presented treatments random between individuals.

## 2.3 Statistical analysis

The results of the two experiments were combined for analysis. First, however, we examined whether there was any significant difference in the amount of time it took the elephants to cross the control twine presented alone versus the control string presented inside the pipe as well as the number of commands given to complete these actions. We found no significant differences in the amount of time (GEE: $\chi^2 = 0.683, p = .408$) nor with the number of commands required (GEE: $\chi^2 = 1.660, p = .198$) or between the two types of control treatments. Thus, we assume that the presentation of the odorants in 2019 and 2020 did not influence the elephants’ responses. To determine whether the time it took for the elephants to walk 5 m and step over odor walls with two front feet was significantly different, we used Generalized Estimating Equations (GEEs) using the geepack package in R.
(Halekoh, Højsgaard, & Yan, 2006). GEEs account for potential non-independence of our data (i.e., the same individuals were repeatedly used in the experiments), which could stem from an individual possibly remembering previous trials. GEEs use a population-level approach based on a quasilikelihood function and deliver population-averaged estimates of the parameters. The coefficients of GEE regressions are marginal effects (Wang, 2014), and model the average time it took to walk 5 m and step over the odor wall with both front feet. The model incorporated an exchangeable correlation matrix and gamma distribution with a log link function. We used an exchangeable correlation matrix and elephant ID as the unit of repeated measurements. Upon finding that two elephants could not be enticed to step over the lion odor string (Experiment 1) no matter the number of oranges presented to them (see Section 3), we coded their time-to-cross as 180 s, which was the maximum trial duration. Similarly, we used a GEE to determine whether the average number of commands given to each elephant for each treatment significantly varied. The model used an exchangeable correlation matrix and Poisson distribution with a log link function. We used elephant ID as the unit of repeated measurements.

3 | RESULTS

We identified 15 compounds that were present exclusively or significantly more in lion feces compared to controls (Figure 1 and Table S2). Of these, we focused behavioral trials on two compounds in particular, phenol and indole, because these matched compounds detected in previous studies of predator fecal odorants, and are not central to non-predator fecal compounds (Mansourian et al., 2016).

Behavioral experiments showed that elephants responded significantly differently to the various odor treatments (GEE: \( \chi^2 = 130.567, p < .001 \)). Treatment effects fell into three distinct categories (Figure 2): (a) not significantly different from the water control trial, (b) intermediate hesitation (i.e., higher than the control but lower than lion feces), and (c) responses similar to those elicited by the feces of African elephant’s main predator—the lion. On average, it took (mean ± SD) 10.5 ± 5.7 s for elephants to walk 5 m and step over the odors of: (a) carcass, (b) giraffe, and (c) wildebeest, suggesting that the odors of both herbivores and odors related to death (carrion) have no significant effects in deterring elephants. It took an average of 22.45 ± 11.48 s for elephants to walk and step over (d) indole, and (e) dog feces. Finally, it took an average of 45.51 ± 49.64 s for elephants to step over the (f) cheetah feces, (g) phenol, (h) indole and phenol combined, and (i) lion feces. While these high risk odors all elicit similar responses from the elephants, the odor of lion dung had by far the most significant effect, which cannot be assessed via a statistical model: three elephants refused to step over the pipe, no matter how many oranges were offered, and one of these elephants chose not to participate in further trials after a single exposure to lion dung during trials. Moreover, no other trials required all of the elephants to be offered oranges (lion odor: two elephants required one orange, and two elephants were offered 50 oranges but would not cross, carcass odor: one elephant required one orange, cheetah odor: one elephant required one orange). The odor treatment that resulted in the second-longest delay (i.e., aversion) was the combination of 1 ppm indole and 1 ppm phenol, which took elephants an average of 52.46 ± 9.49 s to walk 5 m and step over, and numerous verbal commands from handlers.

We also found that the number of commands...
significantly varied across treatments (GEE: $\chi^2 = 951.468$, $p < .001$, Figure S2), with the felid predator odor treatments (i.e., cheetah, phenol, indole and phenol, and lion) requiring significantly more commands than the other treatments.

4 | DISCUSSION

Our results show that African elephants show strong aversion to the scent of lion feces—their main predator. We do, however, also find a significant aversion towards cheetah feces as well, which is likely due to the fact that the odor signature from cheetah feces likely carries similar odor signatures to lion dung, given that they are both felids. The elephants’ aversion is highly specific—they are not deterred by fecal materials of herbivores, indirect predator scents (carcass), or non-felid carnivores (dog). Further, our results show that the deterrent effect can be replicated using a combination of two major components of lion dung scent—phenol and indole, used in miniscule concentrations. The fact that both are water soluble in these concentrations, commercially available, inexpensive, and effective even in extremely low concentrations (1 ppm), means that their application can be implemented safely and cheaply.

Lion dung had a stronger deterrent effect on elephants in our study than phenol and indole, though this may result from the use of very low concentrations of these compounds (1 ppm). Additionally, the difference in response to lion dung and phenol and indole was statistically non-significant, indicating that the deterring effect may be triggered by miniscule amounts. This would allow minimizing potential negative effects of widespread application of these chemicals during elephant encounters. Further, we used an equal concentration of the chemicals, whereas our chemical analyses indicate that phenol is more common in lion dung headspace by a ratio of $\approx 3:1$. Synthesizing phenol: indole ratios more accurately may elicit a stronger response. In addition, we chose to exclude one compound (dimethyl disulfide) due to its strong and foul smell, which would render the mixture less useful for widespread application, though future studies may test whether its addition increases behavioral aversion.

The presence of bees, bee sounds, and bee pheromones have been shown to successfully deter elephants from crop raiding or incursion into a given area (King, Douglas-Hamilton, & Vollrath, 2007; King, Lala, Nzumu, Mwambingu, & Douglas-Hamilton, 2017; Wright et al., 2018). While elephants have thick skins, it is hypothesized that their aversion to bees results from aversion to bee stings, particularly in the delicate tissues inside of their noses (Vollrath & Douglas-Hamilton, 2002). While proximity to bees may result in pain to elephants, proximity to predators may result in
Our approach harnesses the long-lasting, indirect (non-lethal) effects of predators, which can shape prey behavior and habitat use, even in the absence of the predator themselves (Brown, 1988; Lima, 1998). African elephants are only at risk of predation from lions, and in some areas, elephants can contribute to a significant portion of lion diets (Creel et al., 2018; Davidson et al., 2013; Loveridge et al., 2006; Power & Compion, 2009; Wittemyer et al., 2005). While lions are unlikely to remove enough elephants from the population via predation events to impact their population sizes and demography, the fear of being attacked by lions will likely have dramatic impacts on elephant behavior, regardless of age. Our results support this notion, whereby we find that African elephants show a strong aversion to the odor of felid predators (i.e., lion and cheetah feces), even when they have not directly interacted with these two predators in over decade. Moreover, our results also suggest that elephants respond to predation risk (i.e., the landscape of fear), which is the psychological topography of the landscape in the mind of prey that is characterized by areas that are considered to be safe while other areas are considered to be risky due to differences in perceived predation risk (Laundré, Hernández, & Altendorf, 2001; Laundré, Hernández, & Ripple, 2010). Much like many other prey species, the elephants in our study weighed up the potential food reward offered to them in an area that had lion odor (signaling danger), which the elephants ultimately considered to be a risky area, and altered their behavior to reflect the trade-off between food and fear. It is likely that in wild situations, elephants would avoid areas where they detect lions, regardless of food availability (thus living in a landscape of fear), however, this requires further investigation.

A further strength of this study is that it likely overrides behavioral-response variation resulting from variation in elephant age-sex classes. It is hypothesized that male-only elephant groups are more risk-tolerant compared with matriarch-led family groups, however, evidence for variation in predator avoidance behavior based on elephant age-sex classes is mixed (Sitati et al., 2003), and extant studies have found that elephants across herd size and composition demonstrate aversion to predator auditory signals (Thuppil & Coss, 2013). While calves are thought to be disproportionately targeted by felid predators, larger elephants are not immune (Power & Shem Compion, 2009).

While our study focused on African elephants, there is reason to expect that this approach could be useful in closely related Asian elephants (Elephas maximus). Analogous to African elephants, Asian elephants are at risk of predation from tigers (Panthera tigris). One study found that when Asian elephants detected auditory cues of tigers, they quietly retreated from the area (Thuppil & Coss, 2013). Interestingly, chemical analyses have revealed that tiger feces, like lion feces, are characterized by the presence of indole and phenol (Vester, Burke, Dikeman, Simmons, & Swanson, 2008), and like their African counterparts, Asian elephants are highly olfactorily-oriented (Plotnik et al., 2014; 2019; Rasmussen, 1998).

While communities living amongst elephants may be acutely aware of the risk posed by elephants to their lives and livelihoods, expensive and labor-intensive methods like bee fencing, or trench digging, tend not to be successful in the long term, as continued maintenance stagnates, or funds run dry (Sarkar et al., 2016). Familiarization is a concern with all human–elephant conflict mitigation strategies, however, by harnessing the indirect effects that lions have on elephants, it is likely that this strategy will have longer-lasting impacts on elephant behavior than other techniques. This is because the consequences of becoming complacent around predator cues could be lethal. While we did not see familiarization in our trials, we suggest that this be explored on a larger scale with additional field testing. It is also possible that our molecular barrier could be used in conjunction with other human–elephant mitigation strategies to create a dynamic deterrent fence that elephants do not become easily familiarized with.

Ideally, elephant-deterrence would also be useful outside of the context of crop raiding, including sudden elephant encounters. A more immediately relevant and effective solution to reducing human–elephant conflict is likely one which requires no maintenance, and which can be deployed in the moment of need, for example, bear spray (Floyd, 1999), as opposed to current deterrent efforts which require planning and maintenance just in case. We hope that these results can be used for the development of products that would prove effective ad hoc repellents of elephants, thus protecting farmers from economic damage, humans from fatality, and elephants from retaliatory killings.

ACKNOWLEDGMENTS

We thank S. Hensman, J. Crosby, staff at Adventures with Elephants and the Rory Hensman Conservation and Research Unit for allowing us to conduct research on their premises. We thank Christine Janks and Carson Springs Wildlife Conservation Foundation, Gainesville, FL, for allowing us to collect fecal samples, and to Laura Haynes and Dominic Mayo for collection assistance. We thank K. Stears, R.J. Schmitt, S.J. Holbrook,
A. Shuttleworth, and Y.D. Jacques for their invaluable help with logistics. Funding: K.V. was funded by the University of Florida. O. N. was funded by Deutsche Forschungsgemeinschaft #NE2156/1-1. M. H. S. was funded by NRF #120670.

CONFLICT OF INTEREST
The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS
Kim Valenta, Melissa H. Schmitt, and Omer Nevo designed the study; Kim Valenta and Melissa H. Schmitt collected data. All authors wrote the manuscript and declare no competing interests.

DATA AVAILABILITY STATEMENT
All data are available upon reasonable request from the corresponding author.

ETHICS STATEMENT
All research was approved by the Duke Institutional Animal Care and Use Committee (IACUC #A248-18-10), and adhered to the laws of South Africa where the behavioral trials took place.

ORCID
Kim Valenta https://orcid.org/0000-0001-9843-0698

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**SUPPORTING INFORMATION**

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

**How to cite this article:** Valenta K, Schmitt MH, Ayasse M, Nevo O. The sensory ecology of fear: African elephants show aversion to olfactory predator signals. *Conservation Science and Practice*. 2021;3:e333. https://doi.org/10.1111/csp2.333