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An Assessment of Perceived Crop Damage in a Tanzanian Village Impacted by Human-Elephant Conflict and an Investigation of Deterrent Properties of African Elephant (Loxodonta Africana) Exudates Using Bioassays

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AN ASSESSMENT OF PERCEIVED CROP DAMAGE IN A TANZANIAN VILLAGE IMPACTED BY HUMAN-ELEPHANT CONFLICT AND AN INVESTIGATION OF DETERRENT PROPERTIES OF AFRICAN ELEPHANT (*Loxodonta africana*) EXUDATES USING BIOASSAYS

by

REBEKAH R. KARIMI

(Under the Direction of Bruce A. Schulte)

ABSTRACT

Human-elephant conflict (HEC) is on the rise in East Africa as habitat that was formerly occupied by elephants and other wildlife is being converted to farmland. African elephants (*Loxodonta africana*) will raid agricultural fields to feed on crops, and many agriculturalists attribute the majority of their crop damage to elephants. The first two objectives of this study were to evaluate the accuracy of this perception by comparing perceived crop damage by elephants and other factors to the actual, quantified crop damage, as well as to evaluate the effectiveness of deterrent methods against wildlife used by local farmers in a Tanzanian village. From May to November 2008, farmers from Miti Mirefu in northern Tanzania were interviewed about both their perception of crop damage and effectiveness of deterrents used. During the same period, the actual damage to their corn fields was measured and compared to the perceived damage. Participants perceived elephants to cause the most damage. Damage from elephants was infrequent, but when it occurred it was on a larger scale than damage attributed to other factors, suggesting that farmers assess damage based on the maximal damage by a single event. Damage from a lack of water was much more frequent and more severe on average than elephant damage. Traditional deterrent methods have not been effective and innovative techniques are difficult to institute on a wide scale. The final objective of this study was to assess compounds that might be used for crop protection. Elephants use chemical signals to communicate keep-away and attractant signals to conspecifics. Compounds within the exudates of African elephants can be identified and used as deterrents around crop fields or to attract elephants to a safe haven. From July to September 2008, at Ndarakwai Ranch in northern Tanzania, (*E,E*)-farnesol and 3-pentanone were bioassayed with wild African elephants. The compounds tested did not elicit bioactivity, but the importance of continued research on biologically meaningful signals is essential to effectively reducing HEC.

INDEX WORDS: Perception, Human-elephant conflict, African elephant, *Loxodonta africana*, Deterrent methods, (*E,E*)-Farnesol, 3-Pentanone, Chemosensory, Bioassay

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Human-wildlife conflict (HWC) is a term used to express all negative interactions between humans and wildlife. It includes rat and cockroach infestations around the world, automobile accidents involving deer, carnivores mauling and killing people, and many more (Woodroffe et al. 2005). A large component of HWC is based upon human perceptions of occurrences that are relatively rare, but significantly damage human properties or lives (Woodroffe et al. 2005). This study examines human-elephant conflict (HEC) from the human perspective.

Humans have had confrontations with African elephants (*Loxodonta africana*) for centuries, but the exponential growth of the human population in much of sub-Saharan Africa in recent years is causing an increase in contact, and therefore conflict, between humans and elephants (Osborn 2002). Elephants damage the crops of subsistence farmers in rural Africa, affecting the livelihoods of communities both directly and indirectly (Osborn & Hill 2005). Directly, families are impacted by reduced yield of their crop and sometimes injury and death by elephants. Indirectly, farmers lose sleep because of the necessity of guarding their crops at night and may invest in a variety of passive deterrents to keep elephants away. The negative effects of the presence of elephants override any appreciation that local people feel toward elephants. With this in mind, I decided to focus on assessing the accuracy of perceived damage by farmers who experience HEC. Understanding perceptions and adjusting attitudes toward elephants and other wildlife is an important step toward HEC mitigation.

Traditionally, farmers have used a variety of techniques to protect crops from damage. In order to mitigate HEC conflict, understanding perceptions of the farmers involved is important. But it is also important to educate farmers and provide them with a reliable mechanism of deterrence. The deterrent methods traditionally used by farmers (e.g. barriers, fire, startle tactics) are not effective and many depend on a constant human presence. Elephants are intelligent and quickly adapt to active and passive deterrent techniques (Sitati & Walpole 2006). Recent innovative techniques to mitigate conflict are lacking in feasibility and have been difficult to implement on a large scale. A second goal of this project was to test elephant chemical compounds that may serve as natural signals to alter elephant behavior. African elephants communicate their reproductive state to conspecifics through chemical signals (Poole 1989a). These signals can serve as a warning to keep away, or an attractant to facilitate coupling for reproduction. Dr. Bruce Schulte and graduate students from Georgia Southern University have been working toward the identification of compounds from elephant exudates that could serve as a meaningful chemical signal (Schulte et al. 2007, Castelda 2008, Nasseri 2009). Because of the evolutionary significance of such signals, elephants should be slow to acclimate to their presence. The development of a deterrent using what has in the past been honest signaling of reproductive state would perhaps be an effective contribution to the mitigation of HEC (Schulte et al. 2007).

These two components combat HEC on two different fronts. The descriptive study of a comparison between actual and perceived damage by elephants and other wildlife is a stepping stone to address the negative perceptions of people living with elephants. The development of a viable deterrent method will equip farmers with a sustainable means to protect their crop fields and maximize their yield. This study, and further research like it, will help bring about more effective management strategies and contribute to the field of elephant conservation by breaking down the aspects of human elephant conflict.

CHAPTER I

AN ASSESSMENT OF PERCEIVED CROP DAMAGE IN A TANZANIAN VILLAGE IMPACTED BY HUMAN-ELEPHANT CONFLICT

ABSTRACT

Human-elephant conflict (HEC) is on the rise in Africa as the human population encroaches on what has historically been wildlife habitat. Crop-raiding by elephants further antagonizes the conflict by damaging the livelihoods of farmers who often retaliate by killing elephants. Farmers may exaggerate damage to their crops based on their background experiences and their perception of wildlife. The objectives of this study were to evaluate the accuracy of perceived crop damage, assess factors causing crop damage, and evaluate the perceived effectiveness of deterrent methods used by local farmers exposed to human elephant conflict on the border of a protected area. The study took place in the village of Miti Mirefu, on the border of Ndarakwai Ranch, in the Kilimanjaro District of northern Tanzania. Agriculturalists were interviewed about their perceptions and attitudes toward crop damage, factors causing the crop damage, and the effectiveness of deterrent methods used. The corn fields of the agriculturalists were measured throughout a growing season and the actual damage was compared to the perceived damage. Most participants were accurate in their perception of damage, but those who were not tended to overestimate damage. This study reveals that the agriculturalists' perceptions are shaped not only by background experiences, but by individuals' experiences with factors that have the most potential to cause damage. Although elephants did damage the largest proportion of a crop, the frequency of elephant crop raids was minimal. Participants attributed the most damage to elephants throughout the season, suggesting they may be estimating based on the maximal damage by any single event. Investigating both the human and elephant sides of HEC and mitigating conflict in such a way as to improve the situation for both species is an essential next step to reduce HEC.

INTRODUCTION

Human wildlife conflict (HWC) is a major concern of conservation efforts. HWC is a broad term encompassing all negative interactions between humans and wildlife (Messmer 2000). A common, ancient example of HWC is crop-raiding, because a variety of mammals, birds, and insects use crop fields as their primary food resources (Webber et al. 2007). Associated damage by HWC does not have to be real, as perceived damage can include economic, aesthetic, social, and political aspects (Messmer 2000). The attitudes (toward wildlife and conservation) adopted by people who deal with HWC affect the conservation of several charismatic species worldwide (Woodroffe et al. 2005).

Conservation benefits both wildlife and people by providing habitat for at-risk species and developing economic benefits derived from the wildlife resource, such as tourism (Gadd 2005). Community development programs concentrating on sharing the revenue from tourism have been examined as potential mitigation instruments in alleviating HWC (Archabald & Naughton-Treves 2001). Ideally, monetary compensation would alleviate the tension humans feel toward problem wildlife, but generally, revenue-sharing and implementing compensation schemes have not been successful because the people experiencing the brunt of impact by the animal species do not relate economic benefits to the presence of wildlife elsewhere (Gadd 2005). More likely, people relate the success of a crop to the absence of problem wildlife. This can result in people neglecting to take steps to protect the wildlife resource, or in some cases sabotaging conservation efforts (Gadd 2005, Naughton et al. 1999). An essential next step in reducing HWC is the creation of more effective mitigation strategies that will replace the negative view of wildlife with an appreciation of the intrinsic value of wildlife resources (Sutton et al. 2004, Sitati & Walpole 2006).

Although understanding the impact of HWC is an important aspect of conservation, it is also necessary to understand the attitudes of the people who deal with the conflict. Inadequate understanding of the attitudes held by the public limits the attainment of conservation goals (Kaltenborn et al. 2006), putting the problem species at risk (Sitati et al. 2005). However, in cases where the needs of local communities and wildlife are considered simultaneously, conservation efforts can be quite successful (Badola 1998). Community-based conservation efforts are more successful than any sort of deterrent method because these programs affect the attitudes of the people within the conflict, particularly when the benefits of a community based conservation program outweigh the costs of dealing with the wildlife (Bajracharya et al. 2006, Kaltenborn et al. 2006, Zhang & Wang 2003). For these reasons, programs that demonstrate the strong customs and traditions of conserving wildlife have been effective by altering the human perceptions of the problem species (Kuriyan 2002).

The customs of local people can influence their modern perspectives on wildlife as these customs have been molded by historic interactions with their surroundings (Cohn 1988). For example, African elephants (*Loxodonta africana*) are respected and admired within the Samburu people in northern Kenya as they appreciate the value of the resource (Kuriyan 2002). Elephants are ecosystem engineers and play a positive role in the ecosystem if not confined to a limited range (Jones et al. 1994, 1997). Their critical role includes creating and expanding waterholes, opening trails for humans and other wildlife, dispersing seeds, and modification of woody vegetation (McKnight 2004, Nyhus & Tilson 2004). The conflict between humans and elephants is quickly escalating; as the human population of Africa has grown, the wild areas needed to sustain elephant populations have dwindled (Newmark et al. 1994, Hoare 1999a), putting the species, and therefore the ecosystem impacted by them at risk.

Human-elephant conflict (HEC) is among the most publicized example of HWC in Africa and Asia, and most individuals in these regions can relate to it. The conflict between people and elephants includes direct and indirect negative interactions that harm both species (Zhang & Wang 2003). The conflict is damaging to subsistence farmers because of crop-raiding, and to elephants as humans retaliate by hunting them (Webber et al. 2007, Zhang & Wang 2003, Osborn & Parker 2002b). The damage caused by elephants can be catastrophic to local subsistence economies. Farmers suffer the brunt of damage, anxiety, and frustration caused by elephants. Costs to the local communities include property damage, human injury or death, competition over water resources for livestock, social disruptions (such as scheduling school around elephant activity patterns), the loss of productivity due to choosing guard duties over sleep, and crop depredation and destruction from raiding (Kangwana 1995, Osborn & Parker 2003a, Kiiru 1995, Hoare 1999b, Tchamba 1996, Naughton et al. 1999). Such negative interactions associated with elephants affect perceptions of those in a community where HEC exists; if elephants damage the livelihood of one family, the entire community is impacted (Woodroffe et al. 2005). If crop loss from elephant damage goes unchecked, rural people express their frustration through passive resistance to, or even sabotage of projects that have been implemented to further the conservation cause (Osborn & Parker 2003a, O'Connell-Rodwell et al. 2000, Nyhus et al. 2000).

Yet, elephants can also be economically beneficial (Dublin & Hoare 2004). Tourists from around the world visit Africa to see elephants in their natural environment. Past studies to evaluate the attitudes of local people toward elephants have shown that most appreciate the economic value of elephants attracting tourism, but they would prefer not to have them around (Newmark et al. 1993, Naughton et al. 1999, Harris 2002, Bauer 2003). HEC has been exacerbated by competition for land and resources; when the human population uses more land for agriculture, less natural habitat remains to sustain elephant populations in Africa (Parker & Osborn 2001, Osborn & Hill 2005).

African elephants require a large amount of productive land to support their expansive diets. They spend up to 90% of their time foraging and consume up to 300 kg of vegetation per day (Osborn 2004). The presence of elephants is often evident from the loss of standing biomass and the changes made to their natural habitat, making them ecological engineers (Osborn 2002). Typically, elephants graze on short grasses during the rainy season and browse on woody vegetation during the dry season (Osborn 2004). Elephants are opportunistic feeders, readily feeding on nutritionally dense, mature crops (Hoare 1999a, Osborn 2004). Crop-raiding is common during the transitional feeding period between grass and woody vegetation. Crop-raiding is exacerbated by the destruction of woody plants in over-crowded protected areas, driving elephants out of these regions. As available browse is reduced by human consumption, elephants enter crops to locate sufficient food (Osborn 2002). Besides feeding on mature crops, elephants may trample seedlings or consume the vegetative material before the harvestable food source for humans is mature (Parker & Osborn 2001). The appetites and extensive movements of elephants make them nuisances for local farmers who are concerned about their personal well-being as well as the survival of their crops.

Farmers and conservationists have tried many ways to mitigate conflict. Traditional methods of deterring the elephants are classified into two categories: passive and active. Passive deterrent methods include barriers such as electric or barbed wire fences, trenches, warning systems, and buffer zones. Active deterrent methods involve people driving the elephants away with loud noises like gunshots or banging on pots, burning dung mixed with chili peppers, throwing stones, or night-guarding (Osborn & Parker 2003a, 2002b). Elephants are quick to adapt to simple barriers or methods of chasing them away (Osborn & Parker 2002b, Barnes et al. 2006), so new methods of deterrence have been explored. For example, when placed around crop fields, hives of bees create a buffer zone. In a recent study, elephants moved quickly away from trees from which the sound of buzzing bees was played (King et al. 2009). Hence, bees may serve as a deterrent and provide an alternate source of income for farmers (Karidozo & Osborn 2005). Likewise, chili peppers have proven to be a sustainable cash crop that is commercially viable and resistant to wildlife due to its low palatability (Parker & Osborn 2006, Osborn & Parker 2002b, Osborn & Rasmussen 1995). While the traditional techniques lose effectiveness over time, in different, changing combinations they may reduce crop-raiding. Integrating community involvement with creative techniques to reduce crop-raiding is an important aspect of achieving conservation goals (Walpole et al. 2006). While sometimes lacking in feasibility, these techniques can be effective, but there is no single magic bullet to end crop-raiding by elephants.

Numerous studies have recommended the use of monetary compensation for farmers who have been affected by elephant crop damage (Nyhus et al. 2000, Naughton-Treves 1998). Unfortunately, when monetary compensation is involved, even in the form of revenue-sharing, the programs become vulnerable to corruption and the people may feel a sense of entitlement rather than an appreciation for the wildlife areas (Archabald & Naughton-Treves 2001). Compensation schemes are popular in India, although the participation of individuals suffering from crop damage is low due to processing delays, corruption, and inadequate remuneration for losses (Ogra & Badola 2008). Additionally, the quantification of damage requires manpower, unless those affected are able to report an estimation of damage experienced and for which they expect to be compensated.

Farmers may exaggerate the damage to crops attributed to elephants because they may not keep accurate damage records, or their recall may not be perfect; or they may overestimate the costs of damage to increase aid received in areas where agencies compensate for wildlife damage (Gillingham & Lee 2003, Sutton et al. 2004, Tchamba 1996). The background of individuals can influence their attitudes toward controversial issues. For example, farming experience, duration of living in one area, level of education, or size of field may determine what attitude is adopted by individuals, and therefore their perception of elephant damage in their fields. Agriculturalists with more experience planting crops where they are familiar with the wildlife would be expected to adapt to the challenges of living in an area impacted by HEC. The size of the field may affect perceived crop damage as it may be more difficult to assess crop damage when the area planted is larger. Level of education may also influence one's ability to adequately assess their crop damage. Other socio-economic opportunity costs such as restriction of movement, competition for water and food resources, and loss of sleep also come into play in determining what a farmer's attitude will be toward elephants (Hoare 1999b, Naughton et al. 1999, Dublin & Hoare 2004, Osborn & Hill 2005).

When an elephant damages a crop, the effect is obvious, potentially catastrophic, localized, yet typically infrequent (Naughton et al. 1999). In a study around Kibale National Park in Uganda, elephants caused the most damage during a single foray, but domestic livestock were responsible for two-thirds of the total crop damage over the growing season (Naughton et al. 1999). Less obvious species such as birds or insects also have proven to be pests to agriculturalists, but are less likely than elephants to destroy an entire harvest in one raid (Sutton et al. 2004, Gadd 2005). The intensity and frequency of problem elephant activity can be recorded, but it is important to judge them alongside the effects of other agricultural pests (Hoare 1999a). To further the creation of optimal conservation strategies, the attitudes of local communities including the magnitude of perceived damage need to be understood better (Messmer 2000).

The quantification of damage caused by HEC has become its own entity within the study of conservation biology. Hoare (1999b) has developed a protocol for collecting standardized data on human-elephant conflict to help evaluate the problem across the African continent (Dublin & Hoare 2004). For the past five years, students and faculty from Georgia Southern University have conducted research on elephants (Vyas 2006) and elephant damage to acacia trees (Napora 2007) at Ndarakwai Ranch, Tanzania. Nasseri (2009) examined the effects of elephant damage on acacia to the herpetofaunal community. In addition, Castelda (2008) initiated research on elephant damage to crops in the nearby village of Miti Mirefu. I continued and expanded on this last line of research by collecting data on the value of crop damage experienced by local farmers and by quantifying the impact of damage by agricultural pests (including elephants) on crop yield. Quantifying the damage attributed to elephants in comparison to other damage factors addresses the elephant side of HEC (Dublin & Hoare 2004).

The best way of determining the attitude of the farmers affected is to conduct interviews. The interview approach has been criticized because of the possible bias in such data, but interviews do provide valuable information on the attitude of the local people (Badola 1998, Kiru 1995, Naughton-Treves 1998, Dublin & Hoare 2004, Gadd 2005). Spatial distribution, frequency and extent of crop loss, as well as sociological factors that shape local coping strategies and perception of risk, all play into the local view of human elephant conflict (Naughton et al. 1999). I conducted interviews to evaluate the attitudes of the farmers on the border of Ndarakwai Ranch in the village of Miti Mirefu toward elephants in comparison with alternative factors (such as lack of irrigation) that may affect crop success. Participants were asked questions and the answers given were assumed to be the correct answer according to their perception. In addition, participants were asked about sociological factors which may have influenced their attitudes toward wildlife. Evaluating farmers' perceptions of damage addresses the human side of HEC (Dublin & Hoare 2004).

The objectives of the present study were to evaluate the accuracy of perceived crop damage, assess factors causing crop damage, and evaluate the perceived effectiveness of deterrent methods by local farmers exposed to human elephant conflict on the border of a protected area. Fulfillment of these objectives required me to a) quantify crop damage, and b) evaluate the farmers' perceptions towards wildlife and factors causing crop damage by conducting interviews.

METHODS

Study Site

Ndarakwai Ranch, Tanzania

My research occurred from May to December 2008 at Ndarkwai Ranch in northern Tanzania. Ndarakwai Ranch is a semi-protected area (anti-poaching ranger patrols but no fences) covering 4300 hectares of woodland and savannah habitat. Elephants move freely through the ranch, which serves as a wildlife corridor between Amboseli National Park (Kenya), Arusha National Park, and Kilimanjaro National Park (Figure 1.1). Ndarakwai Ranch has become an established study site for elephant research. Previous graduate students at Georgia Southern University, D. Vyas and E. Napora successfully completed studies on elephant land use and elephant chemical ecology. Graduate students S. Castelda and N. Nasseri investigated aspects of HEC and tested the responses of elephants to chemicals identified in elephant secretions and excretions.

Miti Mirefu

Neighboring Ndarakwai Ranch is a small village called Miti Mirefu. The border between the protected area of Ndarakwai Ranch and the agricultural village of Miti Mirefu is the Engare Nairobi (North), also called the Simba River (Figure 1.1). Over the years, the river has proven to be an ineffective barrier to elephants and other wildlife, as crop-raiding occurs in the farms of Miti Mirefu. In the village, there is a mixture of Masai, who are mainly pastoralists, and people who depend primarily on agriculture such as the Wachagga and Pare tribes. In the course of a year, multiple crop seasons correspond to the expected rainy seasons. Farmers are able to irrigate their crops by diverting water from the river into their fields causing the fields to flood, at which point the water furrows are blocked and the water is diverted elsewhere. The community has set up an informal system of which days the water is diverted to which areas, but the frequency of irrigation was highly variable among individual farmers. Common crops include corn, beans, tomatoes, and green pepper.

Part A. Quantification of crop damage

<u>Field Characteristics</u>

Nineteen caretakers (e.g. owner, renter, family of renter/owner, employee of renter/owner) of fields agreed to participate in the study. Due to a variety of complications (Table 1.1), only fourteen fields were measured using the following methodology. All fields were in full sun with no shade trees. Fields were used in analysis if damage was measured within the week prior to the day it was harvested. Several fields were measured more than once, although the data analyzed are representative of the last damage measurement. I estimated the perimeter of the village by walking around the majority of dwellings with a Garmin GPSMAP ® 60 CSx tracking tool. The perimeter was uploaded into MapSource™ software to create a map of the village, which was used to determine the location of individual fields within the village (Figure 1.1). Damage quantification was limited to fields of corn because it is semelparous, and therefore easy to estimate yield. After a field was identified and permission to measure damage was obtained from the owner or renter of the field, I walked the perimeter and took GPS coordinates at all the corners of the field. I counted paces and recorded the distances by sketching the shape of the field. One pace was equivalent to 1.2 meters. If a 1 pace x 1 pace belt transect along the perimeter did not cover 10% of the area of the field, I also counted paces of a belt transect through the middle of the longest side. The stage of the field was classified as: (1) less than a foot tall, (2) location of ears visible but not yet present, (3) immature ear present, (4) mature ears present on less than 50% of corn stalks, (5) mature ears present on the majority of corn stalks, or (v) varying, indicating two or more of the previous five stages were present in a single field. Soil samples were collected 5 meters towards the center of the field, away from the compacted corners of the field. Samples were mixed together so that there was one mixed sample per field. Nitrogen, phosphorous, and potassium levels were estimated using a soil NPK kit (LaMotte™) which classified levels as low, medium, or high. The small sample size of fields from which NPK was estimated eliminated the possibility of performing multivariate analyses to identify the optimal combination of NPK levels. Moisture, light, and pH were estimated with a Soil Master meter (Mosser Lee™) during the first visit to the field, regardless of the time of day or irrigation state of the field. Fields were visited between 0830 and 1530.

Yield Estimate

A yield estimate was measured for the fields that were classified as (3) immature ear present, (4) mature ears present on less than 50% of corn stalks, or (5) mature ears present on the majority of corn stalks. Two perpendicular samples of ten paces without damage were selected in order to estimate the yield of the field if it had not experienced damage (Figure 1.2). I walked five paces toward the center of the field to minimize the edge effect. For each subsample, the number of stalks present within a one pace line transect was recorded. The same line transect was repeated to count the number of ears of corn present. I calculated mean ears per stalk for each field using these values.

Micro-damage

I measured micro-damage (damage to the leaves) by walking from the perimeter toward the center of the field five paces (Figure 1.2), at which point I estimated the proportion of damage to a leaf on the nearest stalk. Leaves were chosen by alternating direction (north, east, south, west) and placement on the corn stalk (second from bottom, middle, second from top). For example, the first measure of a field's micro-damage was a leaf growing on the north side of the stalk near the bottom, as the lowest leaves were usually completely dry. The second measure was taken from a leaf growing in the middle of a stalk five paces from the previous plant growing out of the east side of the stalk. For each designated leaf, I estimated the proportion of the leaf that was affected by the factor indicated. I measured leaves five paces in from the perimeter because I found preliminarily that there was a significant edge effect where it was obvious the stalks were not getting as much water as those in the center of the field. If a 1 pace x 1 pace belt transect along the perimeter did not cover 10% of the area of the field, the same method was used to measure micro-damage along a transect of the longest side of the field. The proportion of micro-damage within one field was estimated by calculating the average leaf damage experienced within each field.

Macro-damage

Macro-damage (detrimental damage to the entire plant) was measured by walking the perimeter of the field with my assistant who was familiar with growing corn and the different types of damage. Initially, she identified the source of damage, and I recorded the number of paces attributed to each damage factor. After a few days of training, I was able to identify the sources of damage (Table 1.2). A lack of water was the one source of damage that could be categorized as both micro- and macro- damage depending on the extent of the damage. If a 1 pace x 1 pace belt transect along the perimeter did not cover 10% of the area of the field, I measured macro-damage along the transect of the longest side of the field. The proportion of micro-damage attributed to each factor within one field was estimated by calculating the proportion of damaged paces attributed to each factor.

Damage from elephants was the most severe and therefore would trump damage by bushpig, baboons, and birds. If a bird damaged one ear of corn in one pace but there was also damage from a bushpig within that pace of the belt transect, the pace was counted as damage by bushpig because the bushpig damage played a larger role in affecting the yield of that pace. Bushpig damage was more severe than baboon damage which was more severe than damage attributed to birds. Therefore, the most obvious damage within a pace was assessed and attributed to individual factors.

Data Summary

The relationship between macro-damage and micro-damage was examined using a correlation model. The mean proportion of macro-damage (P_d) was calculated for each factor in order to determine the most prominent source of damage. Crop damage was examined further by calculating the frequency of damaging visits (F_d) by each of the damage factors. The frequency was multiplied by the average proportion of damage caused ($F_d \times \overline{P_d}$). Frequency of damage by individual damage factors was also multiplied by the maximum amount of damage caused by each factor ($F_d \times P_{d(max)}$). The resulting ranked damage factors were used to compare quantified damage to the perceived damage.

The yield of a field that was damaged by each damage factor was estimated by calculating the total undamaged yield (Y_u) of a field which was multiplied by the proportion of damage (P_d) attributed to each damage factor $(Y_u \times P_d)$. The result was an estimate of the yield damaged by each factor for individual fields. A box plot was created to display the first and third quartile, and the entire range of the yields of fields affected by different damage factors.

The GPS coordinate that was nearest to the perimeter of the village was used to calculate the distance from the perimeter, with negative values indicating fields located outside the village perimeter. Field locations were compared to the total proportion of damage to each field. Naughton-Treves (1998) found that fields located nearer to protected areas experienced more independent damage events than fields located further away. I investigated if the village perimeter would identify the same pattern, with fields located in the center of the village experiencing less damage than those fields on the outskirts of the village's perimeter.

Part B. Assessment of farmers' perceptions

Two interview sessions were held with each participant. The first interview was used to get a consent form signed and establish a relationship with a participant. GSU's Institutional Review Board (H08138) approved the interview technique and questions asked. I gathered background information such as how long they had been farming and if they accrued income from any other activity (Table 1.3). This session lasted about 10 minutes and was conducted on the first visit to the field after damage quantification.

The second interview session took place at least two weeks after the first visit. Questions were divided into three sections because the interview was rather lengthy (Table 1.4). Participants were given the choice to stop the session between sections to resume the next day. Two participants completed the interview session in two consecutive days, while the remaining 12 completed the entire session in one sitting. The first section of questions assessed the participants' perception of damage that they experienced in the past and included the use of pictures of differing amounts of damage categorized into 10%, 25%, 50%, 75%, or 100% of a field. Pictures were used throughout the interview to ensure the participant had a clear understanding of the possible answers. The second section of questions assessed the participants' use of and perception of deterrent methods and included pictures of possible active (burning fires, making noise, guarding crops at night) and passive deterrent methods (fences, wind chime noise makers, trench) or crop maintenance such as using pesticides, herbicides, or irrigation. Crop maintenance was excluded from the analysis because although there was evidence that all crops were maintained throughout the study, not all participants answered accordingly. Pictures used in the interview process are available from the author upon request. There were questions within the second section that were Likert items, as the participants were asked to identify to which extent they agreed with particular statements. The third section of questions focused on the present growing season and the perceived damage. At this point, participants were asked to attribute damage to particular biotic factors, specifically insects and rodents, domestic animals, non-domestic animals, and elephants. Participants were first asked to state which animals were causing damage to their crops and then were shown pictures and asked to identify animals from the pictures that had damaged their crops.

<u>Extension</u>

Quantifying crop damage and establishing a relationship with the farmers required an extensive time commitment. I determined that a larger sample size for the perception portion of the study would better facilitate fulfilling the objective. Therefore, an additional twenty-five participants were questioned about their perception, increasing the sample size for the perception questions to thirty-nine. Crop damage was not quantified in the fields of these additional participants. Questions that focused on the quantification of damage in the farmers' crop field were omitted during this second round of interviews

(Tables 1.3 & 1.4: see asterisks indicating questions included only in the interviews with participants within the quantification sample set).

Attitude Analysis

The answers to background information were used to establish the demographics of the participants interviewed. These answers were categorized to examine potential differences in the background experience of the participants. For questions involving ranking answers from most to least, scores were assigned to each answer. When a participant reported that they were most worried about elephants damaging their field, elephants were scored a 5 for that question. If the next factor ranked was bush pig, bush pig would be assigned a 4. Likert item questions were categorized by level of agreement, which were represented on a figure.

C. Comparison of Crop Damage and Farmers' Attitudes

Actual quantification of crop damage and the factors that caused it were compared to the factors the farmers perceived were contributing to damage. In order to identify if the actual damage aligned with the perceived damage, I performed a correlation to determine if the two variables were associated. If the farmers perceived damage to their crops accurately, then I would expect the slope of the best fit line between data points of perceived damage and actual damage to form a line with a slope of one. If data points fell above the modeled accurate perception, farmers were overestimating damage. Conversely, data points that fell under the modeled accurate perception indicated that famers were underestimating the damage occurring in their fields. Analyses were performed to determine if the slope of the regression lines dividing groups were significantly different. Accuracy of perception was calculated by using the difference between perceived (P) and Actual (A): P-A. A negative accuracy of perception indicated that the farmer underestimated damage, while a positive accuracy of perception indicated damage was overestimated. A P-A of zero would indicate perfect accuracy. The slope of a best-fit line between data points within each group was used to determine if different groups were able to perceive changes in actual damage. A positive y-intercept would indicate that farmers overestimated damage (e.g., at zero damage, farmers would estimate some damage). A negative y-intercept would indicate that farmers were not good at assessing low levels of damage (i.e., they would perceive less damage than was measured). Interview answers were used to identify distinguishing characteristics of the groups of data points, which were compared using a student's t-test or a Mann-Whitney U test if the data did not meet assumptions of normality and equal variance.

RESULTS

Perception Assessment

Perception of Factors affecting Crop Success

The majority of participants (77%: 30/39) had lost an entire crop's yield in the past. Participants attributed complete loss of their crops to elephants (83%: 25/30), bushpig (47%: 14/30), baboons (33%: 9/30), or a lack of rain or irrigation (33%: 9/30). Sixty-seven percent (20/30) of complete damage was perceived to be caused by combinations of the factors listed. At least three participants attributed crop damage to elephants, bushpigs, baboons, insects, lack of water, porcupine, and dikdik. Other damage factors named by participants included cows, goats, rabbits, zebra, donkeys, aardvarks, blue monkeys, impalas, and cold weather. Rank scores for elephant, bushpig, and baboon were higher than rank scores for insects, lack of water, porcupine, and dikdik (Figure 1.3). When participants were asked to choose among insects, rodents, domestic animals, other wildlife, and elephants, the majority predicted that elephants were most likely to damage their crop during the current growing season. The majority of participants (72%) perceived elephants had caused the most damage to their fields in the past. The majority of participants (59%: 23/39) strongly agreed that they were worried about factors that had damaged their crops in the past affecting their crop yield again. Using past experiences, participants perceived that elephants, insects, and other wildlife, respectively, have potential to cause the most crop damage, while no participants chose domestic animals or rodents. Participants were most worried about elephants damaging their crops (Figure 1.4). Ninety-five percent of participants (37/39) had had repeated problems with the same damage factor.

Perception of Deterrent Methods

Ninety-two percent (36/39) of participants had used deterrent methods against crop damage in the past, but 74% (29/39) felt they were only partially effective at preventing crop damage. Fifty-nine percent of participants (23/39) strongly or mildly agreed that deterrents would be effective. Fifty-six percent (13/23) of the participants who did think deterrents would be effective did not use them because they felt deterrent methods were too expensive. Six participants (26%) felt materials needed for deterrent methods were too difficult to find and four participants (17%) did not use deterrent methods because setting them up was too much work. All participants felt that passive and active deterrents would be effective at minimizing crop damage when they were shown pictures of deterrent types; however, participants did not perceive that either active or passive deterrents would be more effective than the other (Figure 1.5). The majority of participants (65%: 25/39) used a combination of active and passive deterrents and 23% (9/39) used active deterrents alone. Five participants (13%) used no deterrents at all and no participants used passive deterrents alone. Eighty-five percent of participants (29/34) who used deterrent methods perceived them to be effective. Ninety-five percent of participants (37/39) believed deterrent methods to be successful on fields in the area, although there was no difference in the effectiveness scores assigned by the participants of passive and active deterrents (separately) in the area (Figure 1.5).

Perception of Past Damage

All participants depended on the yield from their crop as a source of income used to care for their families, but only two participants (5%: 2/39) exclusively sold their entire crop at the local market for income. Fifty-four percent of participants reported that the most crop damage their families could withstand was less than 10% (Figure 1.6). Thirty-six percent of participants perceived the minimum amount of crop damage they had experienced in the past as <10%, and 69% perceived the minimum amount of crop damage they had experienced in the past as <25% (Figure 1.6). Most farmers had reported a maximum of complete crop damage in the past (Figure 1.6).

Demography of Participants

The participants that completed both interview sessions had similar backgrounds. The average duration of living in Miti Mirefu was 18 ± 2.1 years, with 77% (30/39) living in the village for over 10 years. Eight participants were born in Miti Mrefu, while 79% (30/38) immigrated from nearby (within 200 km) towns or villages. Participants depended on agriculture as their primary source of income for 19.8 ± 2.1 years. The majority (77%: 30/39) did not have an occupation outside of farming, while only seven (18%: 7/39) had a previous occupation other than farming but had changed to farming only. The majority of participants had attended school for seven years (64%: 25/39), while two participants (5%) had attended school for over seven years, and five participants (13%) had not attended school at all. Two participants (5%) had taken agricultural courses, but the majority (95%: 37/39) had no formal agricultural education.

<u>Crop Damage Quantification</u>

Biotic Factors affecting Crop Success

The maximum total proportion of damage measured within the fields was attributed to other wildlife, followed by elephants and domestic animals, respectively. There was no difference between average proportions of damage caused by domestic animals and other wildlife (Mann-Whitney-*U*, elephants were excluded from analysis due to small sample size, U= 42, z= 1.56, p= 0.12; Figure 1.7). This calculation resulted in low proportions because it included fields that had no damage, driving down the average. The largest median of estimated loss of yield (ears of corn) in a field was attributed to elephants; however, the ranges of damaged yield overlapped (Figure 1.8). The maximum amount of estimated loss of yield of one field was attributed to elephants (Figure 1.8). Insects damaged the most fields, but domestic animals were also a common contributor to crop damage. Elephants caused damage to fields significantly less frequently than other wildlife (Likelihood ratio, χ^2= 13.07, df= 3, p= 0.0045; Figure 1.9). The calculated average damage indicates that elephants damaged the largest area of fields, but when the damage factors were categorized by combining bushpigs, baboons, and birds, the maximal damage was similar to that caused by elephants (Figure 1.10). This calculated value was low because the majority of fields had low or no damage. The calculated maximum amount of damage frequency also indicated that when elephants damaged fields, they damaged more than any other single biotic damage factor (Figure 1.11). The calculated maximum amount of damage frequency resulted in low numbers due to the small sample size for each category. However, when other wildlife encompassed bushpigs, baboons, and birds, this category bypassed elephants (Figure 1.12).

Use of Deterrent Methods affecting Damage

There was no difference in mean proportion of damage in fields using active only, active and passive, or no deterrent methods (ANOVA, F= 0.70, df= 2, 11, p= 0.52; Figure 1.13).

Abiotic Factors affecting Crop Success

Although the measured degree of soil moisture did vary in the quantified fields, there was no association between soil moisture and the average yield estimate for each field (Spearman's rank correlation, r= 0.03, p= 0.65; Figure 1.14). There also was no association between measured light levels and the average yield estimate for each field (Spearman's rank correlation, r= 0.05, p= 0.88; Figure 1.15). Levels of pH in the soil samples from each field did not vary (all but one soil sample had a pH of 8); Spearman's rank correlation, r= -0.15, p= 0.37). The pH levels were not associated with the average yield estimate for each field. No pattern was evident based on NPK levels from soil samples from each field affecting the average yield estimate from each field (ANOVA; Nitrogen: F= 1.65, p=0.23, df= 2, 12; Phosphorus: F=0.2, p= 0.60, df= 1, 13; Potassium: F= 0.0003, p= 0.99, df= 1,13; Figure 1.16).

Micro Leaf Damage and Macro Plant Damage

The primary source of observed micro damage to the corn leaves was a lack of water. Wind and insects also caused damage, although at times it was difficult to determine the specific cause of micro damage. Therefore, the sources of micro leaf damage were not analyzed extensively. The leaf micro damage and plant macro damage were not associated (pairwise correlation, r= 0.30, p= 0.30) (Figure 1.17).

Perceived Damage and Actual Damage

Comparing Perceived and Actual Proportions of Damage

Of the fourteen fields from which damage was quantified and perceptions assessed, nine participants were accurate in their perceptions of crop damage experienced (Figure 1.18). The difference between perceived damage and actual damage experienced was less than 0.2 in the group of participants with accurate perception, with all but one data point falling in the area of underestimation (Figure 1.18).

The remaining five participants overestimated crop damage (Figure 1.18, Table 1.6). The sample sizes of the two groups (over-estimators: n= 5; accurate: n= 9) prevented adequate statistical analysis. However, the slopes of the best-fit lines of the two groups were notably different (over-estimators: 0.41 ±0.28; accurate: 0.98 ±0.10). The sum of absolute values of the difference between perceived and actual values

$$\sum|P - A|$$

for each participant indicates that participants who underestimated damage (0.58) were more accurate than those who overestimated damage (2.41). Four over-estimators reported 75% of their fields were damaged, while one estimated their crop damage at 50%. The y-intercepts of the best fit line of the two groups also differed notably (over-estimators: 0.61 ±0.07; accurate: -0.05 ±0.05). There was no difference in mean years of formal education, mean field size, mean farming experience, and mean duration of stay in Miti Mirefu for the farmers from these two groups (Table 1.7).

Comparing Perceived and Actual Biotic Damage Factors

Biotic damage factors perceived to be responsible for the majority of crop damage did appear to play a prominent role in the quantified crop damage (Table 1.5). Elephants were perceived to cause the most crop damage but insects, domestic animals, and other wildlife also contributed to quantified crop damage (Table 1.5).

Comparing Perceived and Actual Abiotic Damage Factor: Lack of Water

While 79% (11/14) of participants strongly or mildly agreed that their crop was irrigated adequately, 93% (13/14) listed a lack of water as a factor that affected crop success. The damage quantification showed that 86% (12/14) of fields experienced damage attributed to a lack of water. The average percentage of area within the fields that was damaged by a lack of irrigation was 18%, while the mean area damaged by other biotic factors excluding elephants was 11% (Figure 1.19). There was no association between farming experience and damage attributed to a lack of water (pairwise correlation, r= -0.33, p= 0.24; Figure 1.20).

Location in Relation to the Perimeter of Miti Mirefu, Actual and Perceived Damage

The total proportion of damage was not associated to the fields' location (Spearman's rank correlation, r^2= 0.49, p= 0.31; Figure 1.21). Perceived damage also was not associated to the location of fields outside the village's estimated perimeter (Spearman's rank correlation, r^2= 0.06, p= 0.48; Figure 1.22).

DISCUSSION

The objective of this study was to compare the perception of crop damage by farmers to the actual crop damage experienced in their fields of corn over a single growing season. During the analysis phase of this investigation, two groups of participants became apparent. The participants who perceived more crop damage than what their fields had experienced were more inaccurate than those who had underestimated the amount of damage based on the absolute value of the difference between perceived and actual damage

$$\sum |P - A|$$

The findings of this study suggest that there are individuals (roughly one third in this study) who are either biased or for some reason predisposed to overestimating damage occurring in their crop fields. The group of over-estimators overwhelmingly chose 75% as the amount of damage experienced in their fields in the current season. There was no correlation between the actual and perceived damage in the group that overestimated damage; as actual damage increased, the perceived damage was static at 75%. It is important to define the relationship between the accuracy of farmers' perceptions and independent variables that could play a role in influencing people's perceptions of wildlife and conservation (Borgerhoff Mulder et al. 2007, Naughton-Treves 1998). I expected that the independent variables of education, field size, farming experience, and time spent in the area would be good indicators of farmers' abilities to accurately assess their crop damage. However, none of these factors was strongly related to perception. Hence, further work is needed to identify characteristics that could be used to predict accuracy in assessing damage.

The perceptions and attitudes of people are influenced by their background experiences, particularly when it comes to evaluating the cause of crop damage, either during the current season or from seasons past. All questions used to identify factors that the people perceived caused the most damage resulted in elephants ranked first. Because elephant damage is so catastrophic when it does occur, people are more likely to remember the devastation resulting from elephant damage than the accumulation of damage from insects and other wildlife (Naughton-Treves 1998). Occurrences of elephant damage are rare, but those incidences have potential to cause more damage than any other damage factor; whereas, damage from insects or a lack of irrigation is so common that agriculturalists may even expect to absorb some cost from them. The catastrophic incidences of elephant crop-raiding do affect the farmers' perceptions of elephants (Gadd 2005, Osborn & Hill 2005). For this reason, community-based conservation programs that inform community members on the positive aspects of elephant ecology would be beneficial (Kuriyan 2002).

Throughout this study, the categorized damage factor of other wildlife included bushpig, baboons, insects, and birds. However, most damage that was not due to a lack of water or elephants was attributed to bushpigs. Bushpig damage was relatively severe because they uproot stalks, essentially killing the corn. Damage by baboons and insects tends to affect parts of a plant without complete mortality, so that farmers may still obtain some harvest from these plants. Several fields had experienced damage from baboons or insects previously but when bushpigs damaged the same fields, the baboon and insect damage was no longer apparent. Therefore, the damage was attributed to bushpigs.

The evaluation of deterrent methods and farmers' perception of their effectiveness were inconclusive due to the small sample size of farmers with matching interview data and damage quantification data. The perceived effectiveness of active and passive deterrent methods did not differ and because none of the fields quantified used passive deterrents alone, a comparison was not possible. However, it was interesting that the presence of passive deterrents did seem to decrease crop damage and that most participants reported the use of a combination of active and passive deterrent methods. Active deterrent methods are dependent on human presence (Nelson et al. 2003, Omondi et al. 2004, Sitati et al. 2005). Passive deterrent methods are in place at all times. The constant presence of passive deterrent methods may habituate elephants and other wildlife that protected fields are off-limits and therefore may be more effective than active deterrents alone (Nelson et al. 2003). Yet, the participants interviewed in this study did not perceive the effectiveness of active and passive deterrent methods differently, and there is no known long-term answer, as elephants have proven their ability to adapt and overcome all types of deterrent methods over time (Sitati et al. 2005, Sitati & Walpole 2006). Rather than one solution, rural farmers should use a myriad of creative deterrent methods in different combinations over different seasons to ensure the maximum yield from their crops (O'Connell et al. 2000, Omondi et al. 2002).

Of the abiotic factors investigated in this study, a lack of water was the most prominent and obvious contributor to crop damage. Participants responded that their fields were adequately watered, but the majority of quantified damage was attributed to a lack of water. Throughout the study, there was no rain and in order for the crops to be irrigated, participants had to divert water from the river using a system of furrows. This activity can be very taxing and participants were possibly making a decision not to irrigate their fields because of the strenuous work it required (Sutton et al. 2004). If participants are willing to absorb the cost of not irrigating their crops rather than actively irrigating to minimize damage from a lack of water, it implies that they are able to withstand the potential damage attributed to a dry field. Most participants perceived that they were able to withstand either 10% or 25% of their field being lost, and the mean area damaged by a lack of water in fields measured was 18%. This study suggests that farmers are willing to minimize the damage of factors only if those factors have the potential to cause more damage than what their family can withstand.

The other measured abiotic factors (soil pH, soil nitrogen, soil phosphorous, soil potassium, light, soil moisture) were similar in all of the fields measured, but before abiotic factors are ruled out as having an effect on crop yield, more data should be collected. Soil samples were collected only 1-2 times throughout the study period. The fields were all in full sun with no trees providing shade to the fields.

Therefore, any variability in light levels was due to cloud cover. Although this study suggests soil moisture does not affect the yield of a field, it is rather inconclusive because if the farmer was present at the field, usually it was being irrigated, which of course would affect the soil moisture on the particular day of crop damage quantification. Optimal levels of soil NPK vary according to the levels of the preceding compounds. For example, if high N is found, low P and K might be optimal. Due to the sample size of fields in this study, the optimal combination of soil NPK was not apparent. In addition, the test kit used in this study reported relative levels of low, medium, or high. To rule out the abiotic factors as contributors of crop damage, it would be necessary to test soil samples for more specific NPK levels, and moisture levels more frequently throughout a growing season. This was not feasible within the context of this study due to a lack of manpower and time.

Elephants were perceived to be the greatest risk to debilitating crop yield. The frequency of elephant visits multiplied by the maximum amount of damage attributed to elephants determined that elephants were in fact, the greatest risk to the farmers' livelihoods. This study suggests that participants perceive the potential of damage factors to cause the greatest amount of damage, rather than assessing the odds (or frequency) of elephants or any other factor damaging their crop during a particular season. Naughton-Treves (1998) found that the tolerance to damage by wildlife is shaped more by the amount of crop loss rather than the frequency of raids, which was supported in the context of this study. The same has been found in studies on crop damage by Asian elephants (Linkie et al. 2007, Madhusudan 2003).

Compensation schemes depend on the quantification of crop damage in order to adequately replace income lost by farmers (Nyhus et al. 2000, Nyhus & Tilson 2004). Relying on the affected peoples' perceptions is not an accurate means for ensuring compensation reaches those who honestly are in need of it. The majority of participants in this study (64%) were accurate in assessing the crop damage to their field. However, participants were told that there was no monetary compensation available for participation in the research. If a government worker asks the same questions under the pretext that there is a fund available for compensation, farmers may overestimate damage to increase their compensation (Bajracharya et al. 2006, Ogra & Badola 2008).

To create a more harmonious relationship between people and wildlife, community outreach and education may be more effective than compensation schemes. By installing innovative and effective deterrent methods, as well as emphasizing the benefits of wildlife areas, crop loss can be decreased and appreciation for wildlife enhanced. If compensation schemes are implemented, the motivation of agriculturalists to minimize crop damage is diminished unless agriculturalists are required to gain eligibility for compensation by implementing deterrent methods. If farmers are paid for their losses rather than for their crop yield, conservation efforts and work invested by farmers are unproductive. With no productivity (and no food outcome), the potential of developing more nutrient dense crops through genetic modification or other agricultural enhancements is nonexistent. However, if agriculturalists continue in their efforts to reduce crop damage so that the yields of their crops are realized, the long term productivity will increase. Future research should be directed at evaluating individual deterrent methods that would help agriculturalists fulfill the maximum yield of their crops.

Land use planning is an important component involving the cooperation of the local communities where HEC is a problem (Osborn & Parker 2002b, Fernando et al. 2005). While land use guidelines are rarely implemented in Africa, they may serve as a guideline for future development. The positioning of fields to avoid areas of high elephant traffic may be easier than any district wide schemes, but for the people relying on fields in an elephant corridor, exchanging their land for land outside an elephant corridor may not be practical (Osborn & Parker 2002b, Fernando et al. 2005). Naughton-Treves (1998) associated a field's location with the amount of elephant crop damage experienced in Uganda. Fields located further from Kibale National Park did not experience as much crop damage as fields nearer to the border of this protected area. The present study investigated the relationship between a field's location relative to the perimeter of the village and the amount of damage endured by wildlife. There was a trend of more damage on the outskirts of the village than in the interior of the village.

A future study could benefit from a larger sample size with more specific questions to determine if there are characteristics of farmers that affect their accuracy of perception. Participants in this study had similar backgrounds and therefore, it was not possible to identify characteristics that could act as predictors of farmers' accuracy. Future research should be directed towards determining which characteristics increase the likelihood of participants' ability to accurately report damage to their crops. When conservationists are better able to understand what influences the perceptions of people living with wildlife, community involvement in conservation strategies will be more effective (Badola 1998, duToit 2002, Kuriyan 2002, Osborn & Parker 2002a, Parker et al. 2007).

The present study attempted to compare the human perception of crop damage with the measured damage by wildlife and abiotic factors. It is imperative to evaluate the accuracy of damage estimates before relying on farmers to adequately report damage in their fields. Farmers have a tendency to attribute crop damage to the factor that causes the maximal damage, rather than the overall average damage. Because this study encompassed only one village of rural farmers, further work is needed to determine if these results have broad applicability. A collaboration of researchers studying HEC across East Africa could determine if these results are universal or specific to Miti Mirefu. In order to be effective, mitigation strategies should benefit both humans and wildlife.

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Table 1.1. Several fields within the original nineteen were not included in the correlation between measured and perceived damage because the quantification of damage was not performed before harvest.

Field Count	Quantification Outcome
9*	Damage was measured twice throughout growing season with the last quantification visit occurring 1-2 days before crop was harvested
3*	Crops harvested without my notification, but damage quantified within the week before harvest
2*	Cows damaged crop and owners harvested remaining crop quickly without a final harvest visit; but damage was quantified within the week before preemptive harvest
2	Crop harvested early without notifying me
1	Elephants trampled field before first full interview session and was harvested before next visit
1	Elephants trampled field and caretaker was from out of town and did not return to field
1	Participant became suspicious of my intentions and declined participation after first visit

*fields that were included for comparison between perceived and actual damage

Table 1.2. Damage was attributed to certain factors based on the appearance of damage and evidence present at the scene.

Factor	Evidence
Baboon	Ears of corn missing or scattered on the ground; stalks upright
Birds	One ear of corn damaged with no other evidence present
Bushpig	Stalks pushed over; ruts present in the soil; damage located along a path; footprints sometimes present
Cow	Leaves torn and missing at the height of a cow's head; greater damage than that from goat
Elephant	Stalks pushed over; footprints present; area of damage greater than the body size of an elephant
Goat	Leaves torn and missing at the height of a goat's head; damage less than that from cow
Insects	Top half of cornstalk shriveled while leaves toward bottom unharmed; stalk very weak when bent; usually affected one stalk in a cluster of stalks
Lack of water	All leaves on stalk were shriveled; usually more than one meter

Table 1.3. Questions asked during the first interview session used to gather background information about individual participants.

1	Participant/Field code
2*	Do you own these fields? (y/n)
3*	Do you lease these fields? (y/n)
4	Duration of stay in Miti Mirefu?
5	Previous location(s)?
6	Duration of dependence on agriculture?
7	Previous occupation(s)?
8	Current occupation (s)?
9	How long have you been farming?
10	How much formal education have you had?
11	Do you have any agricultural education? (y/n)
12	If yes to #11, what agricultural education have you had?
13	Which crops do you harvest and when?
14*	Do you depend on rain or irrigation?
15	Other notes on the participant:

* indicates questions that were excluded for the extension portion of study

Table 1.4. The second interview session was divided into 3 groups of questions and assessed the perceptions of participants' past damage, use of deterrents, and current damage attributed to certain factors.

Group A. *Past Damage Perception*	
Participant were asked to assign an extent to the following questions: *1= some; 2= medium amount; 3= large amount; 4= near complete; or 5= complete damage.*	
A1.*	What is the most damage you have experienced in the past?
A2.*	How much damage did you experience last season?
A3.	What is the minimum amount of damage you have experienced in the past?
A4.*	How much damage can you withstand and still have enough to feed your family?
A5.*	Is this income earned from the crop? (y/n)
A6.*	Is this food from the crop itself? (y/n)
Participant were shown pictures depicting: *1= some damage (<10% of a field); 2= medium amount of damage (10-25%); 3= large amount of damage (25-50%); 4= near complete (50-75%); or 5= complete damage (75-100%)*	
A7.	How much damage can you withstand and still have enough to feed your family?
A8.	Is this income earned from the crop? (y/n)
A9.	Is this crop used to feed your family directly? (y/n)
A10.	What is the most damage you have experienced in the past?
Group B. *Deterrent Method Perception*	
For some of the following questions, participants were asked to identify to which extent they agree with the statements: *A= Strongly Agree; B= Mildly Agree; C= Undecided or Unsure; D= Mildly Disagree; or E= Strongly Disagree.*	
B1.	Have you used methods to prevent damage in the past? (y/n)
B2.	When I used methods to prevent damage, it was effective and less damage was experienced.
B3.*	Do you use pesticides? (y/n)
B4.*	Have you used pesticides? (y/n)
B5.*	Do you use fertilizer? (y/n)
B6.*	Have you used fertilizer? (y/n)
B7.	I provide adequate water for the crops in my fields.
B8.	There are deterrents I believe would be effective for my crops.
B9.	If you strongly agree with B8, why haven't you tried them? a) they are expensive; b) they take a lot of work; c) it is difficult to find the needed materials; d) other
Using Pictures: Participant were presented with a number of pictures including: *(1= Active) a guard, a gun, a fire; (2= Passive) a trench, a string fence, a string fence with "bells" attached, a chili pepper, a 3m clearing on both sides of a fence; (3= Crop Maintenance) pesticides, fertilizer, water diversion*	
B10.	Do you see any pictures of methods that you feel will reduce crop damage in your fields? (y/n)
B11.	If yes to #B10, which pictures show the methods you feel will be effective?
B12.	If more than one answer to B11, rank them.
B13.	Have you used any of the deterrent methods pictured? (y/n)
B14.	If yes to #B12, which pictures shows the methods you have used?
B15.	If yes to #B12, were they effective? (y/n)
B16.	Are any of these deterrent methods are successful in farms in the area? (y/n)
B17.	If yes to #B16, which methods are successful in the area?
B18.	If more than one answer to #B17, rank them:
Group C. *Perceived Factors causing Damage*	
Open- ended	
C1.	In the past, have you lost an entire season's yield? (y/n)
C2.	If yes to #C1, which factor was the loss due to?
C3.	What has caused damage to your crops in the past?
C4.	If more than one answer to #C3, rank them from most damage to least damage caused:
C5.*	What factors are you worried will affect your crop success?
C6.*	If more than one answer to #C5, rank them from most worried to least worried:
Using Pictures: Participant will be presented with a variety of pictures including: *1/2= insects & rodents: locusts, grasshopper, beetles, tomato insects; field mice, rats; 3= domestic: cattle, goats, sheep, donkeys; 4= non-domestic: bushpig, impala, wildebeest, zebra, baboons; 5= elephants*	
C7.	Which of these pictures is most likely to damage your crop this season?

C8.	Which factor has caused damage to your crop this season?
C9.	Using pictures of damage, how much damage did the factor from #C8 cause? 1= some damage (<10% of a field); 2= medium amount of damage (10-15%); 3= large amount of damage (25-50%); 4= near complete (50-75%); or complete damage (75-100%)
C10.	Which factor has caused the most damage in the past?
C11.	I am worried that the factor from the answer to #C10 will again cause damage during the present growing season. A= Strongly Agree; B= Mildly Agree; C= Undecided or Unsure; D= Mildly Disagree; or E= Strongly Disagree.
C12.	Using past experiences, which factor could cause the most damage?
C13.	Have there been repeated problems with a particular factor(s)? (y/n)
C14.	If more than one, rank them from most worried to least worried.

* indicates questions that were excluded for the extension portion of study

Table 1.5. Responses to interview questions regarding which species were responsible for crop damage and methods of analyzing actual damage attributed to different factors. Ranks were established either by calculating the proportion of participants responding with each answer or by *calculating the average rank score based on the order in which factors were ranked by participants; n = 39.

PERCEIVED:	**Rank by proportion or mean rank score:**				
Questions regarding perceived factors causing damage	**#1**	**#2**	**#3**	**#4**	**#5**
Which factor was responsible for total loss of an entire season's yield?	Elephants[1]	Bushpigs[2]	Baboons[3]	Lack of water	-
Which factors have caused damage to your crops in the past?*	Elephants[1]	Other wildlife	Insects	Rodents	-
Which factor is most likely to damage your crop this season?	Elephants[1]	Insects	Other wildlife	Rodents	-
Which factor has caused the most damage in the past?	Elephants[1]	Other wildlife	Insects	Rodents	-
Which factor could cause the most damage (using past experiences)?	Elephants[1]	Insects	Other wildlife	-	-
Which factors are you most worried about damaging your crops?*	Elephants[1]	Other wildlife	Insects	Rodents	Domestic
ACTUAL:	**Rank of factors from most damage to least damage:**				
Method of analysis for measured damage	**#1**	**#2**	**#3**	**#4**	**#5**
Sum proportion of damaged area per field	Other wildlife	Elephants[1]	Domestic	-	-
Mean proportion damaged area per field	Elephants[1]	Other wildlife	Domestic	-	-
Estimated median yield damaged	Elephants[1]	Bushpigs[2]	Lack of water	Birds	Insects
Estimated maximum yield damaged	Elephants[1]	Lack of water	Bushpigs[2]	Domestic	Insects
Frequency of damage events	Insects	Domestic	Other wildlife	Elephants[1]	-
Calculated average damage (non-categorized)	Elephants[1]	Insects	Bushpigs[2]	Domestic	Baboons[3]
Calculated average damage (categorized)	Elephants[1]	Other wildlife	Insects	Domestic	-
Calculated maximum damage (non-categorized)	Elephants[1]	Domestic	Bushpigs[2]	Insects	Baboons[3]
Calculated maximum damage (categorized)	Other wildlife	Elephants[1]	Domestic	Insects	-

[1]*Loxodonta africana;* [2]*Potamochoerus larvatus;* [3]*Papio anubis*

Table 1.6. The comparison between participants' perception of damage and the actual damage their fields experienced in the current growing season. Education, size of field, farming experience, and time spent in Miti Mirefu were examined to distinguish differences between participants with accurate perception from participants who overestimated damage to their fields. Note: Participants were asked to choose a category of damage to assess their perception; shaded rows indicate an accuracy of perception > 0.2.

Field	Actual Proportion of Damage	Perceived Proportion of Damage	Accuracy of Perception (Actual – Perceived)	Education (years)	Field Size (m^2)	Farming Experience (years)	Time Spent in Miti Mirefu (years)
1	0.29	0.10	-0.19	7	1609	24	20
2	0.38	0.25	-0.13	7	635	6	18
3	0.83	0.75	-0.08	5	2156	18	5
4	0.82	0.75	-0.07	7	2277	15	13
5	0.31	0.25	-0.06	7	1552	30	1
6	0.13	0.10	-0.03	8	1590	12	12
7	0.27	0.25	-0.02	7	1266	24	20
8	0.26	0.25	-0.01	7	4102	20	5
9	0.47	0.50	0.03	7	1195	7	1
10	0.48	0.75	0.27	0	2755	52	6
11	0.29	0.75	0.46	0	1016	31	58
12	0.02	0.50	0.48	7	2482	10	21
13	0.22	0.75	0.53	7	2482	22	13
14	0.11	0.75	0.64	7	406	36	10
Mean	0.35	0.48	0.13	6	1823	22	15
±SD	0.24	0.27	0.28	2.6	969	12.5	14.3

Table 1.7. Statistical tests were performed to see if there was a difference in backgrounds of participants who overestimated damage and those who were accurate in their perception of crop damage.

Independent Variable	Statistical Test	Test Statistic	P-value	Df
Mean formal education (yrs)	Mann-Whitney Wilcoxon	Z = -1.42	0.16	
Mean area of field (m^2)	Student's t-test	T = 0.50	0.63	1
Mean farming experience (yrs)	Student's t-test	T = 1.80	0.13	1
Duration living in Miti Mirefu (yrs)	Mann-Whitney Wilcoxon	Z = 1.14	0.26	

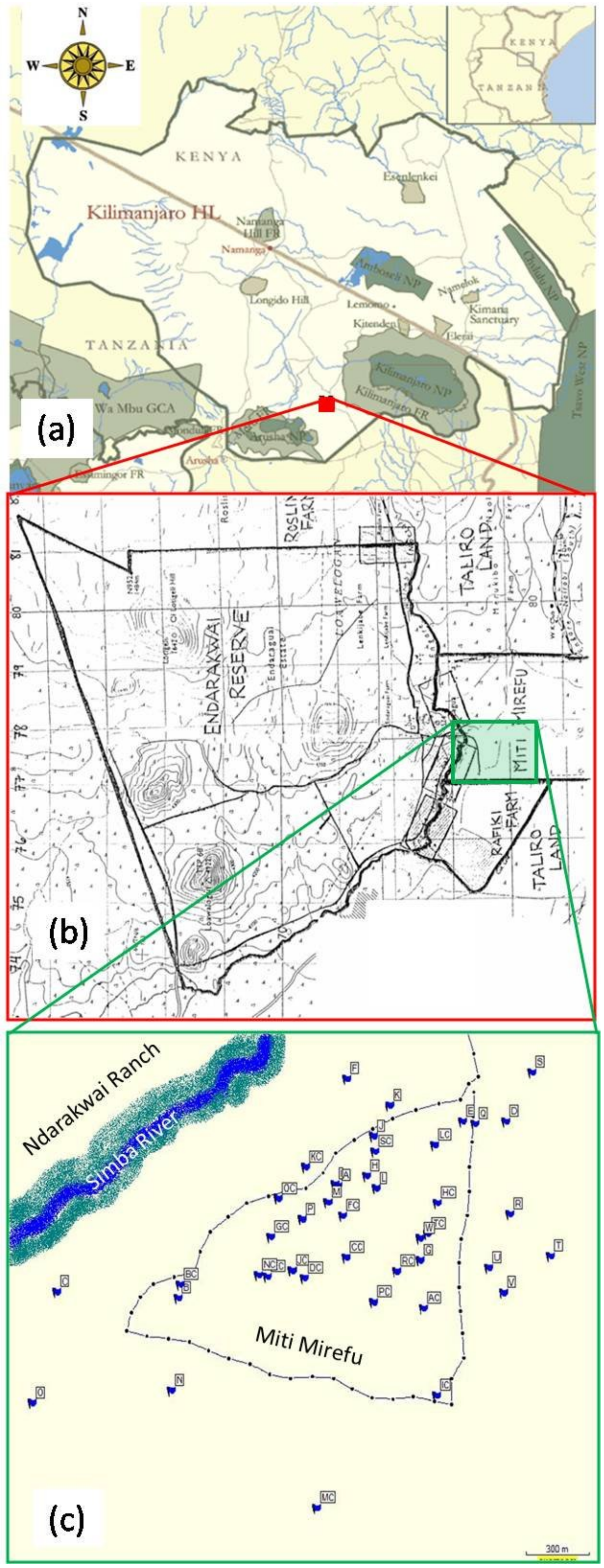

Figure 1.1. (a) Location of Ndarakwai Game Ranch in the Kilimanjaro district of northern Tanzania (b) map of Ndarakwai Ranch and Miti Mirefu (c) estimated perimeter of Miti Mirefu with flags marking the location of each field.

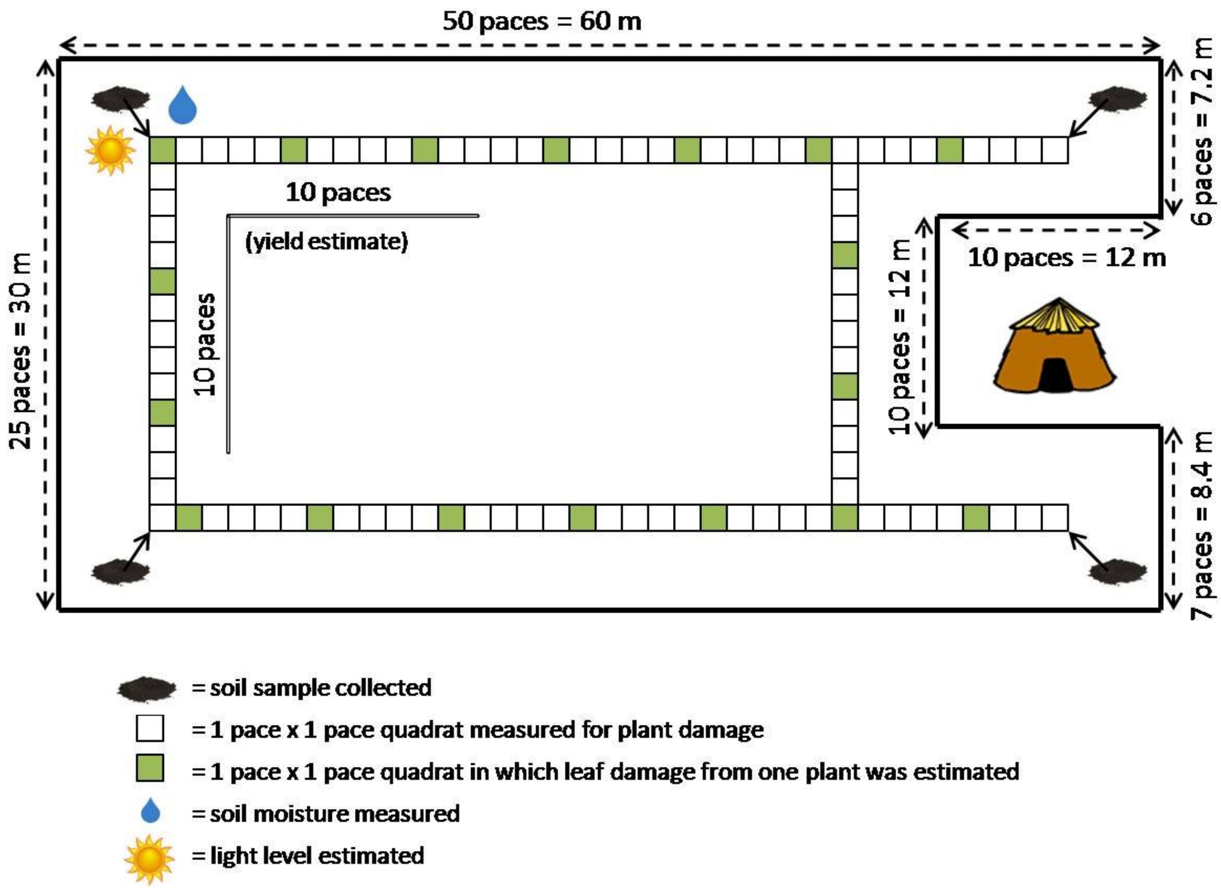

Figure 1.2. Example of a field measured (not to scale and not actual field) and what data were collected from each field. Soil samples were collected from four corners and mixed together for one measure of N, P, K, & pH per field. Soil moisture and light levels were estimated from one corner of the field. The perimeter of the entire field was measured by counting paces (1 pace = 1.2 meters).

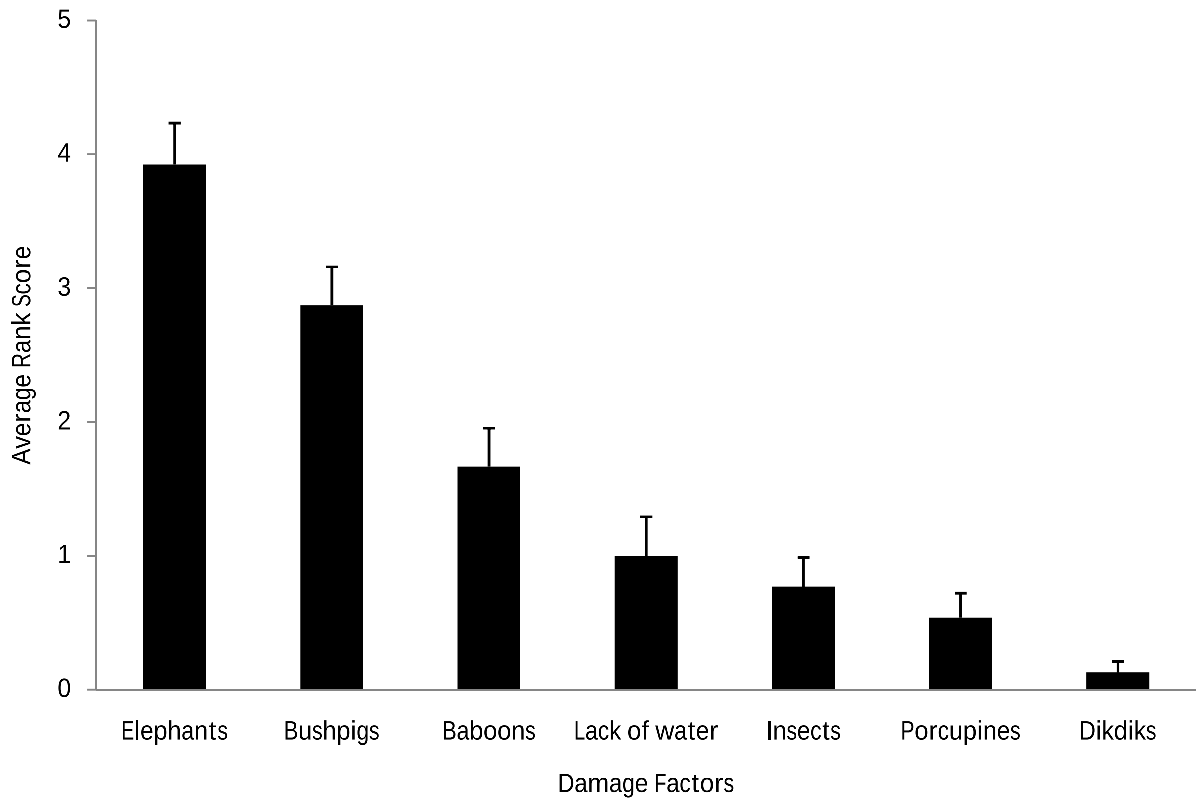

Figure 1.3. Average rank scores of perceived damage factors determined by the order in which participants ranked damage factors from most to least damage. Maximum rank score = 5, indicating the participants' ranked factors with a score of five first and therefore perceived rank scores of five to be most responsible for crop damage in the past; n= 39.

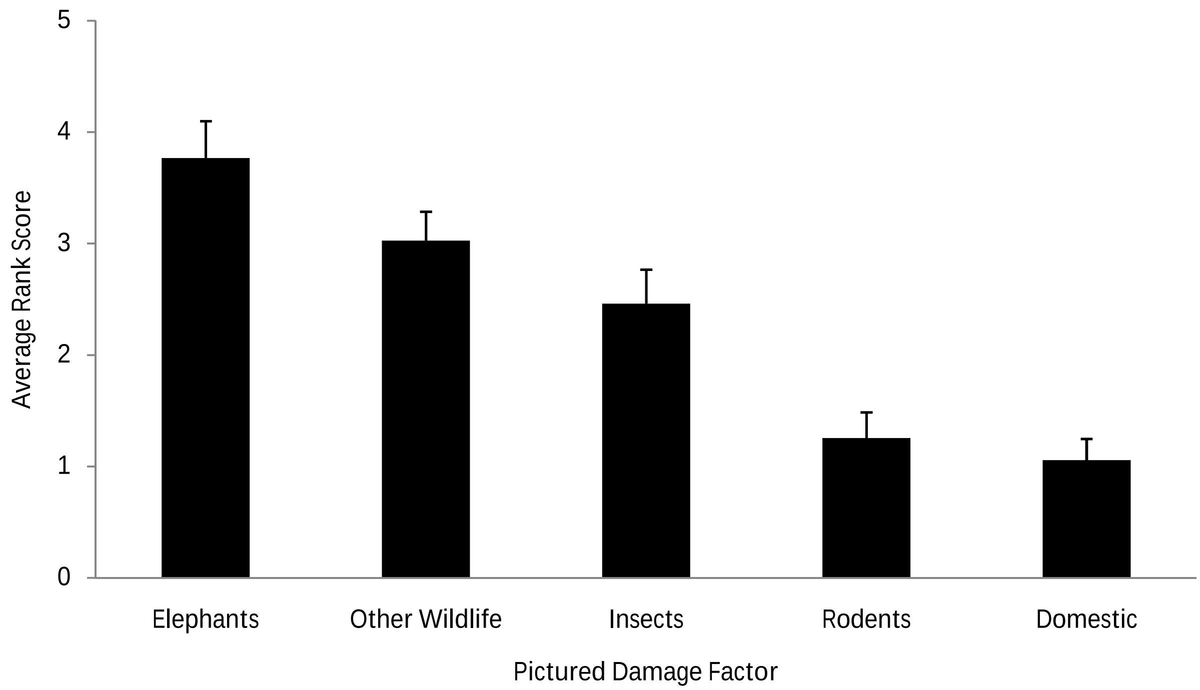

Figure 1.4. Pictured damage factors ranked based on how worried the participants were about them causing damage. The average rank score was determined by assigning a "5" to the factors ranked first, and a "1" to factors ranking fifth. Therefore, the maximum score is "5," and the minimum is "1;" n= 39.

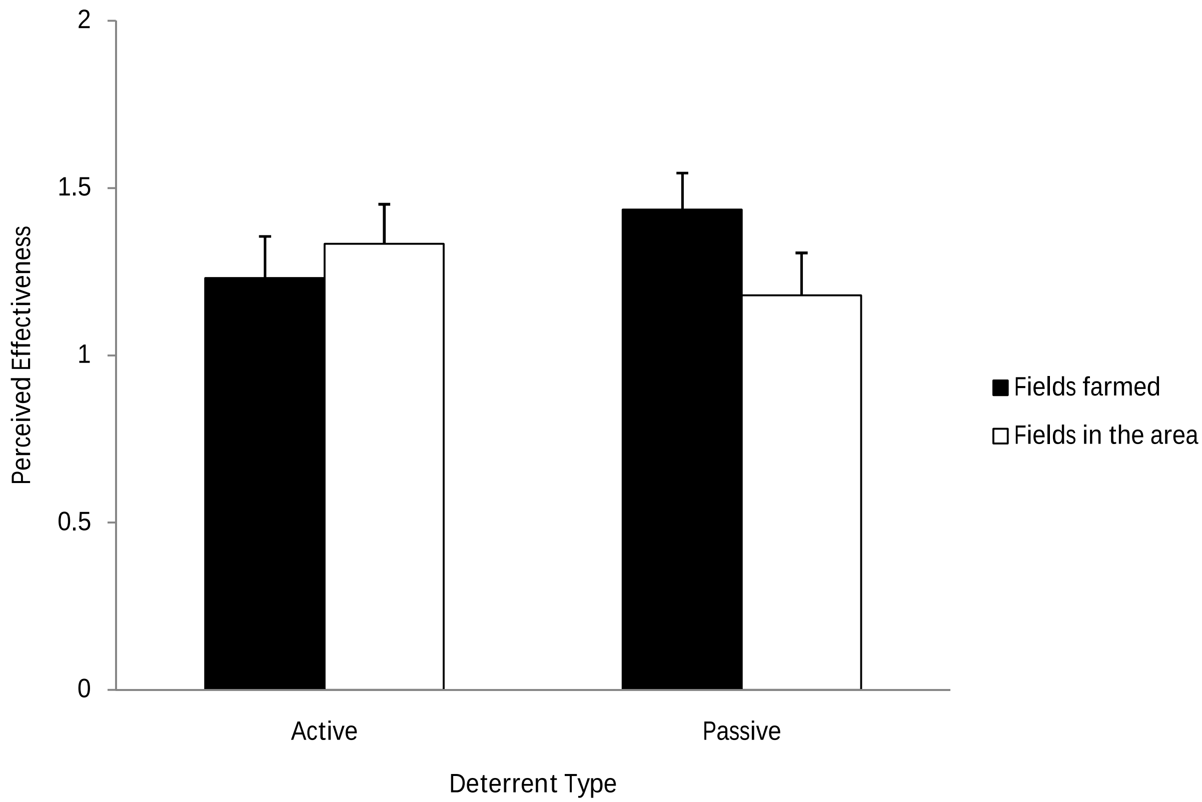

Figure 1.5. Perceived effectiveness of active and passive deterrents set up in fields farmed by the participants and in fields around their fields. Perceived effectiveness is the calculated score from ranking the deterrent types whereby a "2" would indicate maximum effectiveness; n= 39.

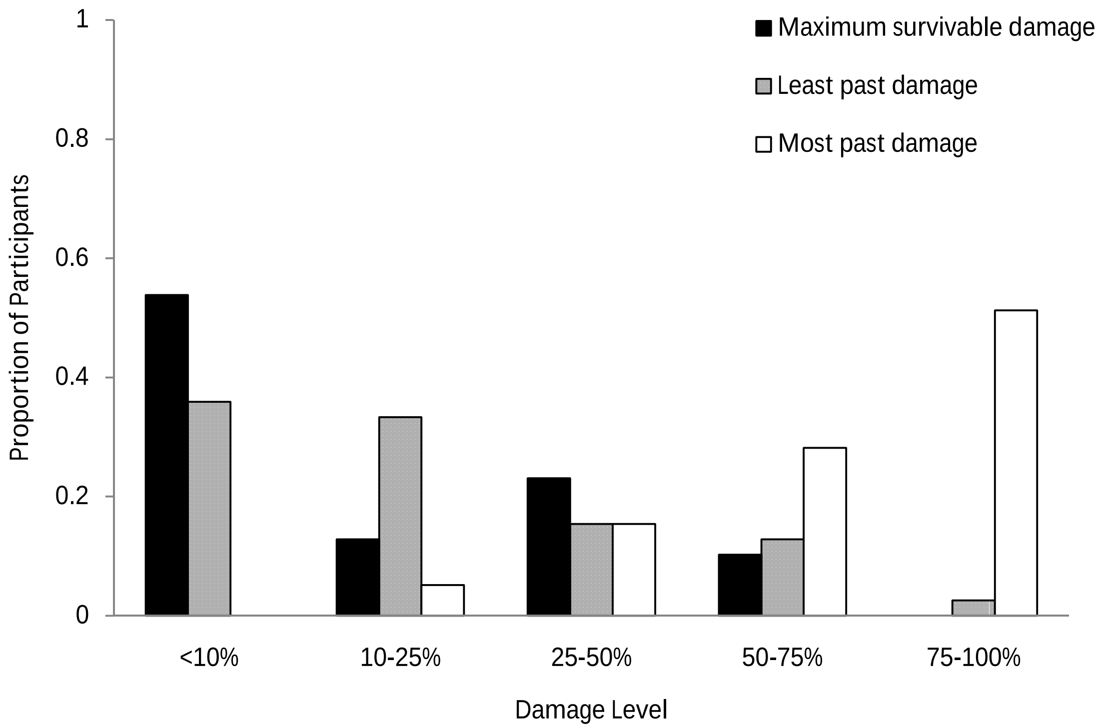

Figure 1.6. Proportion of participants who reported the level of corn crop damage they were able to withstand and still have enough corn to feed their families and the proportion of participants who reported the minimum and maximum amounts of crop damage they had experienced in the past. Damage levels were presented pictorially to participants who were asked to choose a level of damage. Note: the proportions on the y-axis sum to 1; n=39.

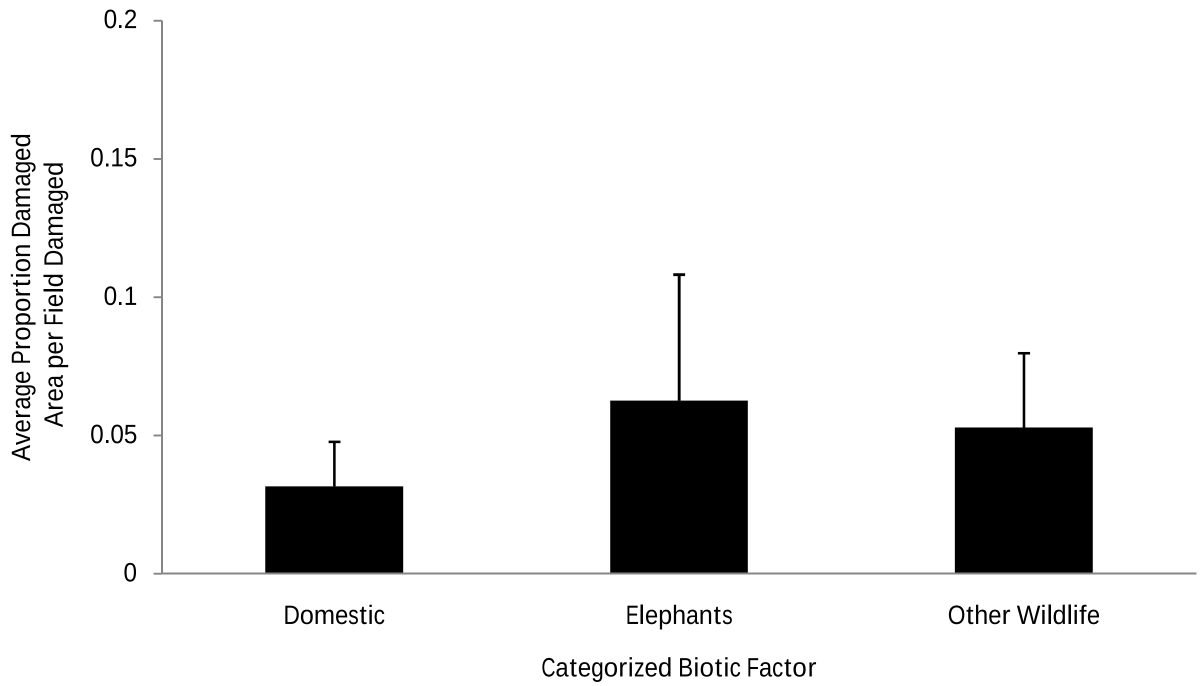

Figure 1.7. Proportion of area per field damaged by each categorized biotic factor. Note: Scale of y-axis is a proportion, but for the sake of clarity is truncated to 0.2; Domestic n= 8, Elephants n= 2, Other Wildlife n= 9.

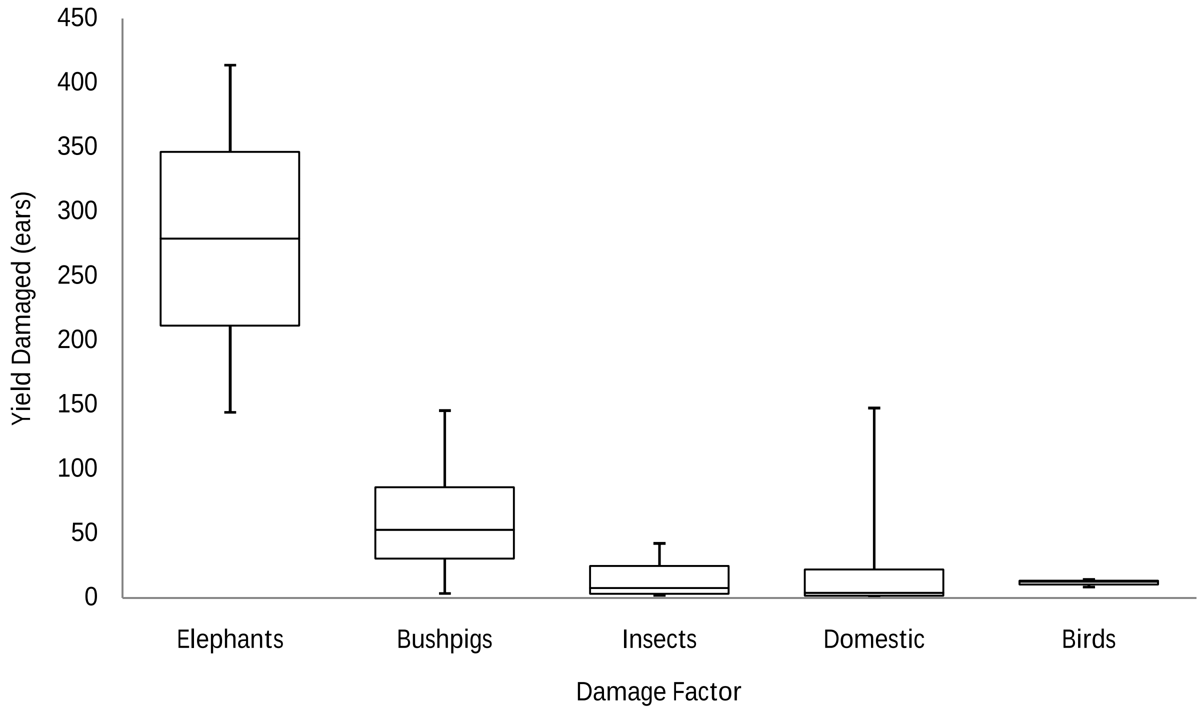

Figure 1.8. Damage occurring in measured fields attributed to several damage factors. Upper box marks the third quadrant and lower box indicates the first quadrant with the dividing line marking the median and bars encompass the full range of measured data.

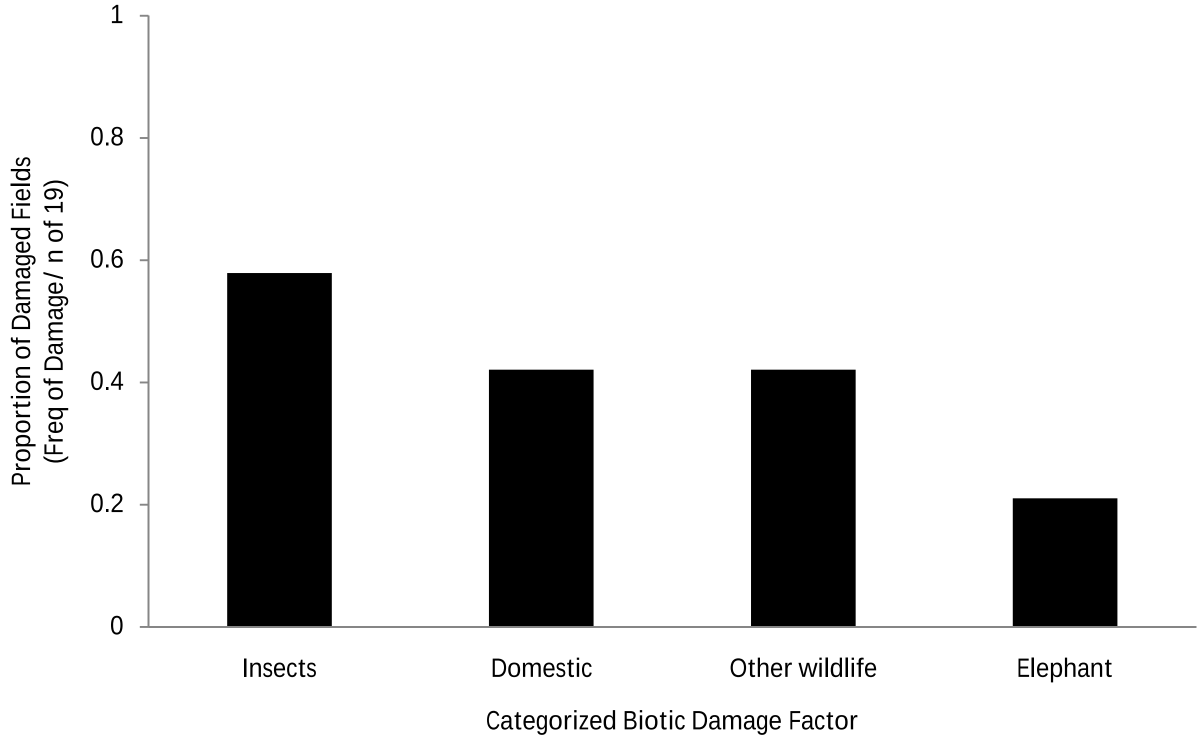

Figure 1.9. The proportion of damaged fields by biotic factors as attributed to insects, domestic animals, other wildlife and elephants. The fields could have multiple sources of damage so values sum to greater than one.

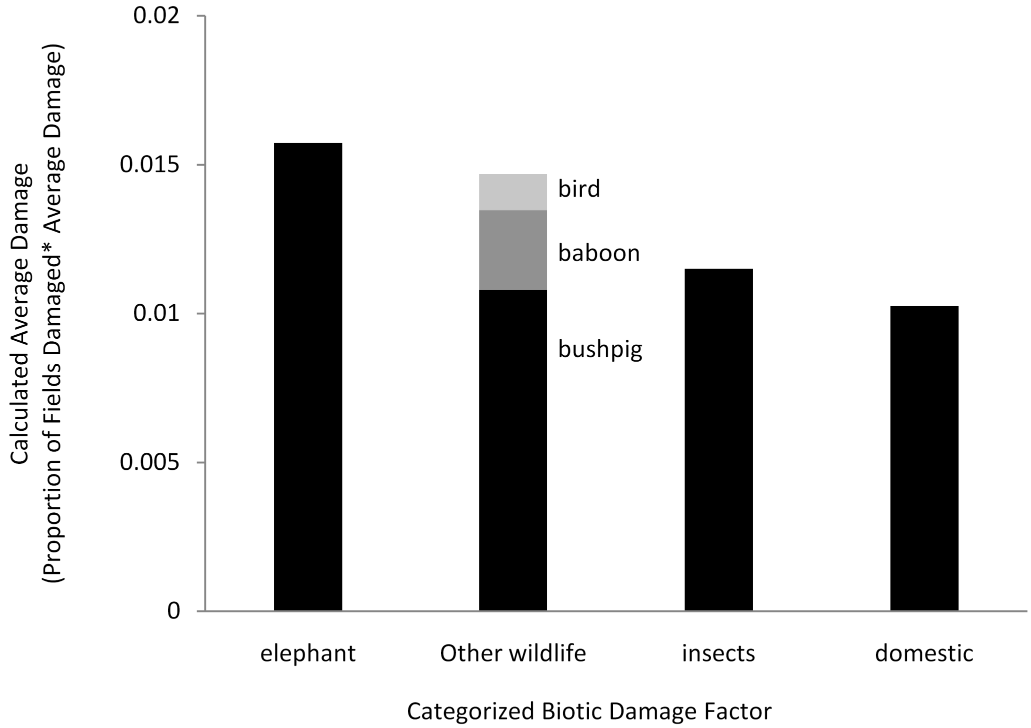

Figure 1.10. The proportion of fields damaged multiplied by the average proportion of damage as attributed to categorized biotic damage factors. The sum of bushpigs, baboons, and birds (categorized into "other wildlife") exceed all but elephants. Note: Scale of the y-axis is a proportion, but for the sake of clarity has been truncated at 0.02.

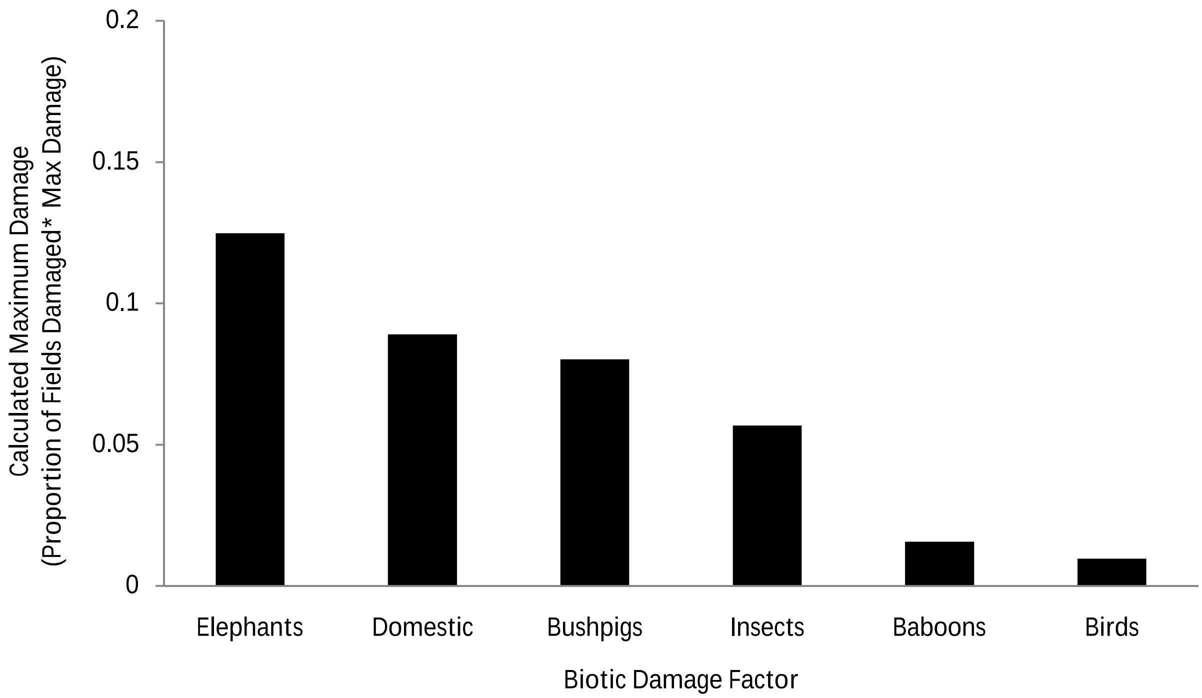

Figure 1.11. Proportion of fields damaged multiplied by the maximum damage proportion of a field by each biotic damage factor. The sum of bushpigs, baboons, and birds (categorized into "other wildlife") exceed all other biotic damage factors. Note: Scale of the y-axis is a proportion, but for the sake of clarity has been truncated at 0.2.

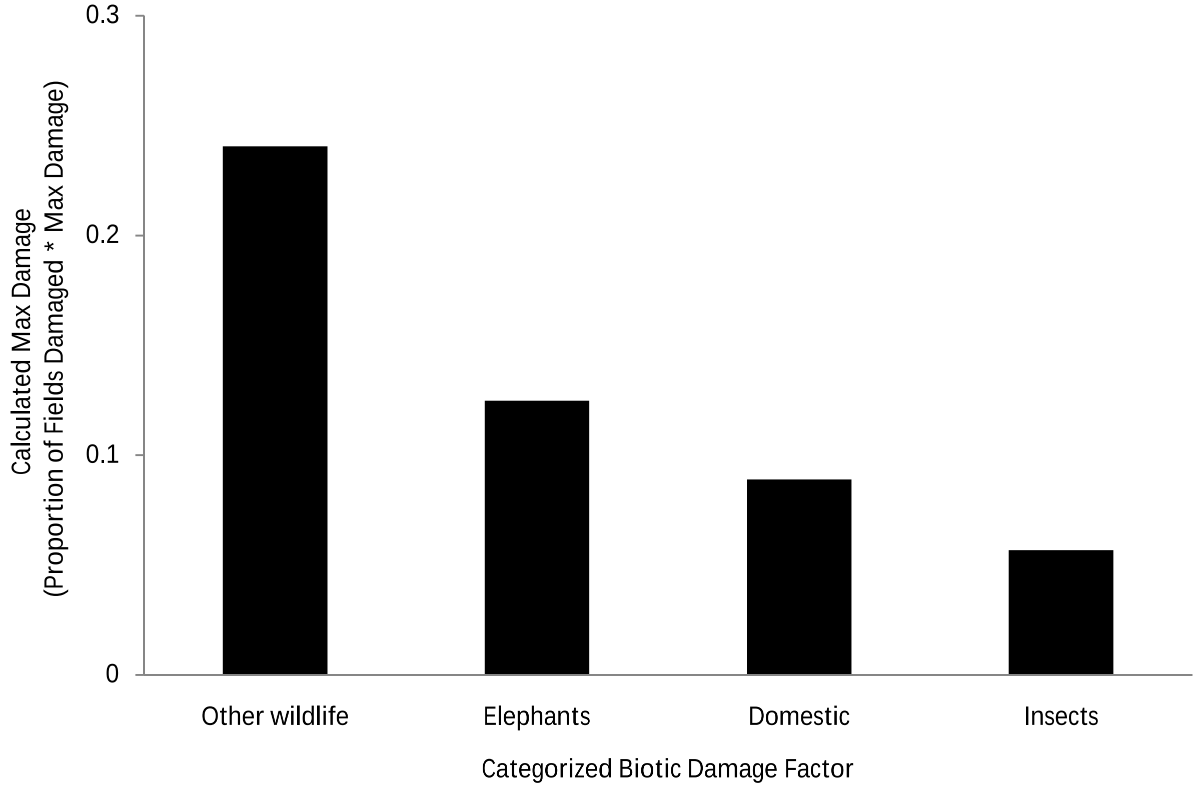

Figure 1.12. The proportion of fields damaged multiplied by the maximum damage proportion of a field while categorizing bushpigs, baboons, and birds into "other wildlife." Note: the maximum possible value on the y-axis is 1, although the axis has been truncated at 0.3.

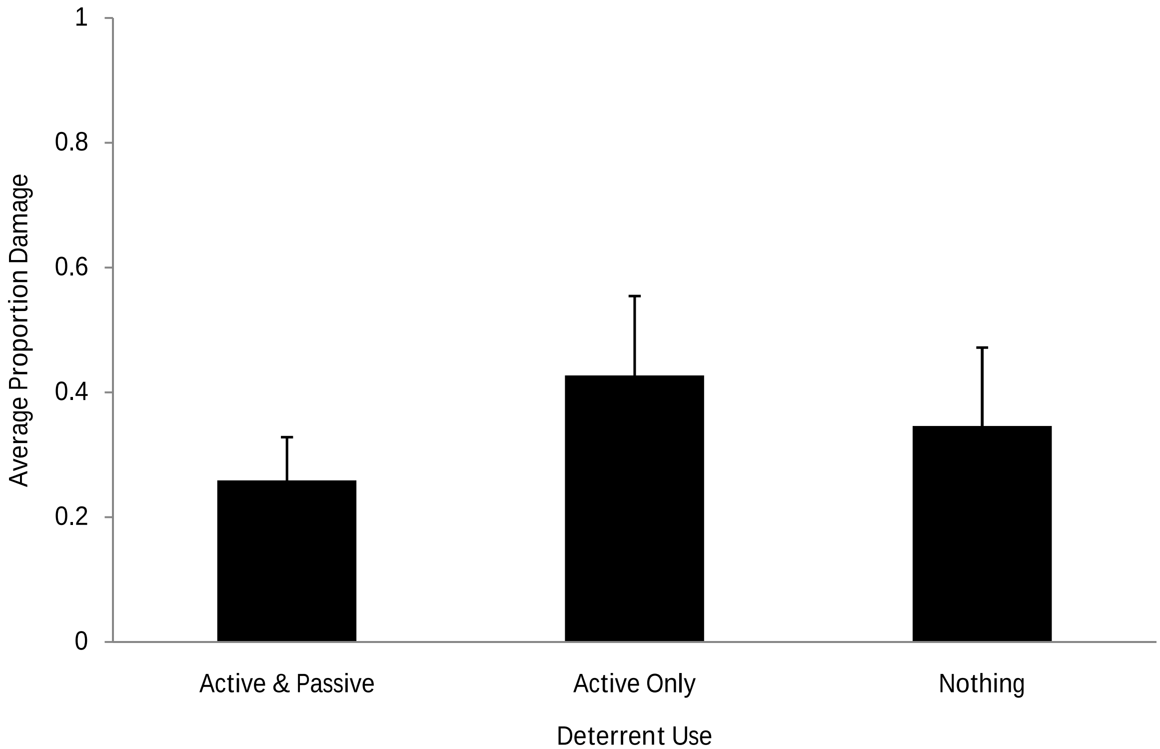

Figure 1.13. Damage experienced in fields that used a combination of active and passive deterrent methods (n=6), active deterrents only (n=6), or no deterrents (n=2).

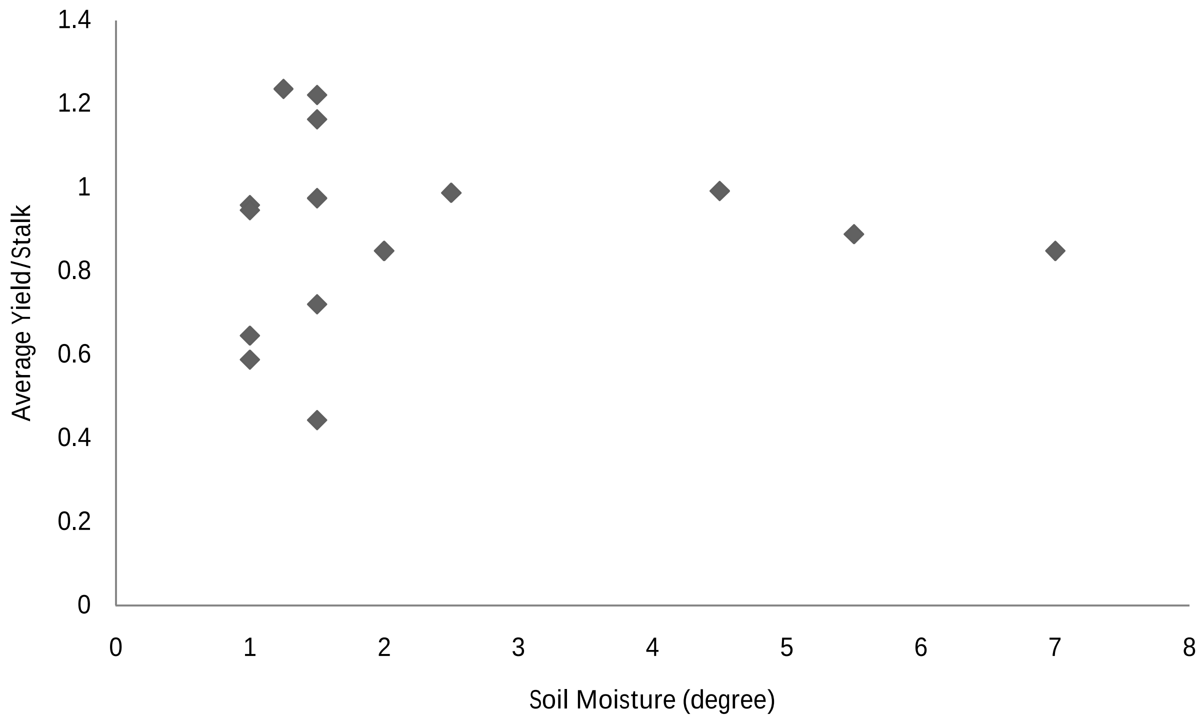

Figure 1.14. Relationship of the estimated average yield of corn per stalk in a field to the measured level of soil moisture; n= 15 (including one field with adequate measure of these two variables, but that did not have adequate measure of macro-damage).

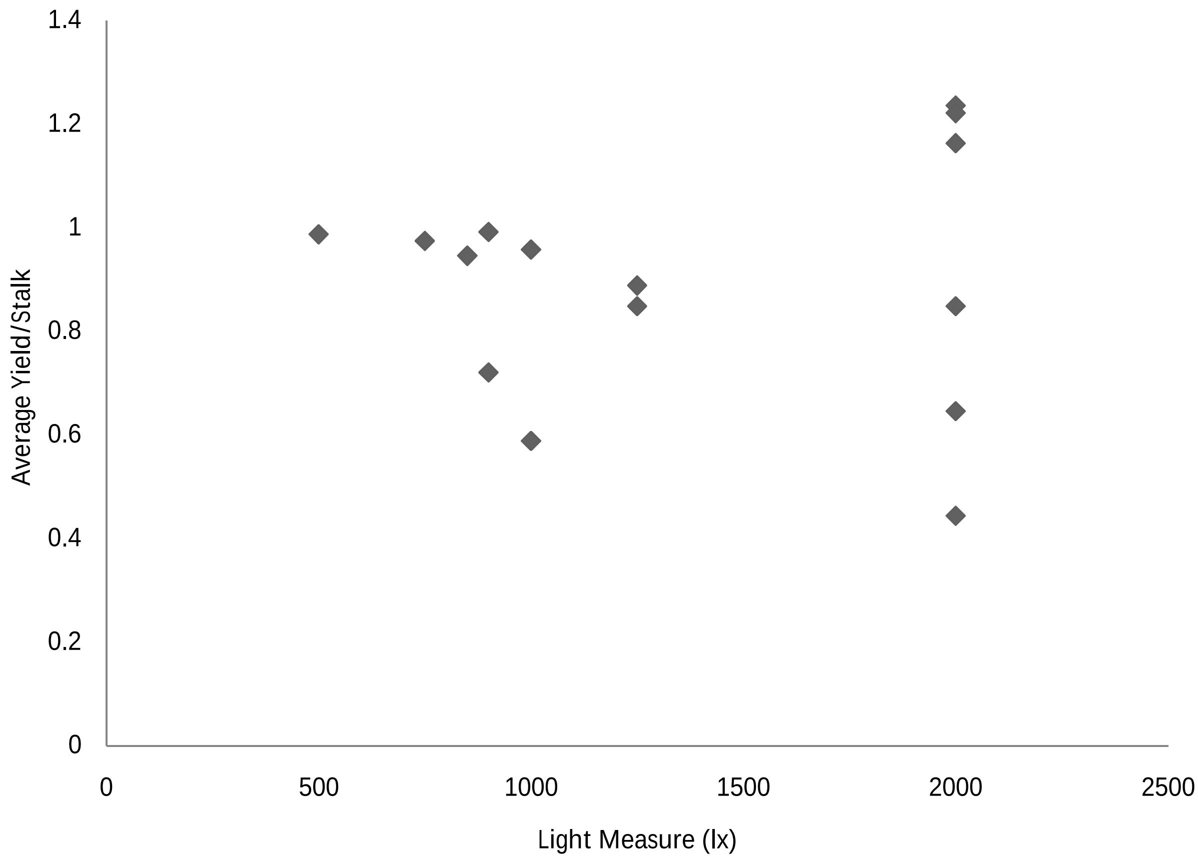

Figure 1.15. Relationship of estimated average yield per stalk to the measured light readings; n= 15 (including one field with adequate measure of these two variables, but that did not have adequate measure of macro-damage).

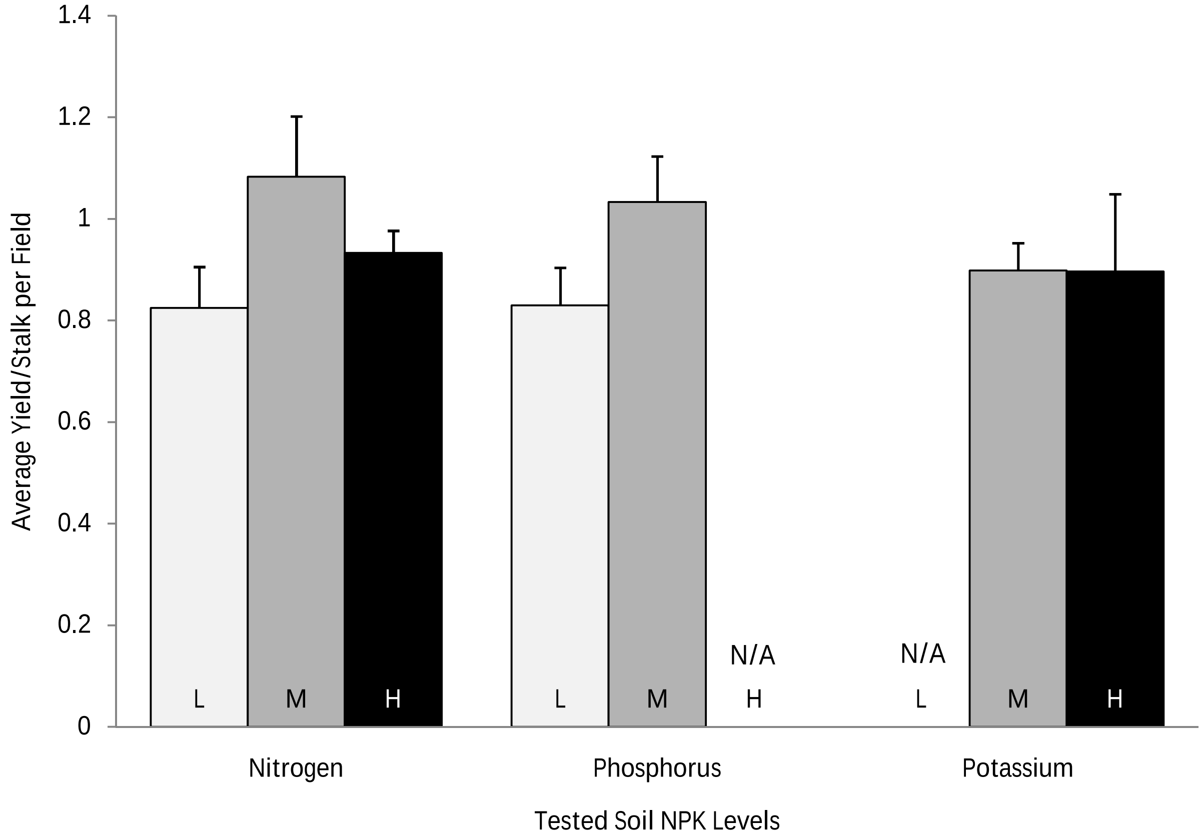

Figure 1.16. Association of levels of Nitrogen (N), Phosphorous (P), and Potassium (K) with corn crop success. No patterns were evident among the sampled fields (Low Nitrogen n=9, Medium Nitrogen n=3, High Nitrogen n=3, Low Phosphorus n=10, Medium Phosphorus n=5, High Phosphorus n=0, Low Potassium n=0, Medium Potassium n=10, High Potassium n=5) (L – Low; M – Medium; H – High).

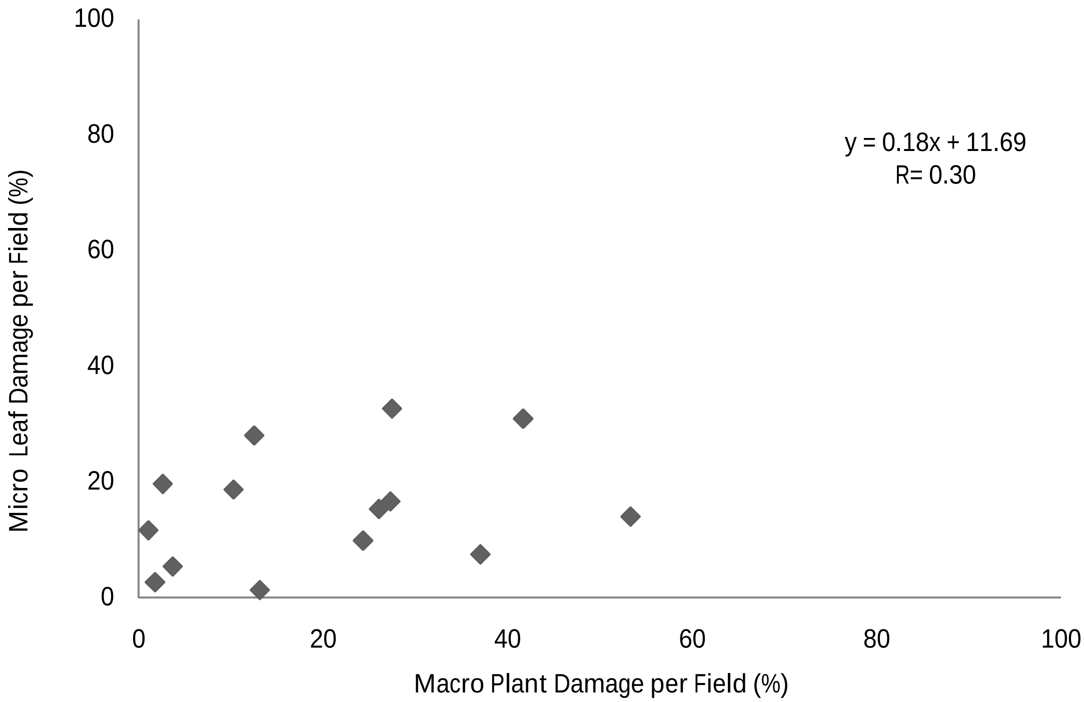

Figure 1.17. The association between the average micro leaf damage and the average macro plant damage attributed to both insects and a lack of water in individual fields, n= 14.

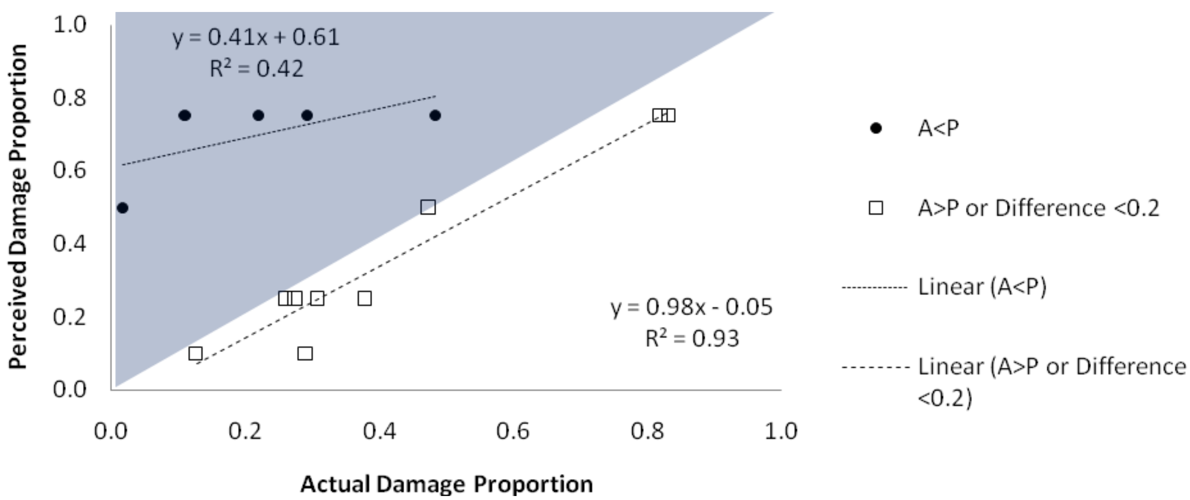

Figure 1.18. Perceived verses actual damage proportions. Nine participants were accurate in their perception of crop damage experienced (n=9). Five participants overestimated crop damage experienced (n=5). Shaded area indicates overestimation, while data points that are not shaded did not overestimate damage to their fields.

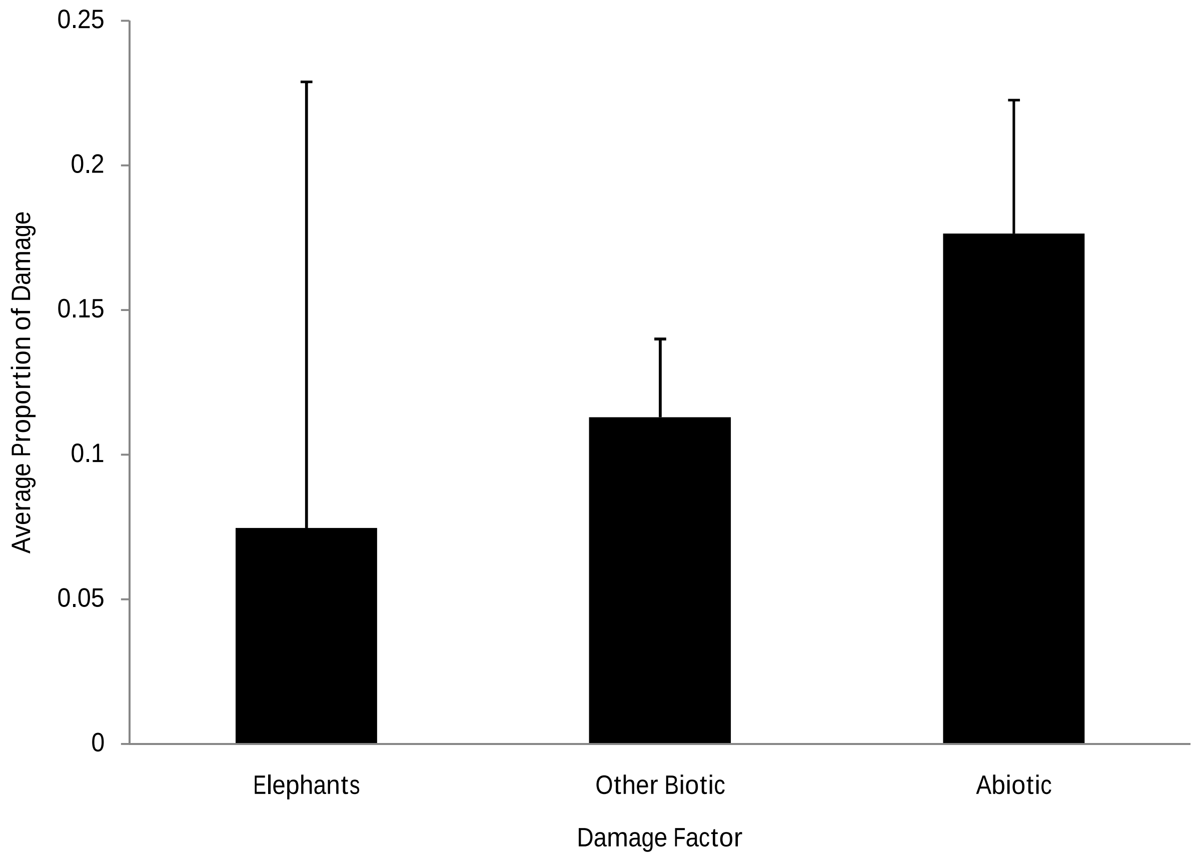

Figure 1.19. Average proportion of damage attributed to categorized damage factors. Note: Scale of the y-axis is a proportion, but for the sake of clarity has been truncated at 0.25; n= 14.

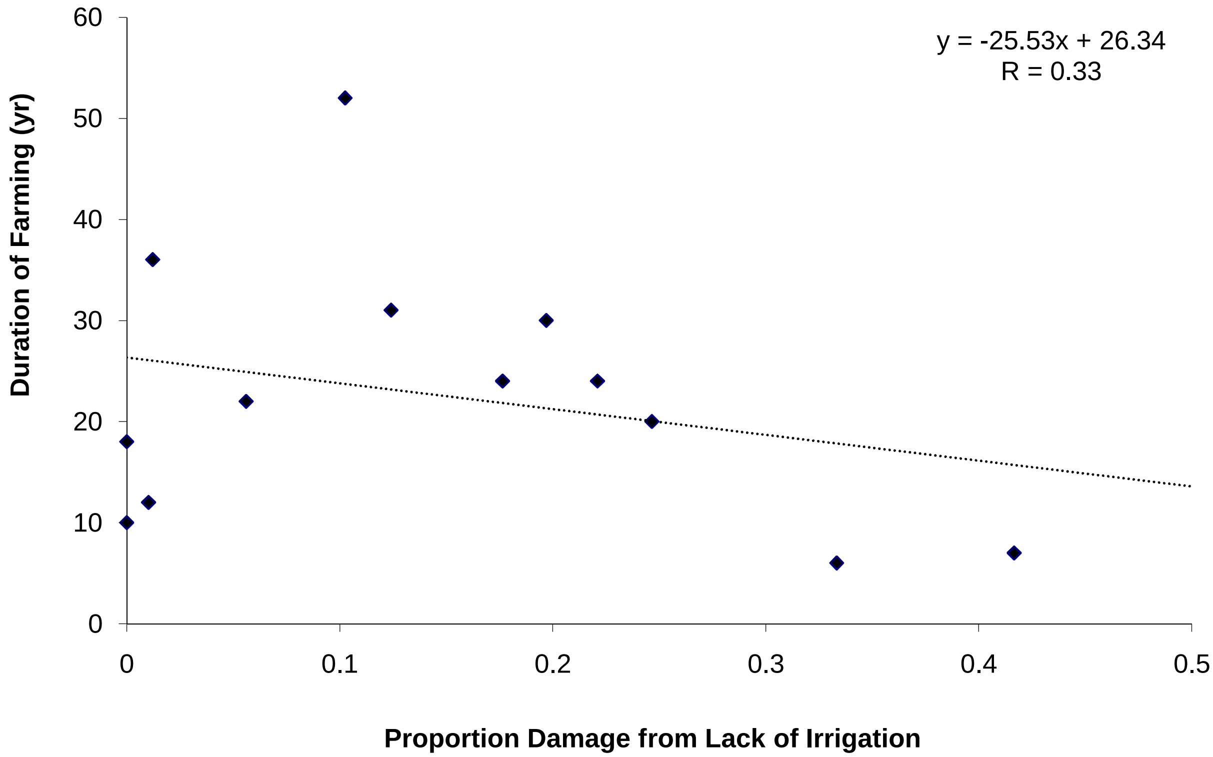

Figure 1.20. The association between the duration participants had been farming and the proportion of field damaged from a lack of irrigation. Note: Scale of the x-axis is a proportion, but for the sake of clarity has been truncated at 0.5; n= 14.

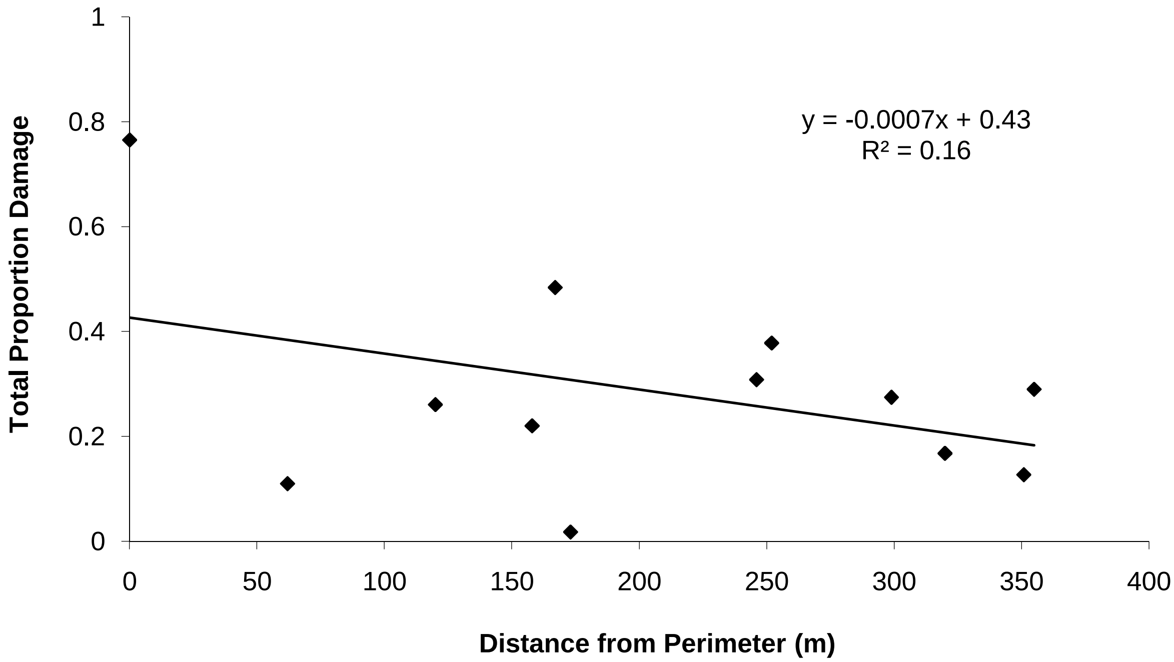

Figure 1.21. The total proportion of damage in corn fields relative to their distance from the village perimeter. Note: Negative distances indicate fields that were outside the village perimeter and as the positive distance increases, the fields get nearer to the center of human habitation within the village; one outlier was eliminated from this figure which was 492 meters outside the village perimeter; n= 13.

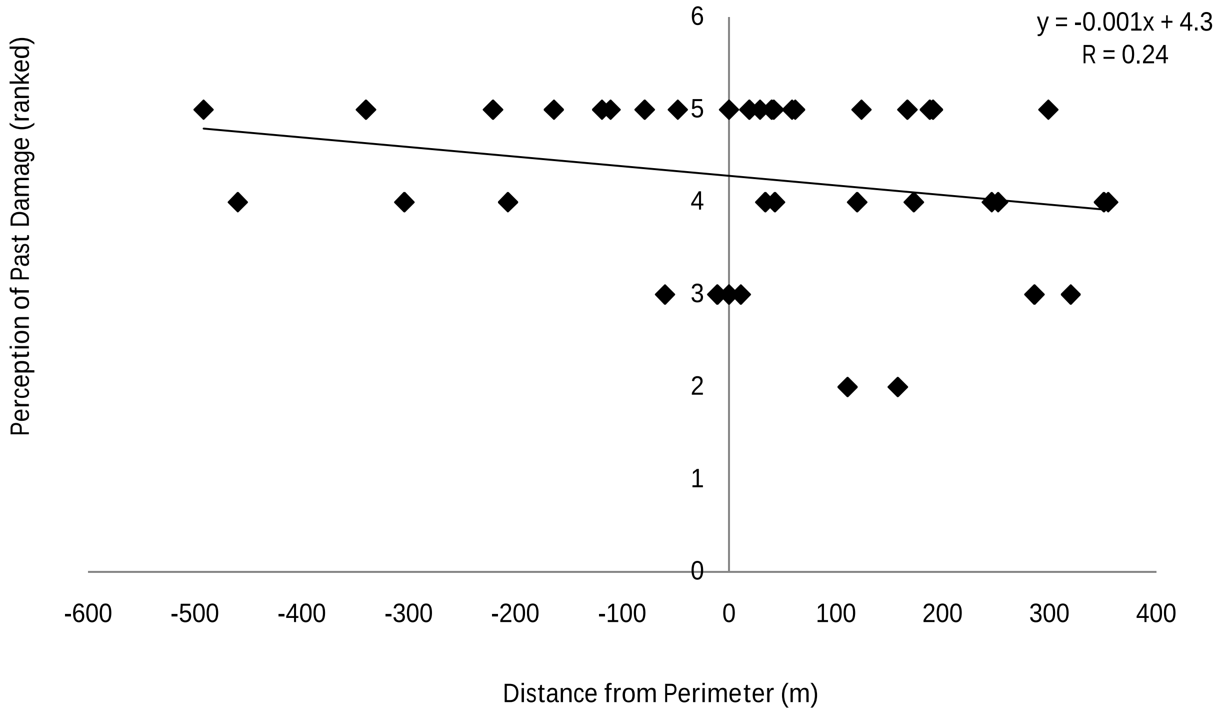

Figure 1.22. The association between past damage to fields perceived by farmers and the distance from the perimeter of Miti Mirefu. Note: Negative distances indicate fields that were outside the village perimeter and as the positive distance increases, the fields get nearer to the center of human habitation within the village; n= 39.

CHAPTER 2

AN INVESTIGATION OF DETERRENT PROPERTIES OF AFRICAN ELEPHANT (*Loxodonta africana*) EXUDATES USING BIOASSAYS

ABSTRACT

The growing population of Africa is leading to greater contact between humans and elephants, thereby increasing human-elephant conflict (HEC). Despite efforts to mitigate conflict, crop raiding by African elephants (*Loxodonta africana*) has become a growing source of contention between the two species. Traditional deterrent methods are ineffective and although some innovative techniques have met with some success, they are lacking in feasibility. Chemical communication is an integral component to the society of African elephants. The exudates of elephants, including urine and temporal gland secretions (TGS), carry chemical signals, which are used to honestly advertise the reproductive state of males and females. Receivers are attracted or repelled based on the composition of volatile chemicals within the excretion of the sender and the receiver's reproductive state. Compounds found in the exudates of elephants have been isolated and identified. (*E,E*)-farnesol is a sesquiterpene alcohol that has been identified in the TGS of African elephants. 3-pentanone is a ketone that is characteristic of musth male urine volatiles. The objective of this study was to determine if (*E,E*)-farnesol or 3-pentanone were active compounds that could act as deterrents by communicating a keep-away signal or attractants to lead elephants elsewhere. Bioassays were performed on wild African elephants at Ndarakwai Ranch in Tanzania. This study suggests that (*E,E*)-farnesol and 3-pentanone are not active components communicating a chemical signal, which could be due to the specific concentrations and ratios of compounds found in elephant exudates. The continued testing of compounds identified in elephant exudates is recommended. With the identification of an active compound that could be used to communicate a meaningful keep-away signal, HEC, particularly crop raiding, could be reduced.

INTRODUCTION

Human-wildlife conflict (HWC) encompasses all negative interactions between humans and wildlife. Costs of HWC include the loss of human lives, property, or opportunities (Messmer 2000). The growing conflict between humans and elephants tangibly affects all three aspects and is therefore the most publicized and relatable example of HWC. Costs to the local communities include property damage, human injury or death, competition over water resources, social disruptions (such as scheduling school around elephant activity patterns), the loss of productivity due to choosing guard duties over sleep, and crop depredation and destruction from raiding (Kangwana 1995, Osborn & Parker 2003a, Kiiru 1995, Hoare 1999a, Tchamba 1996, Naughton et al. 1999).

In Africa, human-elephant conflict (HEC) is a mounting problem that creates tension between humans and elephants. The population in East Africa is growing at an exponential rate and as more land is used to feed larger communities, wilderness areas are being cultivated (Vanleenwe & Lambrechts 1999, van Aarde & Jackson 2007). The growth of the population of subsistence farmers has caused a strain on protected areas available to elephants, as well as an increase in contact between humans and elephants, leading to a rise in HEC (Osborn & Parker 2003b, Hoare 1999a). The increase in negative interactions between humans and elephants necessitates the implementation of viable deterrent methods.

Subsistence farmers have used numerous active and passive techniques to deter elephants from damaging their crops. Active deterrents require human presence such as night guarding, lighting fires, banging on pots, and yelling. Such activity is not only exhausting for the farmers, but can contribute to the habitat change as fuel for the fires is used throughout the night (Osborn & Hill 2005). Passive deterrents are present at all times and include trenches, vegetative barriers, fences, or open spaces between forested land and crop land (Osborn & Parker 2003a, 2002, Sitati & Walpole 2006). However, the great size, strength, dietary flexibility, adaptability, and nocturnal activity patterns of elephants makes them formidable crop raiders who are not easily stopped with these traditional techniques (Osborn & Hill 2005).

Recently, more inventive techniques have been designed to enhance farm productivity and to curb crop damage. Open-pollinated varieties of maize are being developed to withstand even the harshest drought conditions so that agriculturalists can harvest in the dry season, boosting their productivity throughout the year (Osborn & Parker 2002). Beekeeping and chili peppers (*Capsicum* spp.) have been investigated as providing a form of deterrent, and a form of potential income (honey and peppers). Elephants retreat away from bees (King et al. 2007) and do not eat chili peppers (Parker & Osborn 2006). While land use planning would be an effective way to dissuade elephants from entering agricultural communities, it is not feasible to coordinate entire communities of agriculturalists to relocate (Osborn &

Parker 2002). The above techniques must be used in different combinations and constantly rotated because elephants are incredibly adaptable (Sitati & Walpole 2006). Therefore, it is advantageous to explore further inventive techniques that can alleviate elephant crop raiding. Exploring the extensive use of chemical communication by elephants may provide insight into developing a chemically relevant deterrent.

Elephants are long-lived social mammals that exhibit the potential of learning within and among different social groups; this learning transmits across generations as culture (Rendell & Whitehead 2001, Bates et al. 2007). Elephant social groups are primarily matriarchal and comprised of related adult females with juvenile to sub-adult females and males (Douglas-Hamilton 1972). Once males reach sexual maturity at approximately 14 years old, they begin to disperse from their natal herd becoming solitary animals. Young adult males form small bachelor groups for protection, but once they reach social sexual maturity, which is the ability to physically challenge for females, they will disperse once again searching for reproductive viable females (Vidya & Sukumar 2005).

Because adult males often travel singly, they have to locate female-led herds to reproduce. Males do this through vocal calls and chemical signals. Males are able to distinguish estrous females from non-estrous females from urine (Bagley 2004, Bagley et al. 2006). Likewise, females chemically evaluate prospective males, favoring males in the rut-like state of musth (Poole 1989a). Males in musth release copious pungent chemical signals (Hollister-Smith et al. 2007). The state of musth is an honest signal which is advertised to conspecifics through chemical signals (Schulte et al. 2007). For the duration of musth, the male's social status is affected, as he displays increased socialization toward females and increased aggression toward males (Ganswindt et al. 2005). A male in musth is dominant over non-musth males regardless of size; outside of musth, larger bulls are dominant over smaller males (Poole 1989b).

A potential deterrent could combine a natural chemical signal and the elephant's ability to learn to associate natural "keep-away" cues with the presence of a crop. Asian elephants, especially subordinate males and luteal (unreceptive) females, perform a high rate of investigatory chemosensory and avoidance behaviors upon approaching secretions from musth bulls (Rasmussen & Krishnamurthy 2000). This response indicates that exudates contain sexual and warning pheromones that affect interactions with both males and females (Rasmussen et al. 1990). Such a response from male elephants would be instrumental in communicating a "keep-away" signal to adult and subadult males, who are responsible for the majority of crop raids (Hoare 1999b).

Rasmussen and Riddle (2004) tested the association of a natural chemical occurring in the Asian elephant's musth state with a mechanical device that proved to be an effective physical barrier. As the elephants learned to associate the musth male odor with the hardship of passing the mechanical device, the number of devices around a field could be reduced. This study suggests that a combination of biologically relevant signals with physical barriers should be more thoroughly investigated, as it may be a highly effective deterrent (Rasmussen & Riddle 2004). Researchers have begun to investigate the possibility of using an elephant's natural "keep away" chemical compound in a technique similar to that of using chili oil and grease on string ropes as barriers (Osborn & Rasmussen 1995, Sitati & Walpole 2006). The difference is that in the case of chili pepper resin, the elephant needs to contact the material to trigger their trigeminal system (Osborn & Rasmussen 1995).

Exudates of Asian elephants contain a multitude of chemical compounds, several of which play an active role in chemical communication. Specifically, (Z)-7-dodecenyl acetate (Z7-12:Ac) was identified and confirmed as a meaningful estrous signal in the urine of female Asian elephants (Rasmussen et al. 1997). The urine of African elephants contains several thousand different chemical compounds (Rasmussen & Krishnamurthy 2000), over 200 of which have been identified (Goodwin et al. 2005). Investigations of responses to the identified compounds will clarify their importance in the chemical communication of African elephants.

Some of this work has been conducted by Bruce Schulte and his graduate students at Georgia Southern University. Captive African male elephants performed more chemosensory behaviors toward urine collected during a female's follicular (sexually receptive) stage than urine collected during a female's luteal (unreceptive) stage (Bagley et al. 2006). Furthermore, Meyer et al. (2008) found that captive female elephants made more contacts to the urogenital area of females approaching ovulation. Loizi (2004) and Loizi et al. (2009) examined the differences in chemosensory behavior of wild and captive elephants. Vyas (2006) conducted a similar study on wild African elephants at Ndarakwai Ranch and found that males performed more chemosensory behaviors than females around a waterhole. Castelda (2008) and Nasseri (2009) performed bioassays on various compounds identified in elephant exudates to determine which compounds are meaningful chemical signals. Castelda (2008) bioassayed *endo*-brevicomin, *exo*-brevicomin, *E,E,*-α-farnesene, and frontalin, which are compounds found in elephant urine (Rasmussen & Greenwood 2003).

Elephants also have a temporal gland that releases chemicals (Rasmussen et al. 1990). In African elephant TGS (temporal gland secretion), 16 compounds have been identified (Rasmussen et al. 1996, Greenwood et al. 2005). In many cases, the compounds found in Asian elephants have also been found in African elephants. Nasseri (2009) bioassayed 2-decanone, 2-nonanone, and cyclohexanone, chemicals found in the TGS of Asian musth males. The compound 2-nonanone is also found in African elephant urine. The compounds tested previously have not acted as significant attractants or deterrents. The present study further examines two compounds found in exudates of African elephants.

(*E,E*)-farnesol ($C_{15}H_{26}O$) (Figure 2.1), a sesquiterpene alcohol, was among the first compounds identified in the temporal gland secretions (TGS) of African elephants (Wheeler et al. 1982, Goodwin et al. 1999, 2002). In addition, (*E,E*)-farnesol is widely distributed in nature, particularly in the glandular secretions of insects, serving as a communication tool for recognition, mate attraction, and territorial marking (Wheeler et al. 1982, Lee et al. 2007). Recently, (*E,E*)-farnesol was confirmed to be the main component in the anal scent gland extract of the nutria (*Myocastor coypus*); the identification of a meaningful chemical signal could be used to attract nutria for population control measures (Lee et al. 2007). Similarly, identification of the meaningful signal in African elephant TGS could be used to either attract or repel elephants, thus preventing them from damaging crops.

The ketone, 3-pentanone ($C_5H_{10}O$) (Figure 2.1), is a colorless liquid at room temperature with a scent similar to acetone. Volatile molecules of this compound are found in the headspace of urine from pregnant female Asian elephants (Rasmussen & Krishnamurthy 2000). Male elephants are not attracted to pregnant females, as they are not sexually receptive. Therefore, if 3-pentanone is the active compound in the urine of pregnant African elephants, males will not pursue or ignore samples of this compound. However, similar ketones have been identified in the urine of musth males (Rasmussen & Wittemyer 2002). Therefore, it is likely that 3-pentanone is found in musth urine and could elicit chemosensory or avoidance behaviors in post-pubescent males.

METHODS

Study Site

Ndarakwai Ranch, Tanzania

This study was conducted from June 2008 to September 2008 on Ndarakwai Ranch in the Kilimanjaro District of northern Tanzania. Ndarakwai Ranch is a semi-protected area with anti-poaching ranger patrols but almost no fences to inhibit the movement of wildlife. It encompasses 4300 hectares of woodland and savannah habitat. Elephants move freely through the ranch, which serves as a wildlife corridor for elephants moving among Amboseli National Park (Kenya), Arusha National Park, and Kilimanjaro National Park (Figure 1.1). Several previous students have studied elephants, including HEC and elephant chemical ecology at Ndarakwai Ranch.

Waterhole

The ranch contains a permanent 4300 m^2 waterhole fed by water diverted from the Ngare Nairobi River. Adjacent to the waterhole is a 6-meter high observation platform ideal for viewing behaviors of elephants and other fauna gathering at the waterhole. Focal animal sampling was performed from the platform, affording the viewer minimal obstacles. Elephant identification files were initiated in 2004 and maintained through 2008; the files include pictures and descriptions of animals that enable researchers to determine which animals have used the waterhole before, and which animals are new to Ndarakwai.

Samples Tested

I tested elephant responses to two compounds found in elephant urine and TGS; (*E,E*)-farnesol and 3-pentanone (Figure 2.1). Synthesized compounds were purchased from Phero Tech Inc. This was a blind study, as the identities of the compounds were unknown at the time of testing. Samples were placed in solution with either water or elephant urine in natural concentrations (100 µl compound / 500 ml water or urine) (T.E. Goodwin, pers. comm.). A solution of vanilla extract and water or urine (5 ml vanilla extract/500 ml solvent) was used as a control when testing the corresponding solvents. In past studies vanillin, a natural component in Asian elephant urine, or synthetic vanilla extract, has elicited a low but regular level of response in both Asian and African elephants (e.g., Schulte & Rasmussen 1999; Bagley et al. 2006).

Elephant urine was used as a higher response control because of its African elephant origin. Rasmussen et al. (1997) bioassayed luteal urine from female Asian elephants. Additionally, they added synthetic versions of *Z*-7-dodecenyl acetate were added to the luteal urine and bioassayed. Following the protocol of Rasmussen et al. (1997), I used female elephant urine as a solvent. As the natural solvent, urine may facilitate bioactivity by increasing the likelihood of binding to chemosensory receptors in the elephant. In the present study, the female African elephant urine was collected from a 10-year-old orphan who is cared for at Ndarakwai Ranch. Urine was collected the evening before the bioassays were set up and was discarded 24 hours after collection if unused.

The reproductive condition of this female was not known as I did not measure her reproductive hormones. Typically, ten years of age would be early for elephants to first cycle; however, in captivity, females may begin cycling at this age or younger (Rasmussen & Schulte 1998). Because behavioral indicators of estrus involve social interactions (Vidya & Sukumar 2005) and the urine donor was a solitary animal, evaluation of her estrous state was not possible by this means. Because I assumed that the female was not cycling, I examined whether responses varied over time to a sample assayed in urine. If the female was cycling and urine was acquired from the follicular and the luteal phase, I expected responses to vary accordingly.

Bioassay Protocol at the Waterhole

Upon arrival at the waterhole, locations for bioassays were established based on their visibility from the viewing platform and the frequency that elephants visited a particular area of the waterhole. Sites were within 10 m of the water and spaced at least 10 m apart to ensure that one elephant could not be in proximity (within one body length) to more than one sample. To prepare a site for the sample, the earth was leveled and saturated with water to slow absorption. Sites were marked using natural available visual aids such as rocks and sticks placed at least 2 m from the actual sample.

When I saw a group of elephants coming toward the waterhole, I poured samples of one compound in designated sites. Usually there were two sites designated for the compound and two sites designated for the control. When elephants came within proximity of a sample, they were videotaped using a Hitachi DZ-HS300A 8GB HDD (25x optical zoom) digital video recorder so that multiple elephants' reactions could be examined later. During an elephant group's visit to the waterhole, the ages, sexes, and any identifying characteristics were recorded in a field notebook. I stopped video recording if the elephants remained at the waterhole two hours after the samples were placed because by this time samples were usually trampled and buried from the elephant traffic. If multiple groups of elephants visited the waterhole, then I replenished the samples every two hours throughout the day. If a group approached the waterhole when there were already elephants present for over two hours, they were not included in the sample set. At the end of the day, the sites were rinsed with water and the markers were disassembled.

Data Collection from Video

When the field season had concluded, videos were categorized by samples tested and watched chronologically. The acquisition of data from video aided in confirmation of elephant identification, group size determination, and aging and sexing individuals within the elephant groups. The exact ages of elephants at Ndarakwai Ranch are unknown. Therefore, age classes were estimated based on morphological features such as shoulder height and tusk size (Moss 1996). Age classes were defined as calves (0-4 years), juveniles (5-9 years), sub-adults (10-19 years), and adults (>19 years). For data analysis, sub-adults and adults were combined and classified as post-pubescent (PP) (Napora 2007). Only PP individuals were included in the analysis.

Exact durations spent in proximity to a sample were recorded for each individual elephant. Focal animal sampling with continuous recording (Altman 1974, Martin & Bateson 2007) was used to identify behaviors of elephants that were within proximity to the samples placed. Behaviors were classified using a modified ethogram developed to identify chemosensory and avoidance behaviors (Table 2.1). All trunk behaviors directed toward the sample were recorded during the period that they were within proximity to that sample.

Bioassay Analysis

The duration that post-pubescent female and male elephants spent in proximity (within one body length) to the control and the sample was compared using a pairwise t-test when data fit the assumptions of normality and equal variance. When data did not fit the normal distribution, the data were log-transformed. If the assumptions of normality and equal variance were still not met, a Wilcoxon Signed Rank (WSR) test was performed (Sokal & Rohlf 1995). The same analysis was performed for two behavior rates (all chemosensory behaviors performed per proximity and avoidance behaviors performed per proximity) for post-pubescent elephants that approached both the compound and the control sample. If one elephant visited the same sample on multiple days, the average durations and rates were used for those animals. Only elephants that were in proximity to the test and control on the same day were considered for the matched pair analysis. The rate of behaviors was determined by calculating the average frequency of behavior performed per instance of proximity for each animal and taking the weighted mean of post-pubescent males and post-pubescent females. The proportion of elephants that came within proximity to the sample and performed any chemosensory or avoidance behaviors was calculated. Proportions of post-pubescent elephants performing chemosensory and avoidance behaviors toward the sample and the control were analyzed using a Chi-square goodness of fit test. All statistical analyses were tested to a 95% confidence limit ($\alpha = 0.05$) using JMP 8.0 (SAS Institute 2008). Descriptive statistics are displayed as mean (± S.E.).

RESULTS

Samples were placed in preparation for bioassays around the waterhole on 39 of 113 days spent at the waterhole (35%). There were 247 elephants individually identified in proximity to the samples, although only 211 elephants were in proximity to the test sample and the control sample on the same day (Table 2.2). The sample size of post pubescent females visiting (*E,E*)-farnesol and urine was 16, but the remaining sample sizes were greater than or equal to 20.

(*E,E*)-Farnesol

Water solvent

(*E,E*)-farnesol was bioassayed for ten days during the month of July 2008. Seventy-two elephants were observed in proximity to the sample and the control, forty-nine of which were post-pubescent. The proportion of post pubescent female or male elephants that performed chemosensory behaviors toward (*E,E*)-farnesol or the vanilla extract in water control did not significantly differ (females: $\chi^2 = 3.21$, df = 1, p = 0.07; males: $\chi^2 = 0.38$, df = 1, p = 0.54; Table 2.4). The proportion of avoidance behaviors performed toward (*E,E*)-farnesol and the control by females or males also did not differ significantly (females: $\chi^2 = 0.00$, df = 1, p = 1.0; males: $\chi^2 = 1.15$, df = 1, p = 0.28; Table 2.4). Post-pubescent females or males did not spend more time in proximity of (*E,E*)-farnesol than the control (females: $T_s = -25.5$, p = 0.55; males: $T_s = 20.5$, p = 0.49; Figure 2.2). Neither females nor males differed in the rate of chemosensory or avoidance behaviors performed toward (*E,E*)-farnesol and the control (females: $T_s = 22.5$, p = 0.08; $T_s = -1.5$, p = 0.75, respectively; males: t = -0.97, df = 20, p = 0.35; $T_s = 2.0$, p = 0.50, respectively; Figures 2.3, 2.4).

Urine solvent

The bioassays involving urine as a solvent occurred over eleven weeks. A typical elephant cycle is 12-18 weeks with the follicular stage spanning 4-6 weeks and oestrus lasting 2-10 days (Plotka et al. 1988). Careful examination of the data collected shows no indication that this female was in estrus during the time of urine collection; there were no peaks of behaviors indicating more interest at any point throughout the 11 weeks of assays (Figure 2.5). Therefore, the data support the assumption that if the urine donor was cycling, it did not affect the behavioral responses observed.

The urine solvent was bioassayed with (*E,E*)-farnesol and the control, vanilla extract, on ten days in July and August 2008. Sixty-one elephants were observed in proximity to mixtures of (*E,E*)-farnesol in urine and vanilla in urine, forty-five of which were post-pubescent sub-adults and adults. The proportion of post-pubescent female elephants that performed chemosensory behaviors toward (*E,E*)-farnesol in urine and vanilla in urine was identical ($\chi^2 = 0.00$, df = 1, p = 1.0; Table 2.4). The proportion of females performing avoidance behaviors toward the sample and the control did not significantly differ ($\chi^2 = 2.91$, df = 1, p = 0.09; Table 2.4). Post-pubescent males also did not differ in the performance of chemosensory and avoidance behaviors toward the two samples ($\chi^2 = 0.77$, df = 1, p = 0.09, $\chi^2 = 1.12$, df = 1, p = 0.29, respectively; Table 2.4). Females did not spend significantly different durations in proximity to (*E,E*)-farnesol in urine and the vanilla extract in urine control (t = -0.46, df = 15, p = 0.65; Figure 2.2). Likewise, post-pubescent males did not spend significantly different durations in proximity to these two samples ($T_s = 58.5$, p = 0.21; Figure 2.2). In addition, neither post-pubescent females nor males differed in the rate of chemosensory or avoidance behaviors toward (*E,E*)-farnesol in urine and the control (females: t = -0.63, df = 15, p = 0.54; $T_s = -1.5$, p = 0.50, respectively; males: t = 0.33, df = 28, p = 0.74; $T_s = -2.0$, p = 0.63, respectively; Figures 2.3, 2.4).

3-Pentanone

On 14 days in August and September 2008, samples of 3-pentanone and the vanilla extract in water control were bioassayed. Seventy-eight elephants were exposed to the samples, forty-one of which were post-pubescent. Females showed no difference in the proportion of chemosensory behaviors toward 3-pentanone and the control ($\chi^2 = 0.10$, df = 1, p = 0.76) and neither did males ($\chi^2 = 2.06$, df = 1, p = 0.36; Table 2.5). Post-pubescent females did not perform any avoidance behaviors toward 3-pentanone and the control, and only one adult male performed a single avoidance behavior toward 3-pentanone, resulting in similarly low proportions showing avoidance (females: $\chi^2 = 0.00$, df = 1, p = 1.0; males: $\chi^2 = 1.41$, df = 1, p = 0.23; Table 2.5). Post-pubescent females or males spent similar durations in proximity to 3-pentanone and the control (females: $T_s = -21.5$, p = 0.47; males: t = -0.12, df = 19, p = 0.9; Figure 2.6). Post pubescent females or males also did not differ in their rates of chemosensory or avoidance behaviors to 3-pentanone and the control (females: $T_s = 0.5$, $p = 1.0$; $T_s = 0.0$, $p = 1.0$: zero rate for avoidance; males: $T_s = -9.5$, $p = 0.44$; $T_s = -0.5$, $p = 1.0$, respectively; Figure 2.7).

DISCUSSION

The purpose of this study was to determine if naturally occurring compounds found in exudates of African elephants elicited attraction or avoidance responses in wild African elephants. Such compounds could facilitate the development of deterrent, or "keep away," methods that could reduce HEC (Schulte et al. 2007). The compounds are evolutionarily meaningful to elephants, reducing the likelihood of them quickly adapting to the deterrent.

The present study does not support the hypothesis that the single compound (*E,E*)-farnesol in either water or female African elephant urine solvent communicated a 'keep-away' signal. None of the analyses showed significant differences ($\alpha = 0.05$) in response to the experimental and control samples, and only two analyses yielded values of $p < 0.10$ (Table 2.3). The first indicates that post-pubescent females performed chemosensory behaviors at a higher rate toward (*E,E*)-farnesol than the control. The second suggests a larger proportion of post-pubescent females performed chemosensory behaviors toward the (*E,E*)-farnesol than the control. Yet, while none of the sixteen female elephants showed avoidance to the vanilla extract mixed with urine, only two performed avoidance behaviors toward (*E,E*)-farnesol and urine. However, the responses to (*E,E*)-farnesol in urine gave no indication that elephants were interested in this solution.

Similarly, post-pubescent elephants did not perform significantly differently toward 3-pentanone and the control mixed with water. The origin of 3-pentanone, as an ingredient in the urine of pregnant females, may account for the lack of bioactivity toward this compound. While elephants may not be repulsed by a compound that signals pregnancy, post-pubescent males may move away from such a signal because it indicates the female is not reproductively receptive. Although similar ketones have been found in the urine of musth males, the lack of bioactivity toward 3-pentanone suggests that it is not a component in communicating chemical signals, and it especially does not act as a 'keep-away' signal that would be useful in deterrents. Only one adult male exhibited avoidance behavior.

Although this study did not provide behavioral support for a naturally occurring signal that could act as a deterrent, it has eliminated (*E,E*)-farnesol and 3-pentanone from the list of elephant exudates that need to be tested for bioactivity as single compounds. It is possible that one or both of these compounds is important as part of a multi-component signal that only shows activity when all components are present in the appropriate ratios (Wyatt 2003). There are over 200 compounds identified from the TGS and urine from elephants (Rasmussen & Krishnamurphy 2000, Rasmussen et al. 1990). Any or all of them could function as part of an intraspecific signal. For applications to HEC management, the goal is to locate signals that strongly repel or attract elephants without showing habituation.

In the future, researchers should concentrate their efforts on investigating the bioactivity of compounds found in the exudates of musth bulls (Rasmussen & Wittemyer 2002, Rasmussen & Riddle 2004). Such compounds include 2-alkanones and alkan-2-ols, as well as additional ketones that communicate musth and pre-musth in the urine of bull African elephants (Rasmussen & Wittemyer 2002, T.E. Goodwin pers. comm.). The development of a deterrent with a naturally occurring ingredient that communicates a keep-away signal among African elephants may be an effective tool agriculturalists can use to construct a chemical barrier around their crops.

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Table 2.1. Ethogram to record behaviors performed by wild African male and female elephants to bioassay samples. Ethogram modified from Meyer (2006) and Schulte (2006).

Categories and defined behaviors	**Definition**
Approach	Presented in order of closeness to sample
Proximity	Elephant within one body length of sample.
Near	Elephant within one trunk length of sample.
Chemosensory	Presented in order of least to most discriminatory
Sniff	Nasal openings hover over sample without contact.
Check	Touch sample with tip of either finger.
Place	Entire nasal opening is placed on a sample and held momentarily.
Flehmen	Tip of trunk touches sample then placed in the VNO ducts in the roof of the mouth.
Sniff, Horizontal	Trunk tip directed below head and oriented somewhat parallel to ground
Sniff, Periscope	Trunk tip raised above head in characteristic J-or-S-shape
Suck	Trunk contracts like a vacuum hose, sometimes hear sound of liquid uptake
Repulsion/avoidance	
Back up	Elephant retreats after performing any chemosensory behavior toward sample while performing any other repulsion/avoidance behaviors.
Circle (bioassay)	Elephant walks a circle around the bioassay while performing any other repulsion/avoidance behaviors.
Ear flap	Ears held out perpendicular to head, oriented towards sample.
Foot stamp, paw	Aggressively placing paw, moving dirt over sample.
Head shake	Vigorous shaking of the head that causes ears to flap.
Trumpeting	Loud vocalization created by forcing air out of the trunk
Trunk seal	Pressing the two fingers of the trunk together to close nostrils.
Trunk shake	Vigorous swinging of the trunk from side to side
Wriggle	Performed after inspecting a sample. Trunk twists and then untwists once at a moderate pace (slower than trunk flick)
Accessory Trunk	
Blow	Performed after inspecting a sample. Air is expelled quickly from nasal openings of trunk; usually audible and visible mucus expelled.
Pinch	The two fingers of trunk pick up dirt around the sample.
Trunk Flick	Performed after inspecting a sample. Bottom ¼ of trunk moves up and down rapidly.
Other	
Motionless	Elephant exhibits no behavior for at least 5 seconds.
Other	Behaviors exhibited that are not defined in ethogram.

Table 2.2. Sample sizes for age/sex classes of compounds tested at Ndarakwai Ranch, Tanzania May to September 2008. These numbers indicate bioassays in which elephants visited the test sample and the control. (PP= post pubescent)

	(*E*,*E*)-Farnesol/Water	(*E*,*E*)-Farnesol/Urine	3-Pentanone/Water
Adult M	7	12	11
Adult F	18	13	16
Sub-adult M	14	17	9
Sub-adult F	10	3	5
Juvenile M	7	4	12
Juvenile F	5	4	11
Calf M	2	4	5
Calf F	9	4	9
Adult	25	25	27
Sub-adult	24	20	14
Juvenile	12	8	23
Calf	11	8	14
TOTALS	**72**	**61**	**78**
PPF (Adult F + Sub-adult F)	**28**	**16**	**21**
PPM (Adult M + Sub-adult M)	**21**	**29**	**20**

Table 2.3. Statistical tests performed and values used to compare bioassays of the tested compound and the control sample of vanilla and respective solvent (water or urine) at Ndarakwai Ranch, Tanzania June-September 2008.

Figure	Sample	Characteristic	Test	Statistic	P	df
2.3	F/W	Proportion CB/Female	Chi-Squared	χ^2= 3.21	0.07	1
2.3	F/W	Proportion CB/Male	Chi-Squared	χ^2= 0.38	0.54	1
2.4	F/W	Proportion AB/Female	Chi-Squared	χ^2= 0.0	1.0	1
2.4	F/W	Proportion AB/Male	Chi-Squared	χ^2= 1.15	0.28	1
2.5	F/W	Duration/Female	Pairwise t-test*	t= -0.65	0.52	1
2.5	F/W	Duration/Male	Pairwise t-test*	t= -0.80	0.43	1
2.6	F/W	Rate CB/Female	WSR	T_s= -22.5	0.08	
2.7	F/W	Rate AB/Female	WSR	T_s= -1.5	0.75	
2.6	F/W	Rate CB/Male	pairwise t-test*	t= 0.97	0.35	1
2.7	F/W	Rate AB/Male	WSR	T_s= 2.0	0.50	
2.3	F/U	Proportion CB/Female	Chi-Squared	χ^2= 0.0	1.0	1
2.4	F/U	Proportion AB/Female	Chi-Squared	χ^2= 2.9	0.09	1
2.3	F/U	Proportion CB/Male	Chi-Squared	χ^2= 0.77	0.09	1
2.4	F/U	Proportion AB/Male	Chi-Squared	χ^2= 1.12	0.29	1
2.5	F/U	Duration/Female	pairwise t-test*	t= 0.46	0.65	1
2.5	F/U	Duration/Male	WSR	T_s= 58.5	0.21	
2.6	F/U	Rate CB/Female	pairwise t-test*	t= 0.63	0.54	1
2.7	F/U	Rate AB/Female	WSR	T_s= -1.5	0.50	
2.6	F/U	Rate CB/Male	pairwise t-test*	t= -0.33	0.74	1
2.7	F/U	Rate AB/Male	WSR	T_s= -2.0	0.63	
2.9	3P/W	Proportion CB/Female	Chi-Squared	χ^2= 0.10	0.76	1
2.9	3P/W	Proportion CB/Male	Chi-Squared	χ^2= 2.06	0.36	1
2.10	3P/W	Proportion AB/Female	Chi-Squared	χ^2= 0.0	1.0	1
2.10	3P/W	Proportion AB/Male	Chi-Squared	χ^2= 1.41	0.23	1
2.11	3P/W	Duration/Female	pairwise t-test*	t= 0.57	0.57	1
2.11	3P/W	Duration/Male	WSR	T_s= 12.0	0.59	1
2.12	3P/W	Rate CB/Female	pairwise t-test*	t= -0.35	0.73	1
2.12	3P/W	Rate CB/Male	pairwise t-test*	t= -0.11	0.91	1
2.13	3P/W	Rate AB/Female	WSR	T_s= 0.0	1.0	
2.13	3P/W	Rate AB/Male	WSR	T_s= -0.5	1.0	

(*E*,*E*)-farnesol/Urine = F/U; (*E*,*E*)-farnesol/Water = F/W; 3-pentanone/Water = 3P/W; CB = Chemosensory Behaviors; AB = Avoidance Behaviors; WSR = Wilcoxon Signed Rank Test
* Log transformed data fit the assumptions of equal variance and normality

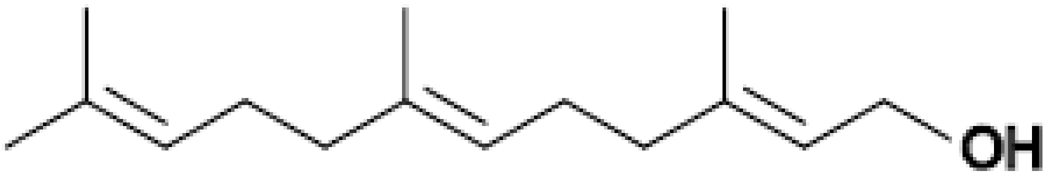
Table 2.4. Proportion of chemosensory and avoidance responders to (*E,E*)-farnesol in water and a urine solution at Ndarakwai Ranch, Tanzania from July to September 2008. Note: PP = post-pubescent

	Proportion Chemosensory Responders		**Proportion Avoidance Responders**	
Sample	*PP Females*	*PP Males*	*PP Females*	*PP Males*
(*E*,*E*)-farnesol/water	0.39	0.52	0.07	0.05
Vanilla/water	0.18	0.43	0.07	0.14
(*E*,*E*)-farnesol/urine	0.56	0.52	0.13	0.10
Vanilla/urine	0.56	0.59	0	0.03

Table 2.5. Proportion of chemosensory and avoidance responders to 3-pentanone in water at Ndarakwai Ranch, Tanzania in August and September 2008. Note: PP = post-pubescent

	Proportion Chemosensory Responders		**Proportion Avoidance Responders**	
Sample	*PP Females*	*PP Males*	*PP Females*	*PP Males*
3-pentanone	0.57	0.55	0	0.05
Vanilla/water	0.52	0.40	0	0

(a)



(b)

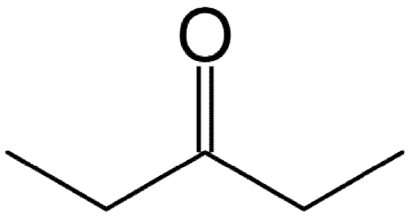


Figure 2.1. Chemical structure of (a) (*E,E*)-farnesol, $C_{15}H_{26}O$, and (b) 3-pentanone, $C_5H_{10}O$.

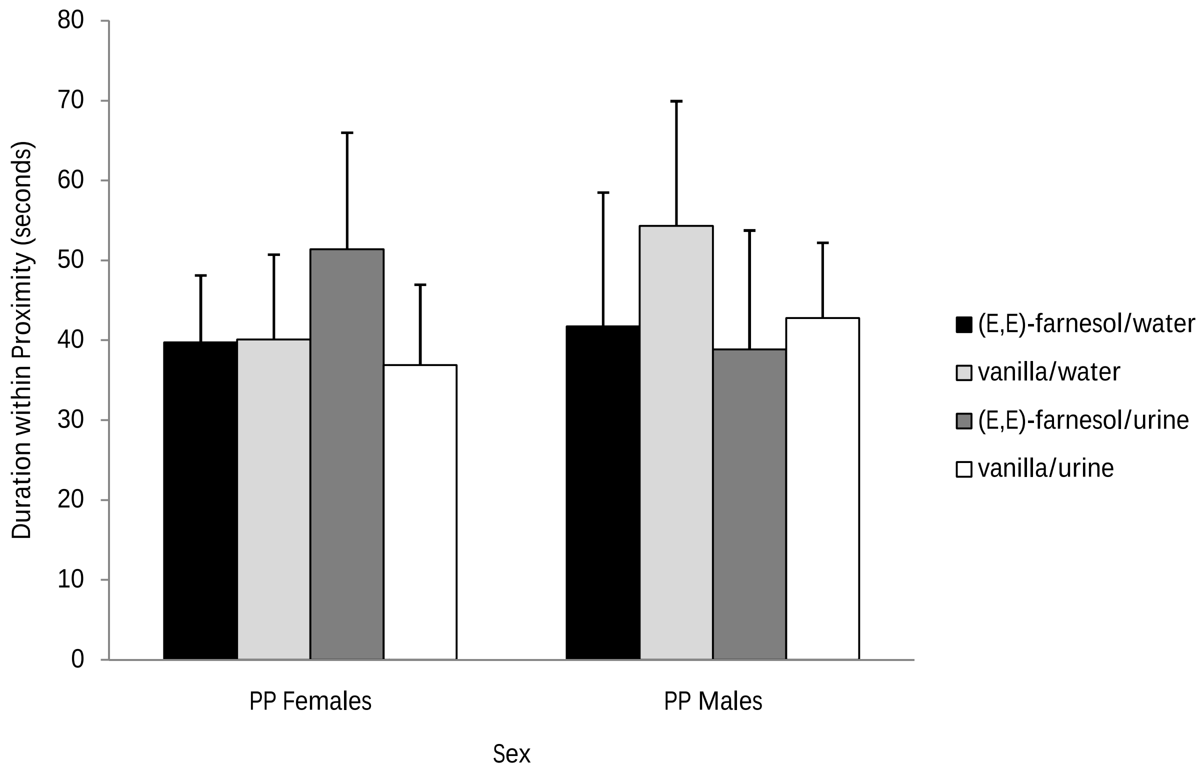


Figure 2.2. Mean duration (± SE) of post-pubescent (PP) elephants within proximity (one body length) of (*E*,*E*)-farnesol and vanilla mixed with water (females: n = 28; males: n = 21) and toward (*E*,*E*)-farnesol and vanilla mixed with urine (females: n = 16; males: n = 29) at Ndarakwai Ranch, Tanzania from July to September 2008. Bars are 1 S.E.

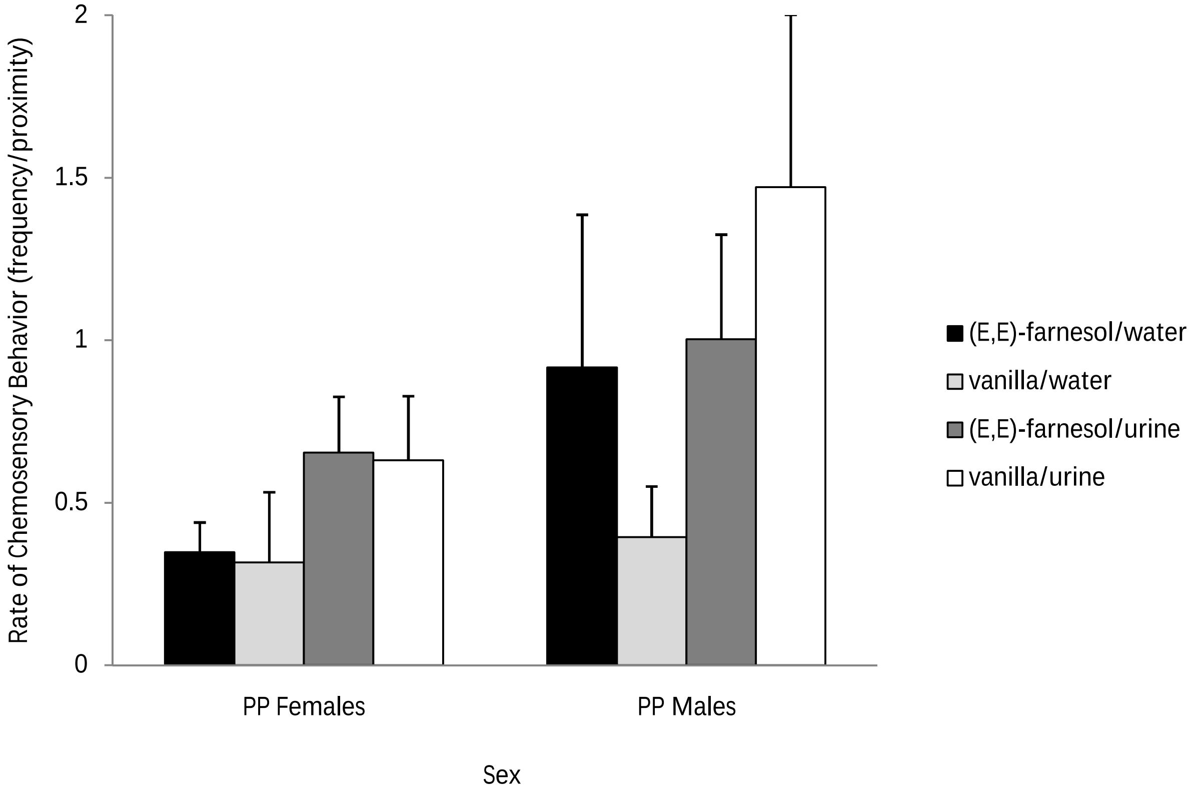


Figure 2.3. Mean (±SE) rate of chemosensory behavior of post-pubescent (PP) elephants within proximity (one body length) of (*E*,*E*)-farnesol and vanilla mixed with water (females: n = 28; males: n = 21) and toward (*E*,*E*)-farnesol and vanilla mixed with urine (females: n = 16; males: n = 29) at Ndarakwai Ranch, Tanzania from July to September 2008. Bars are 1 S.E.

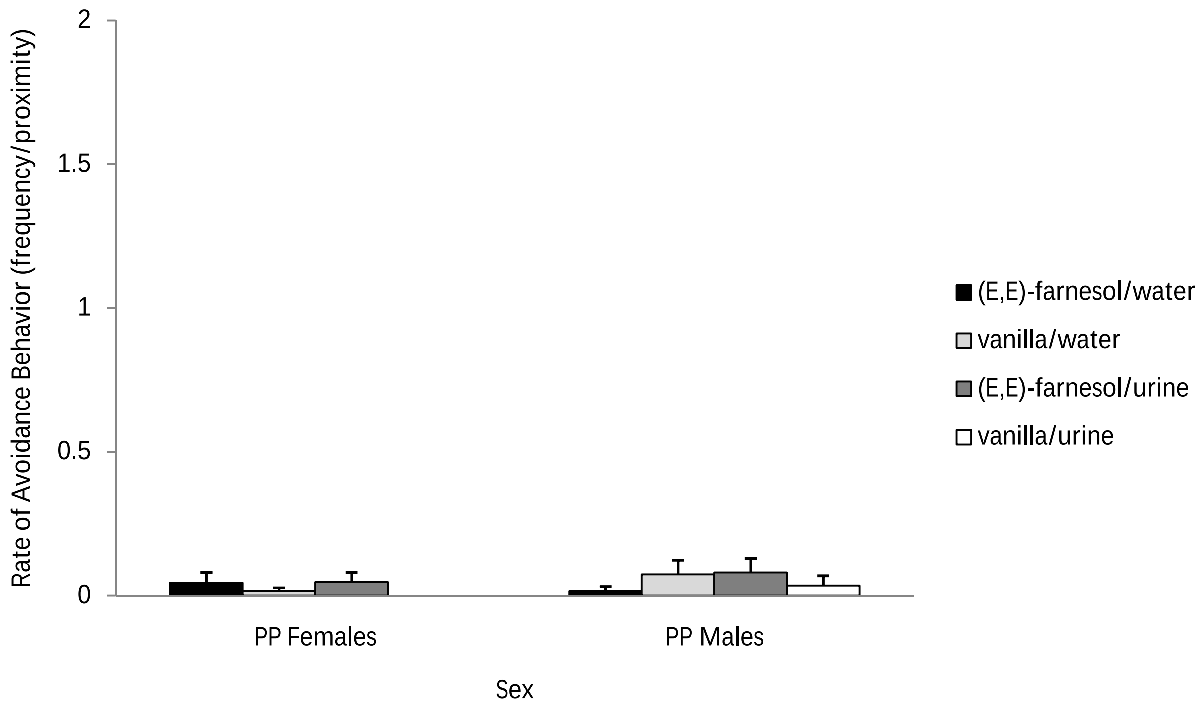


Figure 2.4. Mean (±SE) rate of avoidance behavior of post-pubescent (PP) elephants within proximity (one body length) of (*E,E*)-farnesol and vanilla mixed with water (females: n = 28; males: n = 21) and toward (*E,E*)-farnesol and vanilla mixed with urine (females: n = 16; males: n = 29) at Ndarakwai Ranch, Tanzania from July to September 2008. Note: PP females did not perform avoidance behaviors toward vanilla/urine. Bars are 1 S.E.

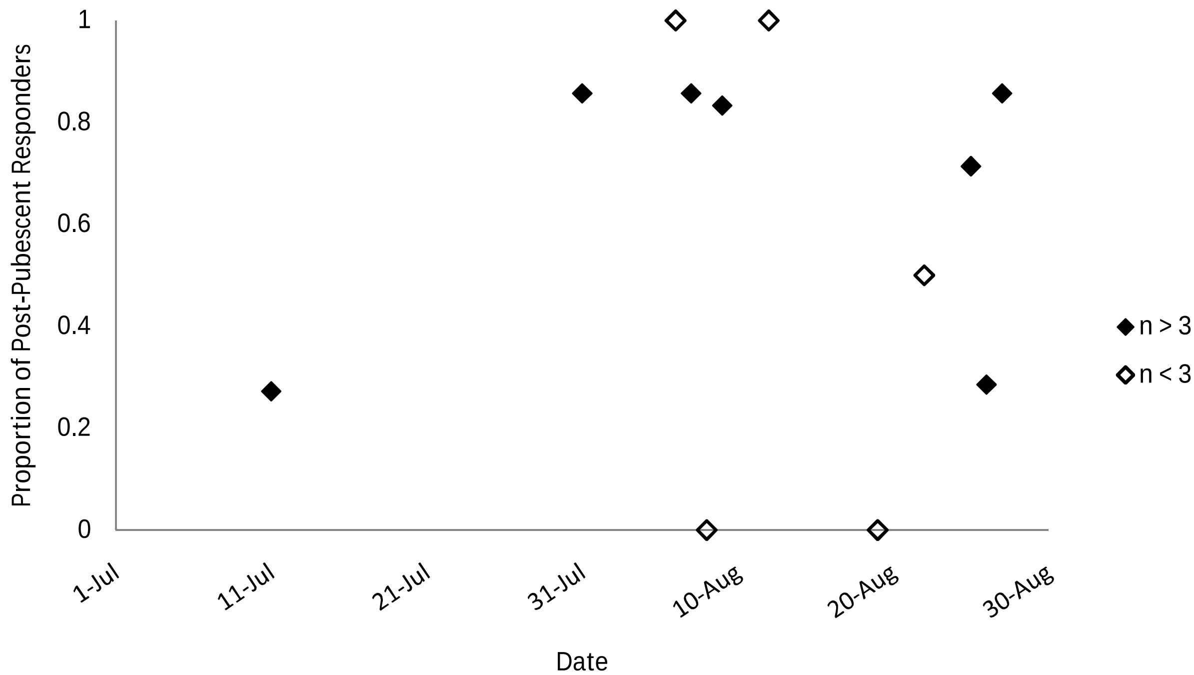


Figure 2.5. Proportion of behavioral responders (chemosensory and avoidance) to either vanilla or (*E,E*)-farnesol mixed with female elephant urine from a ten-year-old orphan on Ndarakwai Ranch, Tanzania, in July and August 2008. On two days, no elephants responded to the sample. Filled in diamonds represent days on which more than three individuals were in proximity to the sample; whereas, the outlined diamond represents days on which there were less than three elephants in proximity to the sample.

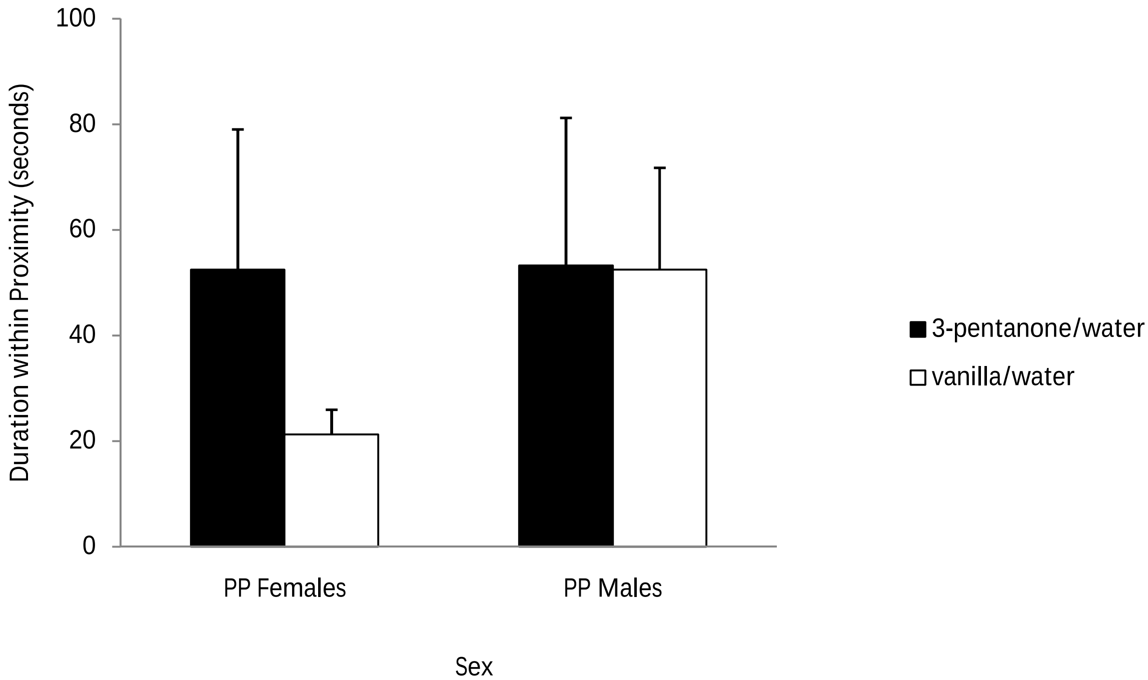


Figure 2.6. Mean duration (± SE) of post-pubescent (PP) females (n = 21) and males (n = 20) within proximity (one body length) of 3-pentanone and vanilla mixed with water at Ndarakwai Ranch, Tanzania in August and September 2008. Bars are 1 S.E.

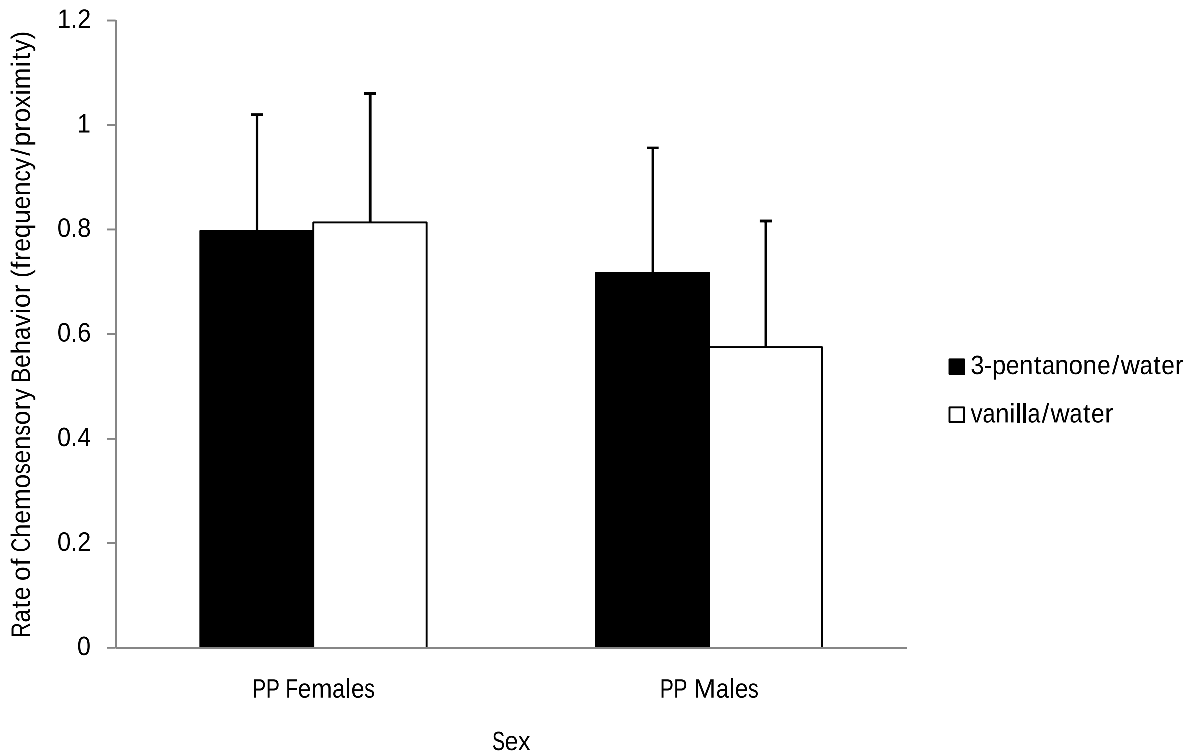


Figure 2.7. Mean (±SE) rate of chemosensory behavior of post-pubescent (PP) females (n = 21) and males (n = 20) towards 3-pentanone and vanilla mixed with water at Ndarakwai Ranch, Tanzania in August and September 2008. Bars are 1 S.E.