these factors to wildlife. When animal behavior research is applied to conservation in practice, it can be successful because it pays careful attention to the underlying causes of the problem from the affected animal's perspective [observing prey-driven antipredator behavior to locate endangered predators—Ale and Brown (2009); e.g., attention to social dynamics in translocations—Shier and Swaisgood (2012); understanding how animals learn from each other in order to manage successful releases into the wild—Berger-Tal and Saltz (2014)]. Here, we focus on one particular conservation issue that centers on the interactions between humans and one significant umbrella megafauna, the elephant.

Human–elephant conflict (HEC) is a term used to describe the variety of negative, physical interactions between humans and elephants. Perceptions and fear associated with the conflict also go far beyond the direct interactions and make mitigation a challenge. In fact, human–elephant conflict flashpoints range widely. They may have an agricultural, environmental and/or financial impact related to crop-raiding or foraging (King et al., 2011; Chiyo et al., 2012; Wilson et al., 2015), damage to property and water and grain stores (Wilson et al., 2015), and impacts on vegetation (Midgley et al., 2005). They may also have a direct impact on the different parties' lives, manifested in the perceived effects of the conflict on human wellbeing (Barua et al., 2013), injury and death of humans and livestock, and retaliatory killing of elephants by humans (Dunham et al., 2010). How often and where each of these events occurs varies widely in Africa and Asia alongside variation in environmental factors such as resource distribution, agricultural practices, human occupation of land, seasonal climatic conditions and habitat connectivity (Bal et al., 2011; Cook et al., 2015; Goswami et al., 2015; Wilson et al., 2015).

For some, the term "conflict" itself is inherently problematic because it suggests an adversarial dynamic and exacerbates tensions, implying that interactions are always negative and that the needs of the different species must be mutually exclusive (Peterson et al., 2010). Some suggest that "coexistence" is a better term because it highlights the fact that positive relationships can and do exist between species living in the same habitats and landscapes (Hoare and Du Toit, 2001; Carter et al., 2012; Songhurst et al., 2016). It is clear, however, that humans and elephants do often compete for resources and are often involved in agonistic interactions across both African and Asian landscapes (Hoare, 2012). Interestingly, the intensity and type of these interactions vary widely, suggesting that there are differences not only across landscapes but also within individuals involved. Understanding the diversity and flexibility of both positive and negative interactions between humans and elephants, as well as the behavior of both are essential for ensuring that conservation practitioners can address all parties' concerns and develop comprehensive policy effectively.

Here, we discuss how the fields of elephant behavioral ecology and comparative cognition as examples can and should be used in the development of comprehensive conservation strategy, specifically human–elephant conflict mitigation action plans in Asia and Africa. We believe this can be accomplished by: (1) applying knowledge of individual variation in life history, personality and behavior to specific, local contexts and (2) taking into account the cognition and sensory perspectives of elephants when developing future conservation strategies. From our point of view, the imperative to take the "elephants' perspective" to prevent conflict between humans and elephants requires that the high resource needs of all parties are satisfied. Unfortunately, the fulfillment of human needs at the expense of the elephants' only delays conflict. Mitigation strategies aimed at preventing conflict by creating physical barriers to it will not, by themselves, solve conflict in the long-term. These strategies neglect details about the landscape in which the conflict occurs, as well as consideration for the individuals involved and their relevant behavior.

One major contributing factor is that the social, physiological and environmental needs of humans and non-human animals are often framed as being opposed to one another, rather than potentially overlapping (Dublin and Hoare, 2004; Barua, 2014). For instance, in the social context, elephants are generally regarded, like humans, as cognitively complex, socially intelligent animals that display empathy toward and learn socially from conspecifics (Lee and Moss, 1999; Plotnik and de Waal, 2014). Elephants cooperate with each other (e.g., McComb et al., 2001, 2011; Plotnik et al., 2011), and there are several anecdotal examples from wild studies of specific targeted helping behaviors in relation to deceased conspecifics and empathy (McComb et al., 2005; Douglas-Hamilton et al., 2006; Bates et al., 2008a). In a physiological context, the pressures on humans and elephants to acquire resources, support the energetic requirements of large bodies and brains over a long life and provisioning offspring means that the resource requirements of both species are high (Shannon et al., 2008; Reiches et al., 2009; Langman et al., 2012).

Long-term research on the complex ecology and life histories of individually identified elephants shows that they exhibit individual-level variation, for example, in responses to changing environmental conditions such as adjusting growth and reproduction in response to droughts (Lee et al., 2011) or workload (Mumby et al., 2015). This individual variation is in addition to age and sex-specific behavior, such as males having different home range use than females because of hormonal changes specific to their sex such as "musth" (Charif et al., 2004). These patterns of variation can inform us about both the elephants' effect on the landscape in relation to humans (Cook et al., 2015; Goswami et al., 2015), as well as the impact of human disturbance on the elephants' social systems (Goldenberg et al., 2016).

Research using individual observations on elephant social intelligence and the complexity of their social relationships (e.g., de Silva et al., 2011; McComb et al., 2011; Plotnik et al., 2014), as well as our growing understanding of how elephants use non-visual sensory modalities —i.e., olfaction and audition (Poole et al., 2005; Bates et al., 2007a,b; McComb et al., 2014; Plotnik et al., 2014; Von Dürckheim et al., 2018)—complements life history and ecological research by suggesting that *how* elephants make decisions may also play a role in the flexibility of environmentally-dependent behavior (Srinivasaiah et al., 2012). Information about how individuals and groups navigate their physical and social environments has direct implications for our

understanding of what causes, and what can mitigate conflict (Chartier et al., 2011).

CURRENT HEC MITIGATION STRATEGIES

One interesting and problematic commonality across many current human–elephant conflict mitigation techniques is their foundation in fear conditioning. This usually includes, for example, the use of negative stimuli such as electric fencing and hand-held firecrackers to force elephants away from crops (**Figure 1**). **Table 1** shows the range of mitigation measures employed, with a majority of the strategies largely focused on the use of a negative stimulus. Most strategies use barrier methods, which have been developed to prevent elephants from accessing crops or areas used by humans. Even softer measures such as coating fences in chili peppers (Osborn and Parker, 2002; Le Bel et al., 2015) or using bees to deter elephants (King et al., 2011) involve "persuading" the animal to avoid a potentially negative experience. These strategies, although potentially effective when consistently implemented and maintained long-term, may be incomplete in their incorporation of what we know (and what we still need to learn) about individual variation and behavior in elephants. The other significant issue is that all strategies need to take the space, landscape and resource needs of both humans and elephants into account (Goswami and Vasudev, 2017); when the needs of the latter are neglected, the mitigation plans are prematurely set up to fail.

In Sri Lanka, for example, pilot programs in which citrus crops are grown that are (a) unappealing to elephants and therefore do not encourage elephants to raid and (b) do not rely on fear-based conditioning to keep the elephants away have been successful (Sri Lanka Wildlife Conservation Society, 2015). In addition to this strategy being feasible at the scale of individual farms, the fruits can be sold for a profit and the rice crops can be grown behind the barrier of citrus trees. Although promising, this mitigation strategy, like most others, relies on the assumption that the primary reason for elephant crop-raiding is access to food; potentially, this is only a secondary by-product of the elephants' migration needs, limited space available in protected areas, the demography of the population and dispersal patterns of male elephants, or some other variable that has not yet been identified (Jackson et al., 2008). This is yet another reason why the collection of baseline behavioral and demographic data for the elephant populations in a given area is essential, as is the need to collect land usage data on individual elephant groups across diverse landscapes. Progress is also being made regarding the use of elephant communication to better inform humans about the presence of elephants and to provide early warnings in areas of human–elephant conflict (for example, by detecting their infrasonic rumbles—Zeppelzauer and Stoeger, 2015).

Thus, whilst together these different strategies represent an important step forward in the monitoring of potential conflict, they only treat conflict "symptoms" with temporary fixes and neglect to address the underlying causes of potentially systemic conflict. The strategies involving negative stimuli largely require elephants to balance the negative experience of the mitigation strategy against potential gains of the conflict activity and only remain effective if the elephants continue to avoid an ever-present negative stimulus. In addition, these monitoring methods and mitigation strategies do not aim to directly alter or impact elephant behavior in a positive way, but only focus on physical, acoustic or olfactory barriers between elephants, humans and their habitats.

FIGURE 1 | Teenage male elephant stepping over non-live electric fence in Kanchanaburi, Thailand. Regular maintenance of mitigation methods like electric fences is crucial with elephants, as they learn quickly about the lack of consequences when the fences are inactive. Photograph published with permission from the Zoological Society of London.

TABLE 1 | Methods of human–elephant conflict mitigation currently employed in Asia and Africa.

Method	Examples	Links to elephant behavior and ecology
Fencing methods	Barbed wire or chain link (Hoare, 2003; Fernando et al., 2008), stone or log (Hoare, 2003; Fernando et al., 2008), electric (Osborn and Parker, 2002; Hoare, 2003; Kioko et al., 2008; Asimopoulos, 2016), chili pepper paste applied to rope (Fernando et al., 2008; Wiafe and Sam, 2014; Wahed et al., 2016), beehives on fences or trees (Ngama et al., 2016; King et al., 2017; Cook et al., 2018).	Some are aimed at preventing elephant movements, while others use a repellent such as electricity, chili pepper or bees to elicit a fear response. Habituation could become an issue with all of these methods.
Perimeter methods	Buffer crops unappealing to elephants (Fernando et al., 2008), perimeter trench or ditch around fields (Hoare, 2003; Fernando et al., 2008), pit traps (Nelson et al., 2003), clear crop boundaries (Fernando et al., 2008), tripwire alarm (O'Connell-Rodwell et al., 2000; Asimopoulos, 2016; Wahed et al., 2016).	Some aim to prevent elephants entering the area or to warn humans, while others, such as trenches, take into account elephant food preferences and physiology.
Repellents	Chili pepper gas disperser (Le Bel et al., 2015), burning chilies and dung (Osborn and Parker, 2002), chili bombs (dried chilis combined with dung and water) (Jones and Elliott, 2006), vehicular disturbance (Hahn et al., 2016), pipe cannon (Asimopoulos, 2016), burning wood or bamboo (Osborn and Parker, 2002; Fernando et al., 2008), spotlights (Zimmermann et al., 2009; Raihan Sarker and Røskaft, 2010).	These methods aim to elicit a fear response that may increase conflict or encourage long-term habituation by the elephants to negative stimuli.
Human strategies	Surveillance methods such as local people recording and monitoring conflict incidents (Osborn and Parker, 2002; Zimmermann et al., 2009; Wahed et al., 2016; Gunaryadi et al., 2017) and occupying watchtowers (Fernando et al., 2008; Wahed et al., 2016). More active monitoring such as hiring guards (Fernando et al., 2008), and using captive elephants ridden by humans to drive away wild elephants (Fernando et al., 2008). Human-focused solutions such as monetary compensation for damage, injury or death resulting from conflict (Distefano, 2005).	Surveillance is more focused on preventing and monitoring conflict, and compensation is human-focused. Driving away animals and guarding crops may elicit fear responses from the elephants that either increase the frequency of physical altercations or result in the elephants finding alternative access points to crops.
Removing elephants	Relocating elephants (Asimopoulos, 2016), killing "problem" elephants (Nelson et al., 2003), culling (Van Aarde et al., 1999).	Removal takes into account that elephants may habitually become involved in conflict but neglects the fact that moving problem elephants to other areas may lead to the spread of problematic behavior to conspecifics via social learning.

Methods have been grouped by strategy, focusing on fencing, perimeters, humans and elephants, with examples of each strategy provided. We also describe the methods' links to behavior and ecology. Although not a fully exhaustive list, these examples highlight the importance of an elephant perspective in HEC mitigation and prevention.

In order to better provide mitigation solutions, we must take into account both human and animal motivations for engaging in potentially risky conflict-causing activities. For example, evidence suggests that elephants that consume agricultural crops are not only accessing calorie-dense food sources, but that they also grow larger than their non-raiding conspecifics (Chiyo et al., 2011). This means that their behavior may be linked to fitness benefits, as dominance and access to mates is linked to body size (Sukumar and Gadgil, 1988; Chiyo et al., 2011). On the human side, farmers have to balance costs of investing in mitigation measures against the value of compensation (Jackson et al., 2008), as well as the social and community-level impact of the conflict. The balancing act maintained by both elephants and humans cannot be seen as static, but in flux because of variation including seasonal availability of resources, social factors and mortality. Any inputs into the system, such as providing farmers with new mitigation tools or compensation could influence this balance in different ways, including stimulating further conversion of land to agricultural use (Bulte and Rondeau, 2005). This suggests that each HEC landscape, even within the same country or region, must be assessed as a unique case with a unique set of confounds and needs for both the individual elephants and the humans involved.

INFORMING HEC MITIGATION

Here, we suggest a holistic approach that focuses on both human and elephant factors. In areas where no mitigation strategy has yet been employed, a careful evaluation of human and elephant behavior and culture should be conducted first, hence the need for collaboration across disciplines in biology, psychology, anthropology and ecology at this level. For instance, both the social dynamics and landscape use of the humans and the elephants must be considered in HEC mitigation (Hoare, 2012); thus, effective strategies would require different types of academic and local community-level expertise.

First, at the level of the community, villages with stable community leaders and good relations between local members may find success with mitigation strategies that require collaboration over large distances (e.g., maintaining several kilometers of electric fence—Wilson et al., 2015). In communities with significant social strife or a lack of cooperation between individuals, attempts at resolving within-group disagreements should be made first to ensure the viability of any HEC mitigation strategy that requires long-term, cooperative investment from all stakeholders. If a mitigation strategy has already been employed and works in a particular site, the strategy's long-term

potential requires that it be applied consistently (for instance, by encouraging community members to be responsible for the upkeep of the specific sections of the electric fence that traverse their land—Chartier et al., 2011). Focusing on consistency in the implementation and maintenance of specific mitigation strategies encourages cooperation among local people but also sends a consistent message to the elephants in their environment. This awareness within human communities, the use of local knowledge and strong local collaborations are vital to the success of interventions or mitigation techniques.

The human dynamic is only one piece, of course; there is a crucial need for a more comprehensive, ecological and psychological understanding of the elephants' behavior and its environmental context. The most important questions we should ask center on why the elephants are coming into conflict with humans, and whether there are individual differences between elephants within and across populations that make them more or less likely to engage in such conflict. We propose to address these questions using two complementary areas of research: the study of elephant behavior and cognition, and the study of elephant ecology and life history. Studies conducted both in Africa and Asia, with both captive and wild populations, show clear evidence for individual differences in a number of ecological and cognitive categories, including parasite load (Lynsdale et al., 2017), body size (Evans and Harris, 2012; Chapman et al., 2016), primiparity (Crawley et al., 2017), social hierarchy (McComb et al., 2011), innovation (Bates et al., 2008b), cooperation (Plotnik et al., 2011), problem-solving (Foerder et al., 2011), aggression (Poole, 1989), and personality (Lee and Moss, 2012; Yasui et al., 2012; Seltmann et al., 2018). Identifying whether or not specific behavioral, physical, demographic or personality traits (collected through future ecological, ethological and experimental research on captive and wild elephants) correlate with an elephant's propensity to crop-raid or engage in conflict may have important implications for preventing or managing these conflicts across different landscapes.

Our growing knowledge about the complexity of elephant cognition and the variability in life history traits suggests that there are most likely substantial differences across populations and between individuals in their propensity for risk taking (Hoare, 1999). For example, from the cognitive perspective, while in-conflict elephant groups in which the leader or other adults are risk averse, fearful of humans or neophobic may only require simple mitigation approaches, areas with risk prone, innovative, curious, or destructive elephant groups may require a more aggressive mitigation strategy to curb conflict. Equally as relevant, these behavioral traits might be linked to life history characteristics such as age, sex, reproductive state or other demographic or ecological traits. Thus, our aim is to gain a comprehensive picture of the individuals in the study area as well as the leadership structure within these groups (McComb et al., 2001, 2011; Wittemyer et al., 2007; de Silva and Wittemyer, 2012) in order to develop protocols that are thus both local community- and elephants-specific and seek positive outcomes from potential conflict scenarios.

In future research, scientists could collect both demographic and trait-based data at the individual level. These data would not be focused simply on the animal's life history stage or sex alone—such as when dispersing adolescent males show a propensity to crop forage or raid (Sukumar and Gadgil, 1988; Rode et al., 2006; Chiyo et al., 2011, 2012)—but would also take into account the size, mortality risk, reproductive status, health status and use of resources of the individual as well as seasonal variation within each. Such research would complement data gathered from ethological (direct, systematic field observations of elephants close to or within crop-raiding zones) and experimental research designs. In the latter, basic cognitive tasks set up in areas frequented by wild elephant groups could help identify individual differences across elephants in confidence, innovation, risk-propensity, leadership and neophobia. Together, this work could be used to develop demographic, physical and personality profiles for individual elephants and groups, which could then be used to inform the implementation of area, group- or elephant-specific strategies to prevent conflict. If the reasons for differences in the type and level of conflict within and across range countries is not purely due to landscape and habitat differences, but instead has demographic, behavioral or personality-level implications, then focusing on influencing the elephants' decision-making process may be a novel approach to mitigating the conflicts across countries. For instance, by focusing on *how* elephants find food—for example, through research on their use of olfaction in both physical (Plotnik et al., 2014; Von Dürckheim et al., 2018) and social (Bates et al., 2007a,b) contexts—and *why* they decide to enter risky crop fields where they may encounter humans, as well as individual differences in their personalities (Yasui et al., 2012; Seltmann et al., 2018), life history traits and problem-solving abilities, conservation planners could focus mitigation on particular elephants.

In addition, instead of using particular strategies haphazardly to see what works in a given landscape, researchers could apply research on specific elephant groups and individual group leaders to the selection and identification of mitigation strategies that work best with particular types of elephants. We also hope that, in the future, research on individual differences in elephants and other species can be used to influence the animal's decision-making process (using techniques such as taste aversion or positive reinforcement conditioning) so that instead of forcing animals away from resources they desire or need, the animals make decisions on their own to avoid them. This would inevitably promote coexistence rather than conflict. Thus, in the case of the elephant, the complement of data on individual differences in life history, cognition and personality would allow conservationists to take the elephants' perspective to both look at the influences of particular traits on conflict as well as to potentially predict it before it occurs.

To be successful, however, this would require a comprehensive approach to wildlife management that accounted for the animals' needs so that alternative sources of food and water were available for animals away from human habitation. The feasibility of such an approach is problematic given that one of the reasons for increasing habitat fragmentation and encroachment is a decrease in natural resource availability for humans (Songer et al., 2016; Acharya et al., 2017). Nonetheless, we believe scientific

research into behavior, ecology and cognition has great promise for helping develop new strategies to prevent conflict between humans and wildlife. When politicians, community leaders and conservationists alike recognize both our growing understanding of the individuality within animal species and the need to take both human- and wildlife-perspectives in conservation practice, current approaches to mitigating conflict will evolve away from short-term stop gap measures that temporarily avoid conflict and toward long-term solutions that effectively prevent it.

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Both authors conceived, designed and wrote this work, and approved it for publication.

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The remaining author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.