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Effect of Lion Calls on African Elephants (*Loxodonta Africana*) in Addo Elephant National Park, South Africa

Margaret Rose Hook
Western Kentucky University, maggiehook86@gmail.com

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EFFECT OF LION CALLS ON AFRICAN ELEPHANTS (*LOXODONTA AFRICANA*) IN ADDO ELEPHANT NATIONAL PARK, SOUTH AFRICA

A Thesis
Presented to
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Western Kentucky University
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In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

By
Margaret Rose Hook

August 2012

EFFECT OF LION CALLS ON AFRICAN ELEPHANTS (*LOXODONTA AFRICANA*)
IN ADDO ELEPHANT NATIONAL PARK, SOUTH AFRICA

Date Recommended ____________________

Bruce A. Schulte

Bruce Schulte, Director of Thesis

Carl W. Dick

Carl Dick

Keith Philips

Michael Collyer

8/20/12

Dean, Graduate Studies and Research Date

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EFFECT OF LION CALLS ON AFRICAN ELEPHANTS (*LOXODONTA AFRICANA*) IN ADDO ELEPHANT NATIONAL PARK, SOUTH AFRICA

Margaret Rose Hook August 2012 70 Pages

Directed by: Dr. Bruce A. Schulte, Dr. Carl Dick, Dr. Michael Collyer
and Dr. Keith Philips

Department of Biology Western Kentucky University

Perceived predation risk alters animals’ behavior. This shift in behavior often comes at the cost of attaining resources. Generally, African elephants (*Loxodonta africana)* experience little predation pressure; however, the risk of predation by lions (*Panthera leo*) increases other prey species are less abundant. In elephant herds, related females and their offspring travel together in family groups, led by the eldest female. Response to predation pressure was examined by playing lion calls to the population of 437 elephants at the Main Camp Section of Addo Elephant National Park (AENP) in South Africa. Unfamiliar lion calls from a single male and two males, static, and running water were played from a remote speaker to elephants at waterholes. These trials were recorded by video. Behaviors of elephants were then extracted from video into focal observations of thirty second segments before, during and after a sound was played. I analyzed these data using parametric t-tests and non-parametric randomization tests. When no sound was played, elephants did not alter their behavior. Water elicited low levels of distress behaviors. Elephants behaved in a threatened or annoyed manner toward static. Elephants changed their behavior more in response to lion calls than to the controls, namely by decreasing drinking and increasing walking and distress behaviors. I also examined how individuals differed in their responses to the lion calls based on a number of demographic factors. Adult and subadult females performed more social behaviors after lion calls when the matriarch was absent than when she was present. Furthermore, when group size was larger and more calves were present, females decreased drinking and increased time exhibiting distress behaviors. Based on this and other studies it can be concluded that elephants of different demographics perceived similar levels of elevated risk when hearing lion calls. Landscape of fear models are useful for assessing habitat use by prey species in response to real and perceived predation risk. The present study corroborates findings from a study in East Africa that elephants perceive threat from lions based on calls alone and appear to distinguish levels of threat by the number of lions calling.

Introduction

The threat of predation alters the behavior and physiology of prey species. In songbirds, playing predator calls reduces the clutch size and offspring survivability, while increasing parent's vigilance behaviors (Zanette et al. 2011)**.** The anticipation of predation can cause changes in foraging behaviors and travel patterns but may result in selecting resources of lower quality. Modeling this preferential resource use based on predation risk is termed the landscape of fear (Laundre et al. 2010). Animals alter their movements based on differential predation pressure and resource quality. However, certain resources like water are necessary and predators can hunt at such locations to acquire prey. For example, lions (*Panthera leo*) prefer areas of high prey abundance, which often occur near water sources (Davidson et al. 2012). Therefore, prey cannot entirely avoid areas frequented by predators.

Anti-predator behavior occurs with both costs and benefits. Numerous types of anti-predator behavior occur in both marine and terrestrial environments including encounter avoidance, escape facilitation, and increased vigilance (Wirsing & Ripple 2011). Performing these behaviors is associated with costs such as taking time from acquiring resources and limiting or changing access to important resources based on predation pressure. Large African ungulates shift their visits to waterholes based on predation and hunting pressure (Crosmary et al. 2012a, b). In addition, in hunting areas ungulates are less likely to drink. Group size, predator proximity, and predation pressure all alter the levels of vigilance displayed by prey (Scheel 1993a, b). When lions are present, the bouts of vigilance increase in duration for African herbivores (Periquet et al.

2010). Compared to the daytime, wildebeest and zebra scan their environment more frequently at night when lions generally hunt (Scheel 1993b).

Lions prey upon a wide variety of mammals in Africa. Their preferred prey size is 350 kg with a range between 190–550 kg with males hunting heavier prey than females (Hayward & Kerley 2005, Patterson 2007, Power and Compion 2009). As the number of lions in a pride increases, so does the size of prey (Scheel 1993a). Differential predation rates occur due to changing prey availability, often reflecting seasonal migration patterns. During the dry season, lions alter their prey selection from wildebeest and zebra to mostly larger prey, such as buffalo (Funston & Mills 2006). Lions also prey upon African elephants (*Loxodonta africana)*.

Animals may gather in groups in part to reduce the costs of anti-predator behavior (Roberts 1996). For example, elephants exhibit lower individual vigilance levels and reduce predation risk when in traveling in family groups versus alone (Wittemyer et al. 2005a, b). African elephants show strong relationships within these families, which consist of related females and their offspring. Age and size determine dominance rank, with the oldest largest female, termed the matriarch, leading the family group (Archie et al. 2006a). When related families fuse, the eldest matriarch, termed the grand matriarch (Esposito 2008), becomes dominant (Wittemyer & Getz 2007). Group living increases protection from threats and the matriarch acts to coordinate responses (McComb et al. 2011). Family groups with lower ranked matriarchs or in areas of higher predation risk move in less predictable patterns (Wittemyer et al. 2008). By varying patterns of movement, elephants put lions at a disadvantage in their ability to predict the location and movement of the elephant family.

Generally, elephants are protected from lion predation by their large body size and dangerous tusks, but they experience periods of risk both seasonally and developmentally. Elephants have four developmental stages: calves (0-4 years), juveniles (5-9 years), subadults (10-19 years), and adults (20+ years). Lee (1987) observed lions preying on calf elephants. In fact, young elephants are included in the weight category lions prefer (Hayward & Kerley 2005). In Kenya, Wittemyer et al. (2005a) found lion predation to be responsible for 23.8% of subadult elephant mortality, the highest known cause of death for that group. Individual male lions are able to capture elephant calves (Loveridge et al. 2006). Predation generally occurs when elephants are traveling longer distances and the young fall behind (Loveridge et al. 1996). The threat to elephants by lions is highest during the dry season when migrating prey is available only at low densities. In Botswana, large prides of lions even prey on adult female elephants during the dry season (Power & Compion 2009). The predation threat is most severe during dark nights that provide greater cover for lions. While adult males are generally too big and with their massive tusks too dangerous for lions, younger males are not so fortunate.

As they age, male offspring become increasingly independent from the family unit as indicated by earlier and greater separation from their mothers compared to female offspring (Lee 1987). They are most vulnerable to predation during this time of development. Males leave their natal family groups permanently, becoming completely self-sufficient as adolescents between the ages of 10–19 years (Evans & Harris 2008). Males congregate with other males as adolescents, establish a hierarchy, and then associate less as they age (Evans & Harris 2008). When males reach 19 years old they are the same size as an adult female, and continue to grow until they are 50–100% larger

(Moss 1996, 2001), at which point, the threat of predation is minimal and less anti-predator behavior would be expected. However, the use of investigatory behaviors increases. Males rely extensively on their ability to detect relevant chemical signals, for example when searching for females for mating (Rasmussen & Schulte 1998, Schulte 2006). However, they play no role in the caring of young.

While adult females also are often too large for lions, females display numerous behaviors that are likely to facilitate the survival of their offspring and relatives (Dublin 1983, 1996). The gestation period for elephants is 22 months with parturition usually occurring during times of high primary productivity (Wittemyer et al. 2007). This gives the mothers a high quality intake of nutrients when offspring are most vulnerable to predation. If calves are distressed, females respond quickly to their calls (Lee 1987). In Central Africa, most of the calves attacked by lions had lost mothers to poaching (Ruggiero 1991).

I hypothesized the response of elephants to the threat of predation would vary with group size, leadership status, sex, developmental stage, and having a calf at my study site in Addo Elephant National Park (AENP) South Africa. The responses by elephants to signs of lions would be more acute when individuals are part of a family group with no matriarch present, with a young matriarch, or when travelling in a smaller group. The responses of individual adult female elephants would be heightened for females that are matriarchs, with young offspring (calves), and when more calves are present. Juvenile and subadult male elephants are hypothesized to be more responsive to the threat of predation because of their greater susceptibility to lions than similarly aged female elephants. I examined sex, age, and the age class of each individual to determine if there were general trends by sex and age (and size) or differences in the developmental stages of elephants.

I used several controls to test my hypotheses and ensure elephants associated lion calls with predation risk. Elephant behaviors were recorded in the same manner without any sound playing. If no sound played, elephants would be expected to show no changes in behavior. Like lion calls, static sounds are loud and unexpected but they should have no evolutionary significance related to predation. The sound of running water was used as a control with an expected effect of invoking walking and investigating as elephants search for the source of the water. Waterholes in AENP are filled with piped in water and elephants are attracted to the sound of water rushing from these pipes (B. Schulte, per. obs.). As a necessary resource, the sound of running water is both evolutionarily and biologically significant but not threatening. Therefore, lion calls were expected to evoke the greatest anti-predator type behaviors compared to no sounds. While static and water each were predicted to elicit responses of awareness, strong anti-predator activities were not expected.

Methods

Study site and population

From 3 June 2010 to 11 January 2011, I conducted research in the main camp section of ANEP located approximately 70 km northeast of Port Elizabeth in the Eastern Cape of South Africa (Table 1, Figure 1). In 1931, South Africa founded AENP to preserve the local elephant population of this sub-tropical thicket habitat. Due to conflicts with farmers, the elephants were enclosed with a fence in 1954 (Whitehouse & Hall-Martin 2000). In September 2003, management reintroduced spotted hyenas and lions to the Main Camp (Hayward et al. 2007). The lions of AENP change their home range only slightly seasonally, with rainfall occurring in both the winter and summer (Hayward et al. 2009). The numbers of other prey items to which lions have access fluctuates little seasonally without migration of other prey species. Therefore, the predation pressure on elephants would remain constant throughout the year.

For the past ten years, graduate students working with Dr. Bruce Schulte at Georgia Southern University or Western Kentucky University and field personnel from Nelson Mandela Metropolitan University in Port Elizabeth have had a continuous field presence at AENP recording all elephant births and deaths and maintaining identification files (Whitehouse 2001, Loizi 2004, Bagley 2004, Gough & Kerley 2006, Merte 2006, Meyer 2006, Esposito 2008). I identified elephants using ear and body morphology along with family associations (Whitehouse & Hall-Martin 2000). The growing population, totaling 437 individuals in Main Camp during the course of this study, is composed of 35 families in six kinship groups (Table 2). Six females in separate families from five of the six kinship groups had a working GPS collar that facilitated locating these families.

Elephants often gather at the man-made waterholes in the park. These open areas are good locations for observations. I conducted experimental studies at five such waterholes. Data were collected with WKU IACUC Animal Welfare Assurance #A3558-01, designation 10-07 and SANParks permit number SCHBA840. I obtained 47.21 hours of video of giving 331 focal observations on 203 unique individuals (Tables 3, 4).

Selection of stimuli

Lion roar stimuli were used to determine the effect of predation risk assessment in elephants. The use of a strictly visual cue (e.g., a lion model) was not reasonable, as the signal would have to be within approximately seven meters of the elephants and the lion stimulus could be destroyed (Bates et al. 2007). Elephants have shown the ability to differentiate perceived risk using chemosensory signals (Bates et al. 2007). Chemical stimuli such as feces placed on a pathway elephants frequently use upon entry to a waterhole was logistically possible; however, odor stimuli are harder to control than auditory stimuli. Therefore, the sound of male lions roaring was used to indicate predator presence.

I played five different sounds to elephants during the period from July to December 2010. To replicate the presence of lions, recordings of male lions were played. I obtained the calls from Drs. Ted Grinnell and Bruce Patterson. I played two different lion calls, one with a single, unfamiliar adult male lion roaring and another with two unfamiliar males roaring concurrently. Dr. Lucy King provided bee sounds, as she found elephants moved away from the sound of buzzing bees (King et al. 2009). I acquired sound files of running water and static from freesound.org.

Static was played to assess that elephants differentiate noise from meaningful sounds such as running water, bee buzzing, and lion calls. Fortuitously, 39 observations occurred in which the intended sound did not play. I used these "no sound" trials as a further control to examine if behaviors differed when elephants heard a sound regardless of type. Each additional sound played decreased the sample size of the other sounds. With a randomized order, each sound had an equal likelihood of being played at any time. The bee treatment was dropped after two months to increase the sample sizes of the other sounds. To avoid habituation, I waited at least two weeks before playing a sound to the same elephants again.

Experimental trials

Initial trials in the field showed elephants flee during lion calls after approximately one minute. By shortening the call duration to 30 seconds, I was able to evoke a range of responses without a majority of the individuals fleeing. This length of time permitted collection on the differential responses expressed by individuals. I edited sounds using Super Sound Joiner software to create 30-second wave files (Softonic International S.L.). A second researcher randomly generated the daily order in which the sounds played each morning. If in one day all five sounds played (or four sounds after I no longer plated bee sounds), I repeated the same order. However, the second time through, the group composition that heard the call earlier in the day was taken into consideration. If I had played four sounds to family groups and one to a lone male, and a new family group was approaching, then the call not already played to that demographic was selected. Conversely, if a lone male was approaching, I would start from the beginning of the day's playlist, omitting the call heard by the previous individual male.

Sound trials equipment

To reduce the risk of elephants being able to associate the sounds with the field vehicle, I used a wireless speaker system. I used a remote-operated Audio Unlimited 900 MHz speaker system with the volume set on high and placed the battery-powered speakers 10-50m from my vehicle. The speaker was enclosed in a tube composed of PVC placed in a bush, either hanging or on the ground. The PVC tube was outfitted with caps on each end with portions drilled out in the middle of the tube from where the sound emanated (Figure 2). Dr. Mark Cambron and Ron Rizzo of the WKU Department of Engineering designed this set up. I painted the PVC cover a mixture of green and brown, and placed elephant feces on and around it to camouflage it from sight and smell. A small antenna plugged into a 12V battery in the vehicle transmitted the sounds played on the laptop to the speaker. Preliminary testing of the speakers included using a Radio Shack sound level meter model 33-2055 to determine how the sound declined with distance from the source. In the initial trials, I used an MP3 player but decibel production was higher using a laptop, so all experimental trials used a Lenovo laptop.

The sound meter's ability to read noise levels produced from speakers when lion calls played carried only 5 m with readings of 100 dB at 0 m and 70 dB at 5 m. After this point, the sound meter did not differentiate lion call sounds from ambient noise. However, humans (N=3) were able to recognize the calls as lions roaring from 75-100 m from the speakers. Testing an elephant's hearing has shown elephants to hear from 16 Hz to 10.5 kHz at 60 dB (Heffner & Heffner 1980). Using Raven Pro's interactive sound analysis, the lion calls played ranged from 110.1 Hz to 195Hz, falling into the category of frequencies elephants can hear (Bioacoustics Research Program 2011). Elephants hear lower frequency sounds better than humans do (Heffner & Heffner 1980). I could ensure elephants would most likely hear by playing sounds when elephants were within 50 m of the speaker.

I was blind and "deaf" to the identity of sounds as they played. A second researcher labeled the sound files as numbers (1-5). She changed these numbers four times to prevent me from learning the calls' identities. Consequently, on the relatively few occasions when I saw what file was used, I did not know what sound was played. Before the sound, I put on headphones and turned on music to cover the sound that the elephants were hearing. The other researcher would then play the sound. The beginning and end of the sound were marked with a quick hand over the camcorder lens. As the call played, the other researcher noted any vocalizations made during the sound. Only after all behaviors were recorded and inputted into a raw data file did I learn which sound the focal elephant(s) heard.

Obtaining focal observations from video recordings

Video recording began as one or more elephants approached the waterhole. After the elephant(s) had been identified, and as many as possible were visible within the camera frame, I played a sound for 30 s. The video camera continued recording for five minutes. After a day in the field was completed, I downloaded all video sequences recorded. To acquire behavior data for a given trial, I watched the tape repeatedly to perform focal observations with continuous recording on each elephant in the visible field one at a time (Martin & Bateson 1993). I muted the sound on the video when the sound was playing from the speaker during each observation to remain deaf to the sound's identity.

I recorded the elephants' state and event behaviors from the video. State behaviors (Table 5a) are longer in duration and were recorded by time spent in the state. Animals perform event behaviors while already exhibiting a state behavior. Event behaviors (Table 5b) are shorter than state behaviors and recorded by frequency of occurrence. The ethogram used for this study included investigative, aggressive, social, and distress event behaviors For each focal elephant, I noted its age and sex, the group size of the family unit, the highest ranked female present (matriarch or non-matriarch), the age of the eldest female present within the family, the total number of elephants that entered together (family unit plus others), and the total number of elephants present (those that entered together plus those already present). I also noted whether a female focal elephant was nulliparous or had a current or past calf, and the age of the most recent calf. Abiotic factors recorded included temperature and wind levels at the time of the call.

Statistical analysis

Elephant behaviors were analyzed using R statistical software (R core Development Team 2009). I divided each focal observation into three equal subsections: the 30 seconds before, during, and after a sound stimulus. Behaviors the elephants performed before a sound played served as an internal control for each focal observation. I calculated behavioral changes by subtracting the value after and during the call played from the initial value before the sound played (after-before and during-before respectively).

State behaviors are continuous and measured in duration. I determined the proportion of time elephants exhibited each state for the 30 s before, during, and after the sound played, omitting any time the elephant was not visible. I examined elephant state behaviors using the changes in proportion of time spent in each state from before to during and after the sound. Three behavioral states comprised over 80% of the elephants' activity budget: drinking ($\bar{x}$ = 0.40 ± 0.09, mean ± 1 se), standing ($\bar{x}$ = 0.25 ± 0.07), and walking ($\bar{x}$ = 0.22 ± 0.07). I analyzed changes in these three groups, as well as the distress state ($\bar{x}$ = 0.02 ± 0.02) comprised of fast walking or freezing, although performed at lower levels, due to its relevance to the study.

I grouped event behaviors by type of behavior and examined the change in number of behaviors performed. The behavioral categories I examined were investigative, social, and distress events. I created these categories due to the low rates of occurrence for individual event behaviors. I combined all investigatory and chemosensory behaviors: check, place, sniff, flehmen, blow, flick, suck, horizontal scope, periscope sniff, and approaching the call with the trunk extended in front of the elephant. I merged all social interactions, whether the individual was sender or receiver, into one category. These social behaviors consisted of all contacts: trunk to behaviors, head into, lean, nurse, present, push, rub, spar, supplant, and displace. Temporal streaming, scream vocalizations, urination, defecation, tail points, ear perks, and fleeing were pooled as distress behaviors. Another category I planned to analyze was aggressive behaviors; however, I could not due to their rare occurrence.

For comparing data within a focal observation, I used paired student t-tests. Paired student t-tests compared the means before a sound played to after for the same elephants. By analyzing focal observations from each sound separately, I could determine what behavioral changes elephants exhibited for each sound. For t-tests, I omitted all but one focal observation if an elephant heard a sound multiple times to avoid pseudoreplication. Inclusion or omission of multiple observations per individual elephant was evenly divided between each possible combination of sounds, with every other elephant being used per sound. I examined behaviors for the 30 seconds preceding, during, and following the sounds within both the control (no sound, static, running water) sounds and experimental (one or two male lions) calls.

When examining behavioral changes by discrete independent variables (i.e., sound type, sex, and age class), I compared changes in behaviors between treatments using randomization tests. These tests calculated the difference between means over many permutations. These tests specifically dealt with non-independence in my observations (as I could not control against multiple measurements on elephants). The tests calculated the sum of squares between treatments (SSB, as a test statistic) over 10,000 permutations, where in each iteration elephants were randomly assigned to treatments. This procedure produced distributions of random SSB using a (null) model of no differences for mean behaviors between treatments. The percentile of an observed SSB in a null distribution is the P-value for the test-statistic. I determined significance of the test statistic based on a type I error probability (alpha) of 0.05 (i.e., if the P-value of the test statistic was less than 0.05, it was considered significant). This procedure is analogous to traditional analysis of variance (ANOVA) but is robust against the stringent assumption of independent observations used in ANOVA (because the test statistic is not based on theoretical probability distributions based on degrees of freedom; personal communication, M. Collyer). Therefore, spurious statistical results (because of pseudoreplication) were not an issue (Hurlbert 1984).

I used randomization tests for several analyses of behavioral changes. First, I examined control sounds and lion calls separately. I merged the different sounds within each of those two categories to compare to each other (lions vs. controls). Although there were differences within each, by combining I could determine if the results were biologically significant as well as statistically significant. Using randomization tests with lumped data was analogous to performing orthogonal contrasts.

To examine the association between state and event behavioral differences and continuous factors (i.e., age and the various group sizes) I used correlation tests (‘cor.test’ function in R). I first created plots examining the data. If the data were heteroscedastic or had error with a non-normal distribution, I used a Spearman’s rank correlation test instead of a Pearson correlation test.

Fisher’s exact test was used with categorical data that can be classified two different ways. I used Fisher’s exact test to compare the number of individuals that fled compared to the total amount of elephants sampled for different sounds. For my data, Fisher’s exact test was preferable to a chi-squared test. While chi-squared gives an approximate p-value based on expected results, Fisher’s exact test gives an exact p-value (Satterthwaite 1946). In addition, chi-squared is based on deviation from expected results while Fisher’s compares the association between two categories.

In addition to determining whether the perceived presence of lions affected elephant behavior, I also considered whether demography (i.e. sex, age, rank) contributed to variation in elephant behaviors in response to lion calls. For these analyses, I divided the data into logical subsets to perform randomization tests. To determine how a matriarch’s absence alters subordinates, I omitted males who no longer travel with their family group. When examining behaviors of matriarchs and non-matriarchs, I used only observations of adult females. Only four females that had no offspring in these age groups were observed when lion calls played, so to increase sample size and examine the effect of having offspring on adult and subadult females behavior, females with calves four and under were compared to females without calves (non-mothers or females older offspring). To test my hypothesis for juvenile and subadult males I compared them only to females of the same age classes. I used correlation tests to assess the relationship between age and changes in behavior for all elephants when lion calls played.

I also investigated whether environmental variation was associated with behavioral responses, especially because my study occurred over several months. I performed correlation analyses on behavioral changes over the focal observations when lion calls played with several factors. The association between the number of days into the study the elephants focal observation occurred was analyzed to determine if the duration or rate of behaviors showed a directional change over the study period. I also examined the correlation between wind levels and responses as well as between temperature and responses. Because I found no significant patterns, these data are presented in an appendix (see Appendix A).

Results

Control sounds

When the speaker system did not play a sound, elephants should not alter their behavior over the 30-second periods of observation (equivalent to before, during, and after a sound). There were no changes in the proportion of time over the 30-second intervals that elephants spent in each state (Figure 3, Table 6a). For events, only social behaviors occurred at measurable levels, with elephants showing no changes over the three time intervals. Therefore, for the trials with sounds, I ascribed any changes in behavior during and after the sound to elephants responding to the sound and not to other components of the experimental design.

I predicted the sound of running water would evoke increases in investigative and walking levels. Elephants displayed little alteration in their behavioral patterns after hearing running water. The proportion of state behaviors showed no significant differences for elephants from before compared to after they heard the sound. Elephants displayed greater levels of distress event behaviors after water was played. No other levels of event behaviors changed. This indicates a somewhat negative reaction to running water, directly opposing the prediction of the sound arousing walking and investigation by elephants.

Static is an evolutionarily non-significant noise that would cause no change in elephant behavior, result in behaviors suggestive of annoyance, or would invoke defensive type behaviors if the sound was considered a threat. The sound of static playing from a speaker placed in the bush elicited changes in the behavior elephants exhibited (Table 6c). Elephants showed a decrease in the proportion of time drinking and an increase in walking (Figure 4). They also showed higher levels of states and events (Figure 5) associated with distress after hearing static compared to before the sound.

When the behaviors of elephants subjected to the three control conditions (no sound, running water and/or static) were compared, differences in state behaviors but not events were evident (Table 7). The proportion of time standing (after minus before) differed significantly when running water ($\bar{x}_{\text{water a-b}}$ = -17.4 ± 0.074%) versus the other control sounds ($\bar{x}_{\text{static a-b}}$ = 10.8 ± 6.9%, $\bar{x}_{\text{none a-b}}$ = 0.7 ± 5.7%) was played. After sounds played, elephants had a greater decrease in proportion of time drinking after static sounds ($\bar{x}_{\text{static a-b}}$ = -19.9 ± 10.5%) than water ($\bar{x}_{\text{water a-b}}$ = 3.8 ± 10.8). No changes in the number of event behaviors performed differed by sound type, with static and water being very similar for all but investigative event behaviors (Table 8, Figure 6). The data were considered as a single category (controls) to compare to the responses by elephants to calls from lions.

Lion calls

Several changes in behavior occurred during the focal observations of elephants over single lion call trials (Table 6e). After hearing the lion call, elephants were expected to display an increase in the proportion of time spent walking and spent in distress states (freezing and fast walking), as well as a decrease in the proportion of time drinking. Also, the rate of investigative, distress, and fleeing behaviors were expected to increase. The proportion of time elephants drank decreased, while standing and distressed states increased after the lion call was played. Elephants did not change the proportion of time spent walking over the course of the single lion call trials; however, elephants did display a higher rate of distress event behaviors. Other event behavioral categories including investigative, social, and aggressive behaviors did not change over the sound trials.

The two lion call produced changes in the behaviors displayed by elephants (Table 6f). Elephants exhibited lower proportion of drinking and higher proportions of time in states of distress and walking after lion call two played. Distress event behaviors and fleeing behaviors were performed at higher rates after the two lion call than before. The number of social and investigative behaviors did not change over the sound trials.

The responses by elephants to the single and two lion calls showed similar directions of change with greater changes to the two lion call for some behaviors (Table 7d, Figure 7). The proportion of time elephants drank decreased more during the two lion call trials. Elephants showed a slight increase in standing after the single lion call played. The change in proportion of time walking increased significantly more after lion call two ended. Elephants increased the proportion of time performing states of distress more while the two lion call played than the single lion call. Elephants exhibited the same changes in social and investigative behaviors for both calls. Distress events occurred at higher rates during lion call two, and flee behaviors did not differ by the lion call played (Fisher exact test p= 0.100). Overall, 15 out of 39 (38.5%) focal elephants fled during or after lion call two played while 11/52 (21.2%) fled over single lion call trials.

Lion and control comparisons

I expected elephants to show stronger behavioral responses to lion calls compared with control sounds, indicating elephants recognize lion calls as threats. Before sounds played, elephants showed no differences in state behaviors. Examining behaviors during and after the call showed elephants' responses vary based on sound type played, responding more strongly to lion calls than control sounds. A greater decrease in the proportion of time elephants drank was displayed after lion calls played (Figure 8). Also, after lion calls, elephants exhibited a greater increase in proportion of time spent walking (Figure 9) and distress state behaviors (Figure 10). The change in rate of elephants performing event behaviors showed significant differences only during the sounds being played, not after. While lion calls played, elephants displayed greater increases in distress event behaviors (Figure 11) and were more likely to flee the waterhole. Including individuals fleeing more than 30 seconds after the call, 28.6% elephants fled during or after lion calls played while only 4.4% fled during or after control sounds (Fisher exact test $p < 0.0001$).

Elephant response to lion calls by demographics

<u>Matriarchs and their effect on other elephants</u>

Elephants experience differential susceptibility to lion predation during different ages and developmental stages. As the leader, the matriarch was expected to respond more strongly to lion calls than other elephants. There was no evidence of this based on behavioral data (Table 9). In adult females, no states or event behaviors were significant by dominance status. Matriarchs were significantly older than other female adult elephants ($\bar{x}_{\text{matriarch}} = 38.6 \pm 2.6$ years (range = 26 - 49), $\bar{x}_{\text{non-matriarch}} = 24.5 \pm 1.2$ years (range = 20 - 36). Therefore, rank was not indicative of a differential behavioral assessment to lion calls.

The presence of a matriarch was examined to determine if elephants would react differently when their leader was not present. Two subsets of elephants sampled were examined to see if matriarch absence would change the way other elephants responded to the call, namely adult and subadult females alone (Table 10) and then all elephants that follow a matriarch (Table 11). Adult and subadult non-matriarch female elephants did not vary their behavior based on the presence or absence of their matriarch. The only change in behavior for adult and subadult females was a decrease in social behaviors during the call when the matriarch was present and an increase in social behaviors when the matriarch was absent. However, this difference was not apparent when all elephants that follow a matriarch were examined. In fact, there were no differences in either state or event behavioral changes found for all elephants that follow a matriarch.

Older matriarchs generally have more experience as leaders; the response of elephants could be associated with the age of their matriarchs to lion calls. The correlation between matriarch age and behavioral responses of elephants with their matriarch present (N = 43) showed some merit. Elephants showed greater rates of fleeing when their matriarch was ranked younger (rho = -0.30, p = 0.02). There was no correlation between the age of the matriarch and the change in state behaviors or the number of other event behaviors. The size of groups was not correlated with matriarch age (rho = 0.14, p = 0.10).

Group size

With the advantages groups afford individuals, I hypothesized that adult and subadult female elephants in smaller groups would respond more strongly, especially in distress and fleeing behaviors. In states, overall there were no differences for all elephants sampled. However, for adult females, there were correlations between group size and change in proportion of time drinking and distress behaviors from before to during the call. Female elephants showed a correlation between group size and drinking decreased more when elephants were in larger groups from before to after the call (corr = -0.42. t = -2.17, df = 22, p = 0.041). Greater increases in the states of distress exhibited were correlated with females in larger groups of elephants (corr = 0.49, t = 2.62, df = 22, p = 0.016,). No changes in event behavior were associated with the size of the group elephants entered with at the waterhole. This lack of correlation with group size and event behaviors was shown for all elephants that heard lion calls, as well as when adult and subadult females were examined separately. When elephant behaviors from all sounds were examined, the number of elephants in the same family group was correlated with social behaviors only. The total number of elephants present did not affect changes in event behaviors (Table 12).

Offspring influence on response

Mothers expend large amounts of energy raising offspring and were expected to react more strongly to the threat of predation than similarly aged females without offspring. Having offspring under five, as well as the age of offspring did not alter females’ responses to lion calls. There were no differences in the levels of change in either state behaviors or event behaviors for these females (Table 13).

The total number of calves present during observations altered female elephant’s responses. Females’ decreases in drinking behavior were stronger with more calves present both during (rho = -0.45, p = 0.022,) and after (rho = -0.38, p = 0.049) the call played. The number of calves present also was positively correlated with group size (rho

= 0.37, p = 0.038). The behaviors of females with offspring were examined to determine if there was a correlation between change in behavior and the age of her latest offspring. In mother elephants, no correlation occurred for any change in behavior from before to after or during the call played with last offspring age.

Male and female response for subadult and juvenile elephants

Juvenile and subadult males showed no greater changes in behavior than comparably aged females in response to lion calls (Table 14). The change in the proportion of time elephants spent performing each state behavior did not differ by sex in these age classes. For event behaviors, there were no differences in the change in behaviors displayed before to after the call between males and females. However, the reasons for predicting males' heightened response were valid. The number of elephants present when the sound was played for females (group size: $\bar{x}_{\text{males}} = 3.4 \pm 1.0$, $\bar{x}_{\text{females}} = 8.3 \pm 1.7$, total number of elephants present: $\bar{x}_{\text{males}} = 4.6 \pm 1.2$, $\bar{x}_{\text{females}} = 15.7 \pm 3.5$) was higher than when males heard the call ($P_{\text{rand}} = 0.0001$). Females had more calves present for when calls played compared to males ($\bar{x}_{\text{males}}$ = 3.7+/- 0.9, $\bar{x}_{\text{females}}$ = 0.6+/- 0.2, $P_{\text{rand}} = 0.0002$).

General examination of responses by age and sex

The relationship between both actual age and the age class (calf, juvenile, subadult, adult) of elephant and the behavioral response to lion calls was examined (Tables 15, 16). There was a positive correlation between the rank in age of the elephant and the rank in change in proportion of time drinking; as age increased, drinking decreased less (rho = 0.20, p-value = 0.026). Juveniles, considered the most susceptible to predation by lions, showed greater decreases in the levels of drinking during the call than adults (Figure 12). The ranks of change in distress state behaviors were negatively correlated with age (Figure 13). However, there were no differences by age class in distress state behaviors. The states of walking and standing showed no change in the proportion of time displayed before to after the call by either age or age class. When examining the rank of change in event behaviors, there were no correlations by age ranks.

To determine the general effect of sex on reaction to lion calls, males and females of all ages were examined by responses to predation pressure (Table 17). The sex of an elephant had little effect on the level of changes in proportions of time and rates of behaviors performed after hearing lion calls. There were no differences found in the change in proportion of time elephants performed any state behavior. In event behaviors, only investigative behaviors elephants displayed differed by sex. Females ($\bar{x}$= 0.83 +/- 0.26 behaviors/minute) showed an increase in the number of investigative behaviors performed after the call played, while males exhibited a decrease ($\bar{x}$= -0.28 +/-0.20 behaviors/minute). There were no other differences found based on the sex of the elephants. However, females were in larger groups ($\bar{x}_{\text{males}}$= 3.9+/- 0.9, $\bar{x}_{\text{females}}$= 9.6+/- 0.9) and had a higher average age than males ($\bar{x}_{\text{males}}$=11.1+/-1.1 years, $\bar{x}_{\text{females}}$= 20.44+/- 1.9). Only six adult males were sampled with the eldest being 29, while 29 adult females were sampled up to age 54.

Discussion

The fear of predation can be influential in animals beyond direct mortality (Martin et al. 2011). Indirect consequences of predation risk can alter a prey population's behaviors more than direct mortality by affecting prey dietary selection (Schmitz 1998). In AENP, elephants recognized lion calls as signs of predator presence and viewed the lions as a potential threat. Their behavioral alterations imply that there is a benefit to performing anti-predator behaviors. The general lack of differential response based on focal elephant demographics suggests the cost to benefit ratio of performing behavioral changes is similar for all elephants or at least above some minimal threshold. The cost for elephants not responding could be great enough that any benefits of continuing in the same behavior (i.e. drinking) would be negated. In addition, the perceived predation risk could be similar for each elephant, regardless of age and social structure. According to the landscape of fear model, animals respond to differing levels of predation (Laundre et al. 2010). In that case, all elephants should show similar patterns for resource use based on predation risk.

Each control type had a different effect on elephants. Elephants did not alter their behavior over the ninety-second observation period when no call was played. The trials with no sound occurred at the same point in elephants' occupation of the waterhole as when the sounds were played. The lack of change in behavioral response supports the assertions of sounds altering elephant behavior. The sound of running water did not act as a control with a positive response as expected. Initial trials showed promise for more approaches to the water sound by sub adult and adult males. If the trials for water had been played for longer than thirty second time intervals, a greater change in behavior recorded may have been observed as elephants become accustomed to the sound’s presence, diminish distress events behaviors, and move toward the speaker (pers. obs.). However, the protocol was balanced against playing lion calls for so long that all the elephants would flee. The thirty second duration for playing sounds was a good compromise between these opposing factors.

The static sound elicited the most changes in elephants’ behavior out of all the controls. Static has no significant evolutionary meaning to elephants; it could be either viewed as a biologically significant threat (by association with humans or as a sound with an unknown source) or as an annoyance. Although there was an increase in distress states and events elephants’ performed after the static sound, the magnitude of these changes was not as large as for elephants responding to lion calls. In some areas, where there is greater human-elephant conflict or elephants are less familiar with human noises, elephants may respond differently, associating this noise with more risk. In that case, there would be a learned response with biologically significant sounds, but not an evolutionary one.

Lion calls evoked responses in elephants, changing behavior. Elephants displayed the highest levels of distress behaviors as well as fleeing after the lion calls played. The predicted behavioral changes were elicited except that elephants did not display higher rates of investigatory behavior after the lion calls were played. Habituation could take place if elephants continually heard lion calls without encountering visual or chemosensory evidence of lion’s immediate presence. However, by not investigating the stimuli, habituation would be less likely to occur. If the elephants fled, there would be no time to gather more evidence of lion presence at the waterhole. No signs of habituation, including evidence of decreases in the change of behavior were shown through the study period. Elephants fled in 28.6% of the lion call trials. For individuals that fled the waterhole, their focal observation were cut short because they left the viewing area Therefore, the changes in the rates of state and event behaviors for those elephants may have been underestimates.

Calls played with one adult male lion roaring and calls with two male lions roaring elicited similar responses in elephants. These results support the findings of McComb et al. (2011) in Amboseli, Kenya, where three lions roaring produced greater changes in behavior than an individual male lion. The number of male lion present in the Main Camp section is small; therefore, the novelty of the calls may be greater factor for the elephants in this study compared with the Amboseli study. McComb et al. (2011) found families with younger matriarchs reacted more strongly those with older matriarchs did while my study showed correlations. However, no matriarchs in my study were all 55 years or older, which is how matriarchs were defined in the Amboseli study. Therefore, if I could have sampled families with older matriarchs, perhaps I also would have seen this trend.

Age rank correlated with several behavioral changes, while sex did not. Younger elephants showed a greater decrease in drinking after the call, and a greater increase in distress state behaviors. This is indicative of a greater fear of susceptibility to lion predation. Another study found little variation in elephant activity patterns when compared by sex (Shannon et al. 2008). In my study, only the change in rate of investigative behaviors performed was different by sex. Females have more kin present, so protecting them would be a greater advantage for indirect fitness than males, who are more likely to be traveling with unrelated individuals.

In general, male juvenile elephants differ in behavior from females of the same age due to males increasing distance from family groups while still developing (Lee 1987). Males of this age group were presumed to be at an increased risk to lion predation (Wittemyer et al. 2005a). Juveniles had the greatest decrease in the proportion of drinking after lion calls. However, elephants that were in the juvenile age class showed no differences in behavioral responses by sex. Juvenile and subadult males travelled to waterholes in smaller groups, decreasing the protection afforded by a larger number of elephants in a herd. Females were in larger groups; however, this difference in group size did not affect the change in behaviors after lion calls were played. The potential pressure predation must be similar enough to elicit no differences in changes of behavior for subadult and juvenile males and females.

The benefits of sociality and larger group sizes include group protection, less individual vigilance, and the dilution effect (Elgar 1989, Roberts 1996). Therefore, elephants in larger groups should show a lessened individual response to predator cues. The behavior of elephants, in this study did not support this. The change in state behaviors of female elephants found larger groups correlated with a greater decrease in drinking and greater increase in distress behaviors. These results opposed the original hypothesis.

In large mammals, individual reproduction can be indirectly altered by risk assessment (Bardsen et al. 2010). Elephants with a calf four years of age or younger did not have different responses after lion calls were played than those without offspring.

Females with calves are expending high levels of energy lactating and therefore require higher quality resources or more low quality resources and is associated with calf growth (Lee & Moss 1986). This differential resource need does not seem to play a role in response to predation risk. The need for higher quality resources would be greater in lactating females; therefore, the costs of not getting them would also be greater. Overall, in adult and subadult females only the number of calves present showed a correlation with the levels of change in any behavior. Drinking decreased at greater rates when more calves were present and groups were larger. With greater levels of protection afforded by living in larger groups, the opposite response was expected to occur, with elephants in larger groups overall responding less strongly to threats. This magnified response indicates females were more likely to decrease the proportion of time spent drinking, a state of vulnerability, when more calves were present. This could be due to kin selection, with related females reacting defensively to possibly protect related calves to increase indirect fitness (Dublin 1986, Archie et al. 2006b). This could also benefit the female directly, allowing her future reproductive success (Clutton-Brock 2002). Females helping others within their herd before they have offspring may help to establish a stronger bond (Lee 1987). When the female becomes reproductively active, she could then expect reciprocation from other group members. These changes in reproductive state can affect the leadership roles, as shown in zebra (Fischoff et al. 2007). However, in elephants, reproductive state does not appear to determine leadership (Wisniewska 2011).

The age of a matriarch did not greatly alter her or her subordinate’s response to the threat of lions for several possible reasons. Esposito (2008) found matriarchs performed more investigatory behaviors in response to more complex social situations. In this study, matriarch age and presence did not alter the response of elephants to lion calls as much as expected. Lions were reintroduced in 2003, meaning all adult elephants have had equal opportunities to gain experience with lions regardless of actual age. Matriarch presence or absence did not affect the behavioral changes of other elephants shown after lion calls played. Esposito (2008) found the matriarch's presence to alter the interactions of unrelated conspecifics. Unlike conspecific interaction among elephants, the threat of predation is mostly independent of age after individuals reach adulthood. Although size greatly determines conspecific interactions in elephants (Archie et al. 2006a), those size differences are less important in interactions with predators. This could explain why adult females of differening rank showed no differences in behavior. Female adult and subadult elephants increased their rate of social behaviors performed when the matriarch was absent, suggesting that in the absence of a leader females may use a more democratic process for decision-making (Conradt & Roper 2003, 2007). Younger individuals taking cues directly from their mother would not change their behavioral response based on matriarch's presence or absence. Younger matriarch's age rank showed correlation with subordinates' increasing in distress and flee behaviors indicating greater responses of fear in these groups. Generally, herds with lower-ranked matriarchs alter their behavior in everyday movements, travelling farther and in less predictable patterns (Wittmyer & Getz 2007). These groups with already more stressed behavior reacted more strongly to predatory cues. Therefore, using lion calls would be more likely to be effective against these herds.

Along with McComb et al. (2011), this work supports the finding that elephants exhibit general anti-predator responses to lion calls. Elephants in AENP show similar behaviors to that of elephants in other parts of Africa (Schulte et al. 2008). Therefore, similar responses would be expected throughout all African elephant populations. The cost for elephants not responding could be great enough that any benefits of continuing in the same behavior (i.e. drinking) would be negated. Elephants have been shown to alter their patterns of movement with predation pressure (Wittemeyer et al. 2008). Habitat use, as modeled in the landscape of fear, can be valuable for estimating prey species response to real and perceived predation risk.

Table 1. Field effort from June 3rd, 2010 to January 11th, 2011 at AENP, South Africa.

Month	***Hours in field***	***Hours / week***	***Notes***
June	75.2	37.6	Fly in June 3rd
July	154	63.5	
August	107.7	26.9	
September	108	27	
October	154	63.5	
November	63	15.8	Land rover issues and week off
December	70	17.5	Week off, Christmas, training in new researcher
January	43.9	29.3	Train in new researcher, leave the 11th

Table 2. Family organization of elephants in the Main Camp AENP.

Clan	1				2	
Kinship group	A	B	H	M/P	L	R
Oldest "Grand" Matriarch (year born)	Andiswa (1956)	Tania (1951)	Heidi (1972)	Megan (1965)	Little Left Tusk (1968)	Rebecca (1964)
# Individuals	81	73	21	95	44	49
#Families/ Kin groups	8	7*	1	10	3	6
Matriarchs (year born)	Andiswa (1956) Aloe-Vera (1961) Little Agatha (1963) Amanda (1969) Allissa (1972) Apple (1974) Amber (1977) Annake (1985)	Tania (1951) Beverly (1970) Caterina (1970) Bluebell (1976) Bonny (1980) Bridie (1980) Bhunya (1986) Byrony (1986)	Heidi (1972)	Megan (1965) Paula (1969) Tipperary (1973) Molly (1981) Mondeka (1981) Phyllis (1981) Pumeza (1984) Melanie (1987) Morag (1990) Madaline (1991)	Little Left Tusk (1968) Laura (1972) Lulama (1984)	Rebecca (1964) Ruth (1971) Rita (1973) Rozalind (1975) Rosie (1981) Ronella (1984)
Collared Females	Amber (1977)	Bubble (1983)	Hilary (1976)	Mushara (1983) Prunella (1980)	None**	Rhiannon (1976)

*B kinship group has 7 families and 8 matriarchs because Tania and Beverly lead the same individuals, however at Tania's advance age she was most often not present. Six months after the conclusion of this study, she was presumed dead.

**Park officials attempted to collar one adult female from each of the kinship groups, Ls were not found on that day. M/P is so large that they collared both an M and a P female.

Table 3. Focal observations of each sound by month during the study. Observations where no sounds played were recorded only in September and October. Bee sounds were only played from September to November.

Sounds	***Number of focal observations per month***						
	July	Aug	Sept	Oct	Nov	Dec	Total / call
Bee	0	0	9	15	4	0	28
Lion 1	1	24	8	11	10	3	57
Lion 2	0	3	13	20	8	9	53
None	0	0	21	18	0	0	39
Static	1	4	22	10	11	7	55
Water	1	20	16	27	9	2	75
Total/month	3	51	79	101	42	21	297

Table 4. Sample size information categorized by age, sex, reproductive experience for females, and rank of females in their social unit.

CALL	*Sex*	*Age Class*	*Number of Individuals*	*Mothers*	*Matriarchs*
BEE	Female	Adult	9	9	6
		Subadult	3	2	
		Juvenile	0		
		Calf	1		
	Male	Adult	3		
		Subadult	6		
		Juvenile	3		
		Calf	0		
Totals			25	11	6
LION 1	Female	Adult	15	15	6
		Subadult	6	4	
		Juvenile	2		
		Calf	7		
	Male	Adult	3		
		Subadult	6		
		Juvenile	4		
		Calf	6		
Totals			49	19	6
LION 2	Female	Adult	15	15	6
		Subadult	4	2	
		Juvenile	1		
		Calf	3		
	Male	Adult	3		
		Subadult	12		
		Juvenile	6		
		Calf	5		
Totals			49	17	6

(Table 4, continued)

CALL	***Sex***	***Age Class***	***Number of Individuals***	***Mothers***	***Matriarchs***
NONE	Female	Adult	14	14	4
		Subadult	3	0	
		Juvenile	5		
		Calf	3		
	Male	Adult	1		
		Subadult	1		
		Juvenile	2		
		Calf	5		
Totals			34	14	4
STATIC	Female	Adult	15	15	7
		Subadult	10	4	
		Juvenile	1		
		Calf	6		
	Male	Adult	5		
		Subadult	11		
		Juvenile	3		
		Calf	2		
Totals			53	19	7
WATER	Female	Adult	17	16	6
		Subadult	9	5	
		Juvenile	5		
		Calf	8		
	Male	Adult	6		
		Subadult	5		
		Juvenile	8		
		Calf	5		
Totals			63	21	6

Table 5a. The ethogram of state behaviors for African elephants used in this study.

State	***Definition of behavior***
Drink	Taking water into the trunk and immediately placing the water into the mouth
Dust	Using the foot or trunk to cover body in dirt
Eat	Take food into mouth
Freeze	Shows no overt behavior for at least 5 s
Mud	Using trunk to splash mud on the body
Play	Includes sparring, gentle, trunk wrestling, and object play
Stand	In a stationary position
Walk	Moving legs to cover a distance
Other	Any behaviors not defined in ethogram
Not visible	Individual is not within view of observer

Table 5b. The ethogram of event behaviors for African elephants used in this study. I divided these behaviors into six general types of behavior: investigative, chemosensory, trunk to, aggressive, distress, and social.

Event	***Definition of behavior***
Investigative*	
Approach	Move towards speaker
Dust	Throws dirt from speaker area on body using trunk
Near	Within one trunk length of speaker
Proximity	Within one body length of speaker
Retreat	Move away from speaker
Chemosensory**	
Sniff	Hovers nasal openings over object without contact
Check	Touches object using trunk tip finger(s)
Place	Flattens entire nasal opening onto object
Flehmen	Touches object with tip of trunk, then places trunk in roof of mouth where vomeronasal organ ducts open
Periscope sniff	Raises trunk above head level and holds this position for at least 2 s
Trunk tip to/from other elephant***	
Anus	Anal region
Body	Torso or areas not listed
Feet	Area below ankle
Genital	Urogenital area, primarily the vulva
Head	Forehead and superior most point of ear
Mouth	Tip inserted into mouth
Tail	Tail

(**Table 5b.** Continued)

Temporal gland	Temporal region or secretion
Trunk	Portion of trunk starting from mouth area, down to tip
Aggressive	
Charge	Rapidly move at sample
Temporal streaming	Secretions from the temporal region
Vocalize	Vocalizes after investigating sample, growls or rumbles
Distress	
Ear perk	Ears held erect with head unmoving
Flee	Leaves the area quickly making no stops
Head shaking	Turning head from side to side quickly
Temporal streaming	Secretions from the temporal region
Urinate	Release urine
Vocalizations	Calls; including screaming or trumpets
Social	
Clumped****	Each member of group approximately one to two body lengths apart
Displace	One approaches and the other leaves, winner does not take site formerly occupied by the loser
Present	Elephant turns so that their rear is facing an incoming individual
Push	One elephant makes contact against another with force
Supplant	One approaches and the other leaves, winner moves into site formerly occupied by loser

*Bagley et al. 2006 ‘
**Schulte, B.A., & Rasmussen, L.E.L. 1999
***Meyer et al. 2008
****Archie et al. 2006a

Daily Observations recorded: date, time, location, abiotic factors, number of elephants, ID of group observing, number of calves present

Table 6. Comparison of the change in elephants' behavior before to after each sound played using paired t- test analysis. The behaviors displayed before sounds played served as an internal control. There are no repeated individuals in these comparisons. The t value is the inferential test statistic and df is degrees of freedom.

Sound	***t value***	***df***	***p value***
6.a No sound			
Drink	-0.63	33	0.53
Stand	1.78	33	0.085
Walk	-0.62	33	0.54
Distress states	NA	33	NA
Distress events	NA	33	NA
Social events	-1	33	0.33
Investigative events	NA	33	NA
Flee	NA	33	NA
6.b Water			
Drink	-0.10	59	0.92
Stand	-1.6	59	0.10
Walk	-0.59	59	0.55
Distress states	1.6	59	0.057
Distress events	-2.38	59	0.021*
Social events	0	59	1
Investigative events	0.95	59	0.35
Flee	NA	59	NA
6.c Static			
Drink	-3.04	51	0.004**
Stand	0.84	51	0.41
Walk	-0.62	51	0.039
Distress states	NA	51	0.03*
Distress events	-2.74	51	0.0096**
Social events	0	51	1
Investigative events	-0.68	51	0.5
Flee	NA	51	NA

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

(**Table 6.** Continued)

Sound	***t value***	***Df***	***P value***
6.d All controls			
Drink	-2	113	0.009**
Stand	1.11	113	0.27
Walk	0.81	113	0.42
Distress states	2.4	113	0.018*
Distress events	-3.27	113	0.0014**
Social events	-0.73	113	0.47
Investigative events	0.52	113	0.6
Flee	NA	113	NA
6.e Lion 1			
Drink	-2.97	39	0.005**
Stand	2.50	39	0.017**
Walk	0.48	39	0.64
Distress states	2.21	39	0.016*
Distress events	-3.63	37	0.0009***
Social	-.33	37	0.74
Investigate	0.44	37	0.28
Flee	-2.37	37	0.023*
6.f Lion 2			
Drink	-4.27	46	0.0001 ***
Stand	-1.15	46	0.26
Walk	4.19	46	0.001**
Distress states	3.94	46	0.026*
Distress events	-3.63	42	0.003**
Social	-1	42	0.32
Investigate	-1.09	42	0.28
Flee	1.99	42	0.027*
6.g Lions combined			
Drink	-4.84	78	0.00006***
Stand	0.65	78	0.38
Walk	2.97	78	0.004***
Distress states	2.98	78	0.002**
Distress events	-4.53	80	0.00002***
Social	-0.83	80	0.41
Investigate	-0.47	80	0.64
Flee	-2.53	80	0.013*

* $p < 0.05$ ** $P < 0.01$ *** $p < 0.001$

Table 7. Comparison of elephants state behaviors by sound trials for all focal elephants. P-values are shown that were based on randomization tests with 10,000 permutations. Results are presented for the analysis of changes in behaviors before to after the sound being played, and before to during the sound (B-A, B-D respectively).

Sound Comparison State	***B-A***	***B-D***
7a. Static vs. Controls		
Drinking	0.028*	0.213
Walking	0.067	0.746
Standing	0.25	0.23
Distress	0.93	0.333
7b. Water vs. Controls		
Drinking	0.056	0.28
Walking	0.18	0.99
Standing	0.012*	0.041*
Distress	0.40	0.83
7c. Controls		
Drinking	0.032*	0.43
Walking	0.075	0.93
Standing	0.042*	0.16
Distress	0.46	0.48
7d. Lion 1 vs. Lion 2		
Drinking	0.66	0.001**
Walking	0.025*	0.099
Standing	0.010*	0.40
Distress	0.93	<0.001***
7e. Lions vs. Controls		
Drinking	0.005**	0.002**
Walking	0.007**	<0.001***
Standing	0.6267	0.95
Distress	0.010*	0.011*

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Table 8. Comparison of event behaviors by sound trials for all focal elephants. Randomization tests with 10,000 permutations were used to examine the change in number of event behaviors performed before to after the sound being played, and before to during the sound (B-A, B-D respectively). The means plus or minus se of the changes in behavior for each sound in the comparisons are noted from after minus before the sound (A-B for each sound). A negative mean value denotes a decrease in the rate behaviors performed after the sound.

Event	***A-B***	***D-B***	***A-B No sound***	***A-B Water***	***A-B Static***
8a. Controls					
Investigative	0.44	0.44	0 ± 0.39	-0.18 ± 0.48	0.39 ± 0.50
Social	0.69	0.69	0.23 ± 0.17	-0.17± 0.21	-0.18 ± 0.22
Distress	0.31	0.31	0 ± 0.18	0.31 ± 0.23	0.34 ± 0.24
Flee	0.42	0.41	0 ± 0.03	0.02 ± 0.04	0 .05± 0.04
8b. Lion Calls	*A-B p-value*	*D-B p-value*	*A-B Lion one*	*A-B Lion 2*	
Investigative	0.34	0.81	-0.05 ± 0.12	0.12 ± 0.16	
Social	0.86	0.76	0.03 ± 0.07	0.05 ± 0.09	
Distress	0.58	0.006**	0.34 ± 0.13	0.1 ± 0.18	
Flee	0.057	0.38	0.13 ± 0.04	0.02 ± 0.06	
8c. Lion calls vs. Controls sounds	*A-B p-value*	*D-B p-value*	*D-B Controls*	*D-B Lions*	
Investigative	0.95	0.45	0.10 ± 0.14	-0.09 ± 0.14	
Social	0.57	0.62	0.05 ± 0.05	0.01 ± 0.08	
Distress	0.26	0.0001***	0.28 ± 0.14	1.45 ± 0.21	
Flee	0.12	0.002**	0 ± 0.02	0.09 ± 0.03	

* $p < 0.05$ ** $p < 0.01$ *** $p < 0.001$

Table 9. Relationship of dominance status to change in elephant behaviors for lion call trials. Randomization tests with 10,000 permutations. The change in behavior was examined from both before the call to after (A-B), and before to during the call (D-B). The group examined was adult females only. $N_{\text{Matriarchs}} = 12$, $N_{\text{non-matriarch}} = 17$.

Behavior	***A-B***	***D-B***
State		
Drink	0.47	0.75
Walk	0.55	0.44
Stand	0.94	0.63
Distress	0.84	0.99
Event		
Investigative	0.68	0.65
Social	0.52	0.42
Distress	0.51	0.52
Flee	0.63	0.61

Table 10. Influence of matriarch presence or absence alters behaviors of lower ranked adult and subadult female elephants. Randomization tests with 10,000 permutations. The change in behavior was examined from both before the call to after (A-B), and before to during the call (D-B). N = 27.

Behavior	***A-B***	***D-B***
State		
Drink	0.84	0.78
Walk	0.23	0.92
Stand	0.13	.85
Distress	0.80	0.71
Event		
Investigative	0.47	0.42
Social	0.19	0.001**
Distress	0.88	0.55
Flee	0.16	0.19

**P<0.01

Table 11. Effect of matriarch presence or absence on behaviors of all other elephants that follow matriarchs for lion call trials. Males no longer following a matriarch were excluded from this sample. Randomization tests with 10,000 permutations. The change in behavior was examined from both before the call to after (A-B), and before to during the call (D-B).

Behavior	***A-B***	***D-B***
State		
Drink	0.94	0.56
Walk	0.16	0.92
Stand	0.50	0.30
Distress	0.23	0.44
Event		
Investigative	0.25	0.74
Social	0.59	0.92
Distress	0.74	0.37
Flee	0.20	0.075

Table 12. Comparison of behaviors exhibited by number of elephants in the same family group and total number of elephants present. For all comparisons, df = 241.

Event Behavior	***Group size***	***Correlation coefficient***	***P value***
Investigative	Family	0.0149	0.5913
	Total	0.044	0.7503
Social	Family	0.158	0.006**
	Total	-0.014	0.4137
Distress	Family	-0.003	0.4831
	Total	-0.134	0.0254*
Flee	Family	-0.056	0.1920
	Total	-0.094	0.0722

* $p < 0.05$ ** $P < 0.01$

Table 13. Comparison of changes in behavior for lion call trials with adult and subadult females by those with and without calves. Randomization tests with 10,000 permutations. The change in behavior was examined from both before the call to after, and before to during the call. $N_{\text{Females with calves}} = 16$, $N_{\text{Females calves}} = 8$.

Behavior	***A-B***	***D-B***
State		
Drink	0.85	0.87
Walk	0.13	0.63
Stand	0.42	0.38
Distress	0.32	0.75
Event		
Investigative	0.47	0.39
Social	0.99	0.42
Distress	0.58	0.70
Flee	0.68	0.71

Table 14. Comparison of juvenile and subadult male to female elephants' changes in behaviors over lion call trials. The changes examined were the proportion of time in each state behavior and change in number of event behaviors both before to after the call (A-B) and before to during the call (D-B). N $_{male}$=28, N $_{female}$=13.

Behavior	***A-B***	***D-B***
State		
Drink	0.64	0.21
Walk	0.46	0.99
Stand	0.65	0.17
Distress states	0.63	0.97
Event		
Investigate	0.12	0.59
Social	0.87	0.12
Distress	0.95	0.61
Flee	0.41	0.12

Table 15. Comparing state and event behaviors by age over lion call trials. The Spearman's rank correlation coefficient between age and each behavior. The change in the proportion of time elephants performed state behaviors from before the call to after the call and before the change from before the call to during was examined. In event behaviors, the change in number of behaviors performed was examined. Rho is the correlation coefficient.

Behavior	***Rho***	***p-value***
A-B		
States		
Drink	0.26	0.013*
Walk	-0.04	0.68
Stand	-0.0001	0.99
Distress	-0.23	0.028*
Events		
Investigative	0.13	0.20
Social	-0.04	0.67
Distress	-0.20	0.051
Flee	-0.12	0.22
D-B		
States		
Drink	0.22	0.036*
Walk	-0.05	0.61
Stand	-0.12	0.27
Distress	-0.13	0.21
Events		
Investigative	0.03	0.79
Social	-0.05	0.60
Distress	-0.06	0.56
Flee	-0.01	0.91

* $p < 0.05$

Table 16. Information on the age class of elephants observed and the change in event behaviors for lion calls. The average age of each age class was determined. Then the change in number of event behaviors performed was examined by age class using a 10,000 permutation randomization test. $N_{\text{Adult}} = 35$, $N_{\text{sub adult}} = 27$, $N_{\text{juvenile}} = 13$, $N_{\text{calf}} = 15$.

Age Class	***Age (in years)***	
Adult	28.8 ± 1.6	
Subadult	14.5 ± 0.46	
Juvenile	6.8 ± 0.3	
Calf	2.7 ± 0.3	
Behavior	***A-B p value***	***D-B p value***
Investigative	0.40	0.72
Social	0.29	0.51
Distress	0.12	0.066
Flee	0.015*	0.60

* $p < 0.05$

Table 17. The change in behaviors by sex of elephants for lion call trials. The change in the proportion of time in each state behavior and change in rate in event behaviors was examined. P-values are shown for changes in behavior before to after the call (A-B) and before to during the call (D-B). $N_{male}=45$, $N_{female}=52$.

Behavior	***A-B***	***D-B***
State		
Drink	0.59	0.37
Walk	0.48	0.84
Stand	0.96	0.46
Distress states	0.99	0.91
Event		
Investigate	0.028*	0.45
Social	0.38	0.30
Distress	0.48	0.65
Flee	0.84	0.33

* $p < 0.05$

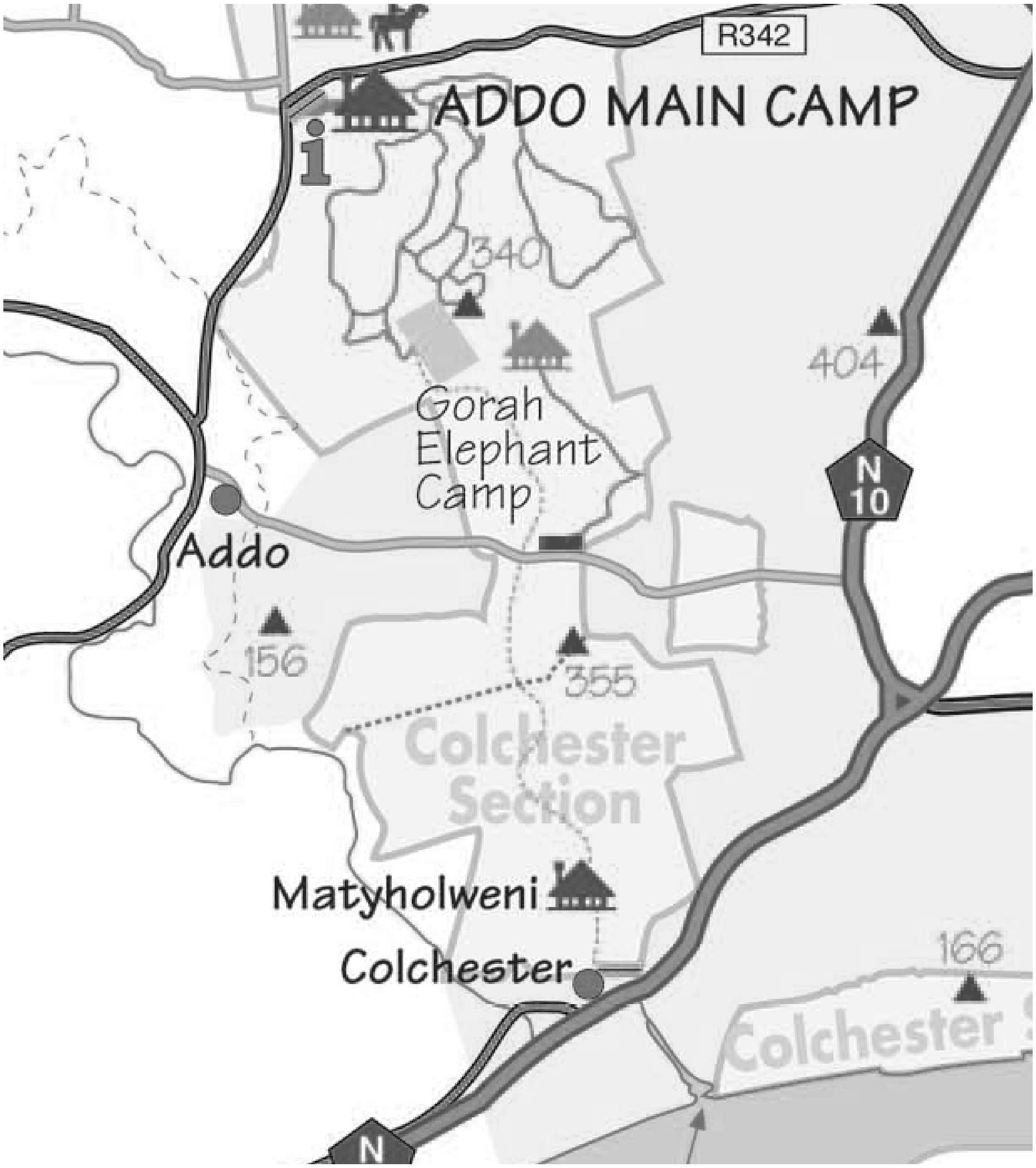

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Figure 1. Map of study area in AENP, South Africa. All data were collected from the Addo Main camp section per SANParks.

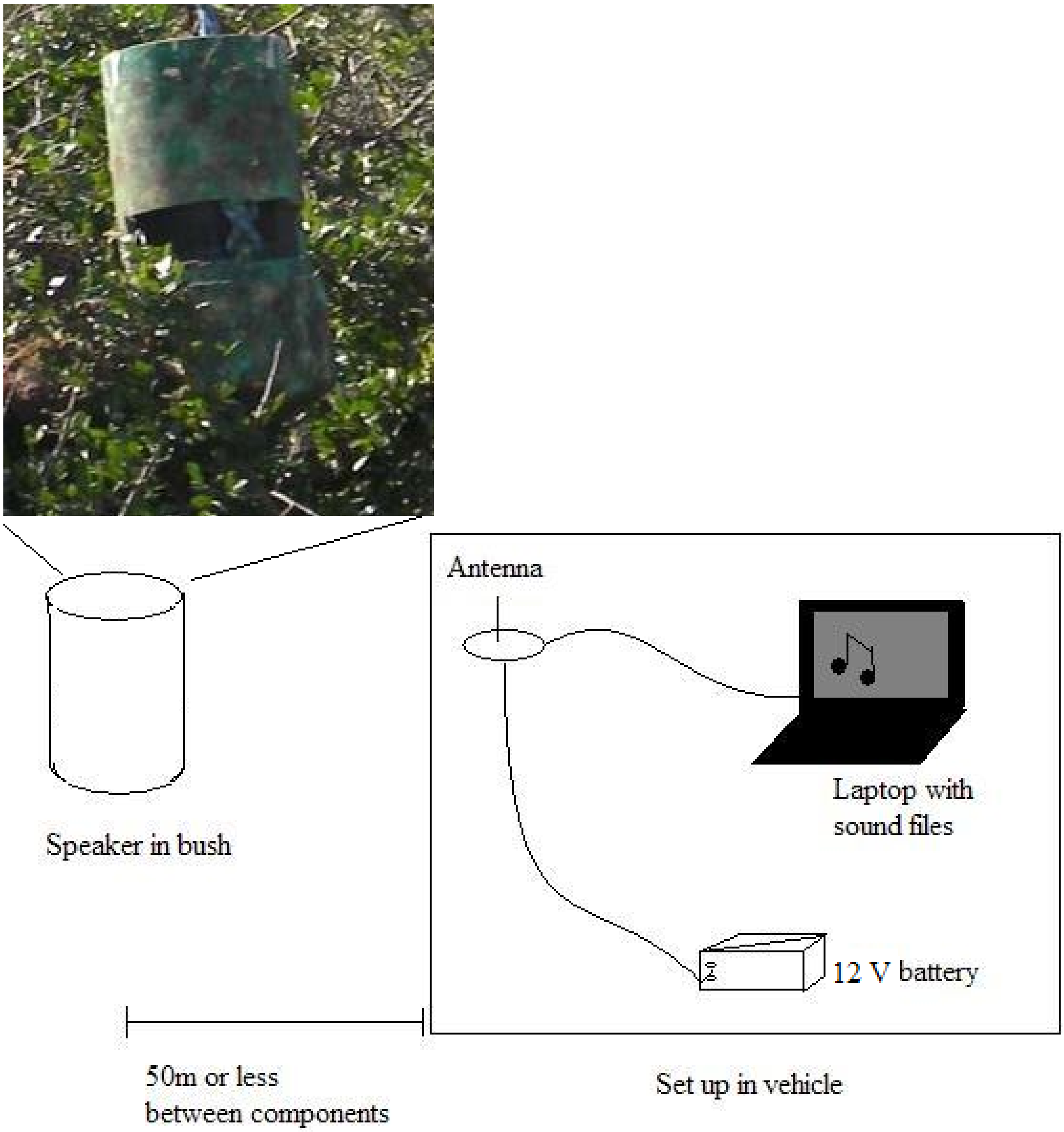


Figure 2. Speaker set up for playing calls.

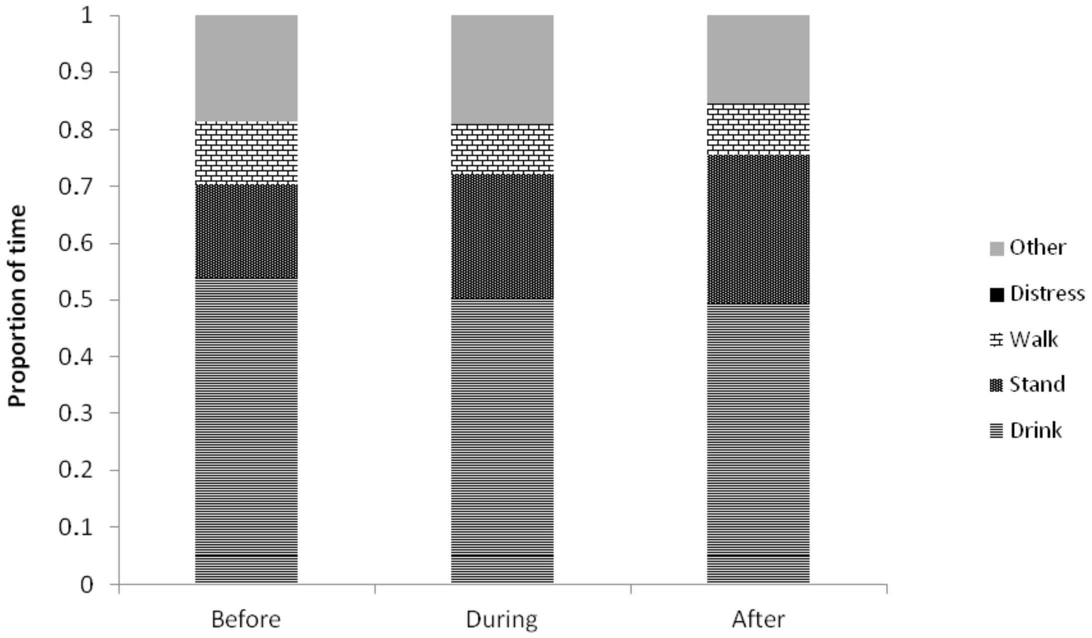


Figure 3. Proportion of time elephants exhibited state behaviors before, during, and after no sound trials. There was little change in behaviors over this 90-second period.

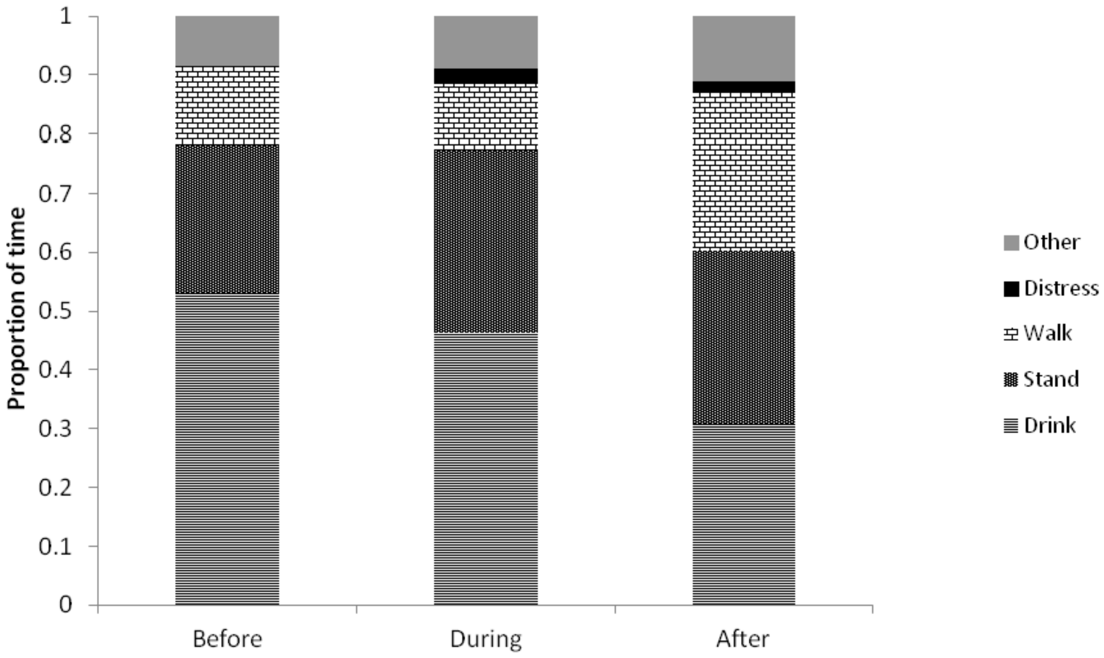


Figure 4. The proportion of time elephants exhibited state behaviors before, during, and after hearing static sound trials. There was an increase in proportion of time elephants walked (p_{rand}= 0.039) and exhibited states of distress (p_{rand}= 0.030). Conversly, drinking levels decreased after the call (p_{rand}= 0.004).

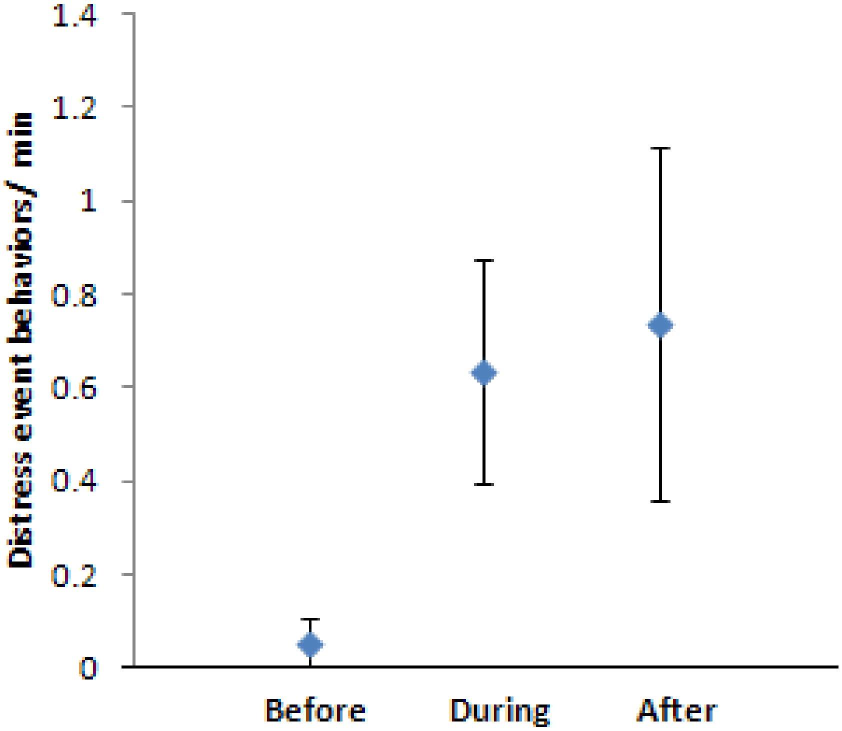


Figure 5. Rate of distress events displayed by elephants before, during and after the sound of static was played. Bars are ± 1SE. (see Table 6a).

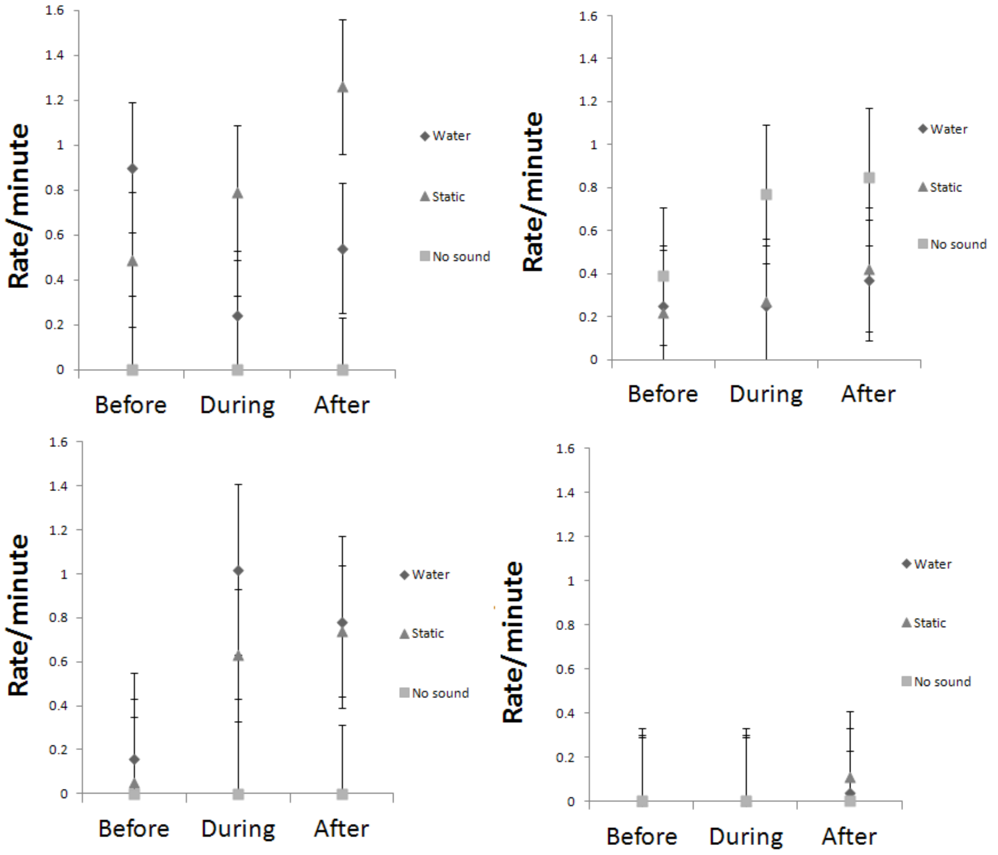


Figure 6. Performance of event behaviors over control sound trials. The rate at which elephant's displayed event behaviors during the control sounds; Investigative (top left), social (top right), distress (bottom left), and flee (bottom right) event behaviors. No elephants fled when hearing no sound (0/26, 0%), static had 2/38 (5.26%), and water 1/48 (2.08%). Bars are ± 1SE. (see Table 8a).

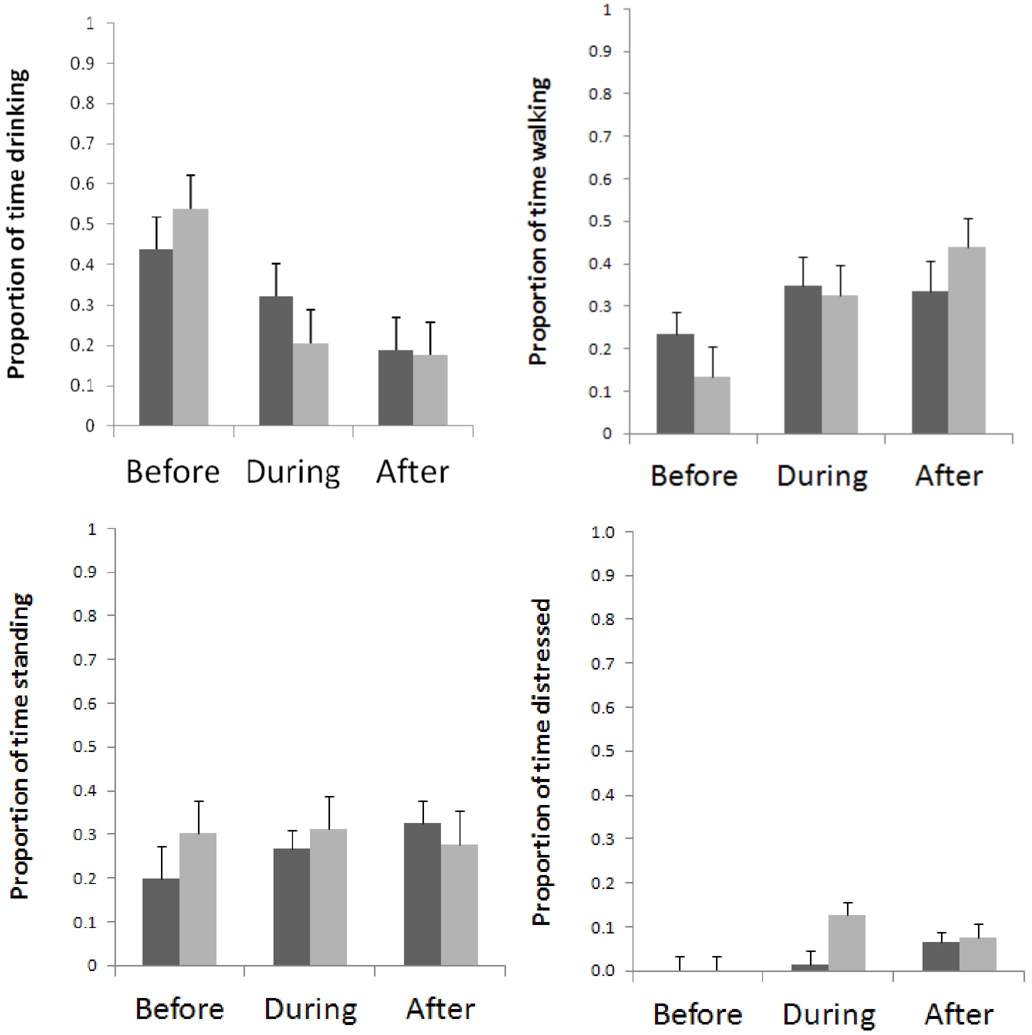


Figure 7. Proportion of time elephants spent in each state by single lion call (dark gray) and two lion call (light gray). Bars are ± 1SE. (See Table 7d).

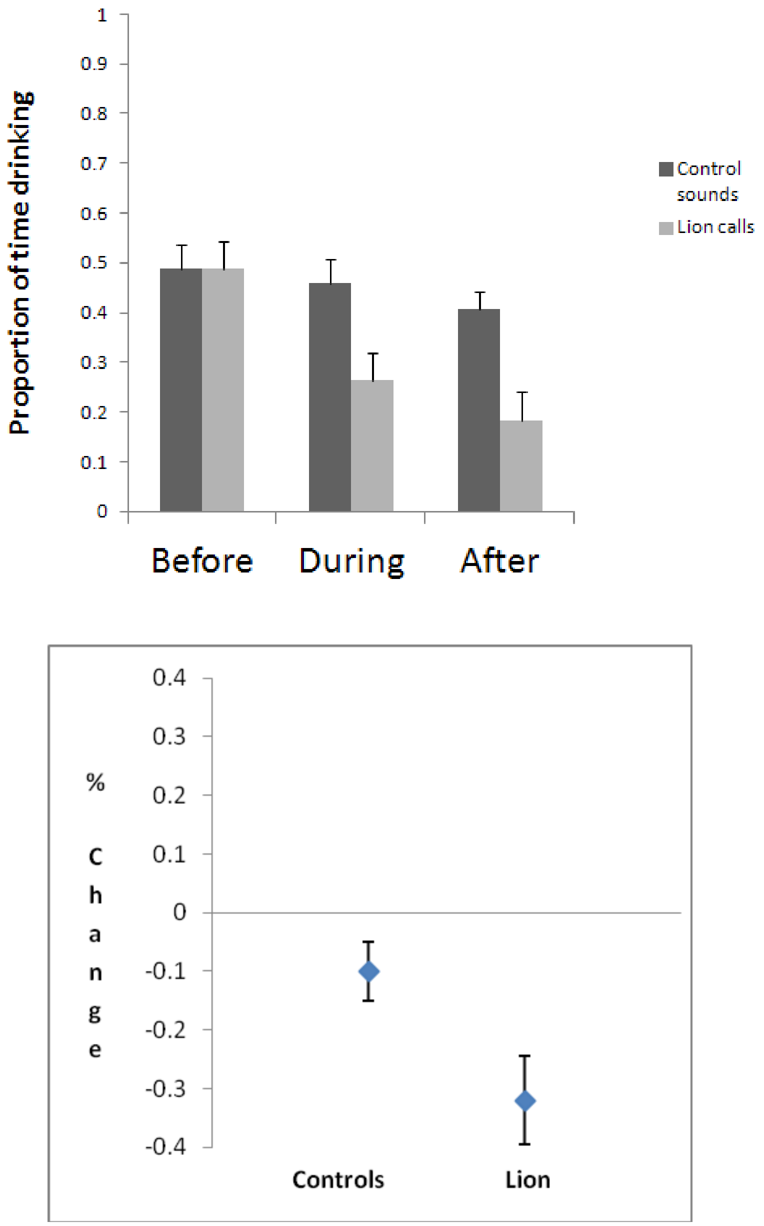


Figure 8. Drinking behavior over controls sounds compared to lion call trials. Proportion of time elephants drank over the course of control sound and lion call trials (top). The change in proporiton of time elephants drank from before to after sounds played (bottom). Bars are ± 1SE. (see Table 7c)

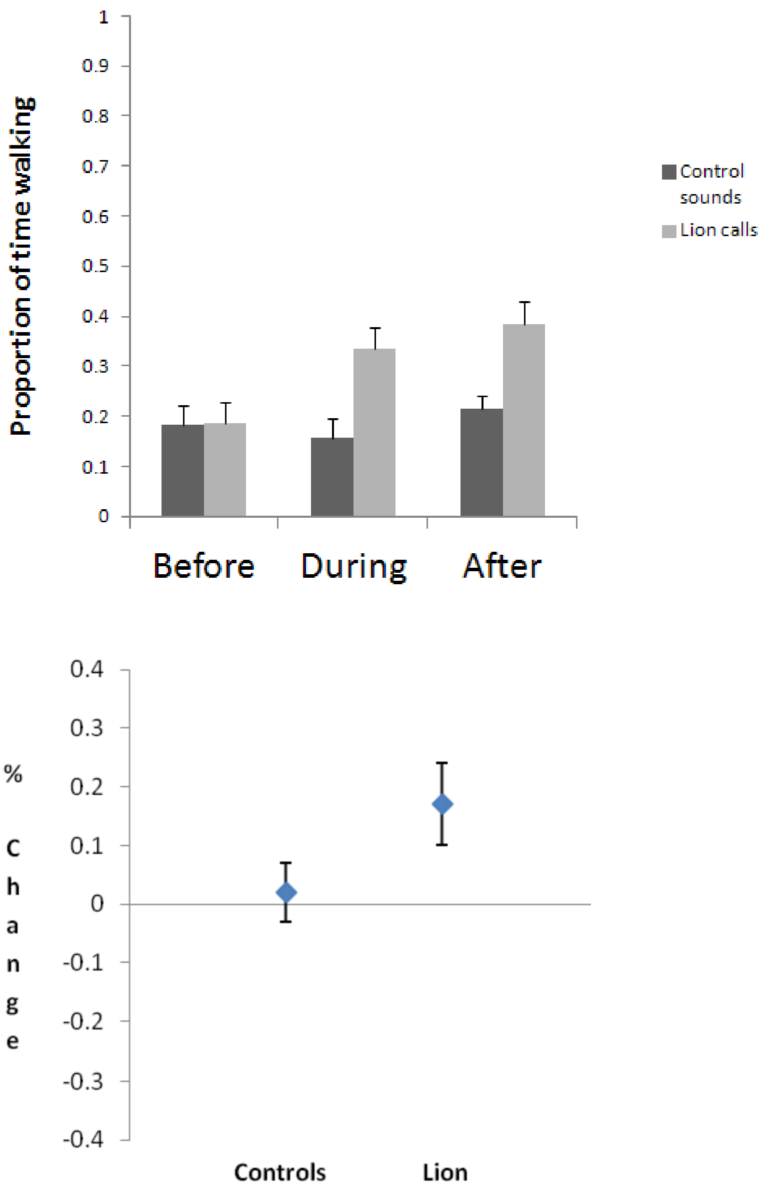


Figure 9. Walking behavior over control sounds compared to lion call trials. Proportion of time elephants walk over the course of control sound and lion call trials. (top). The change in proportion of time elephants drank from before to after sounds played (bottom). Bars are ± 1SE. (see Table 7e)

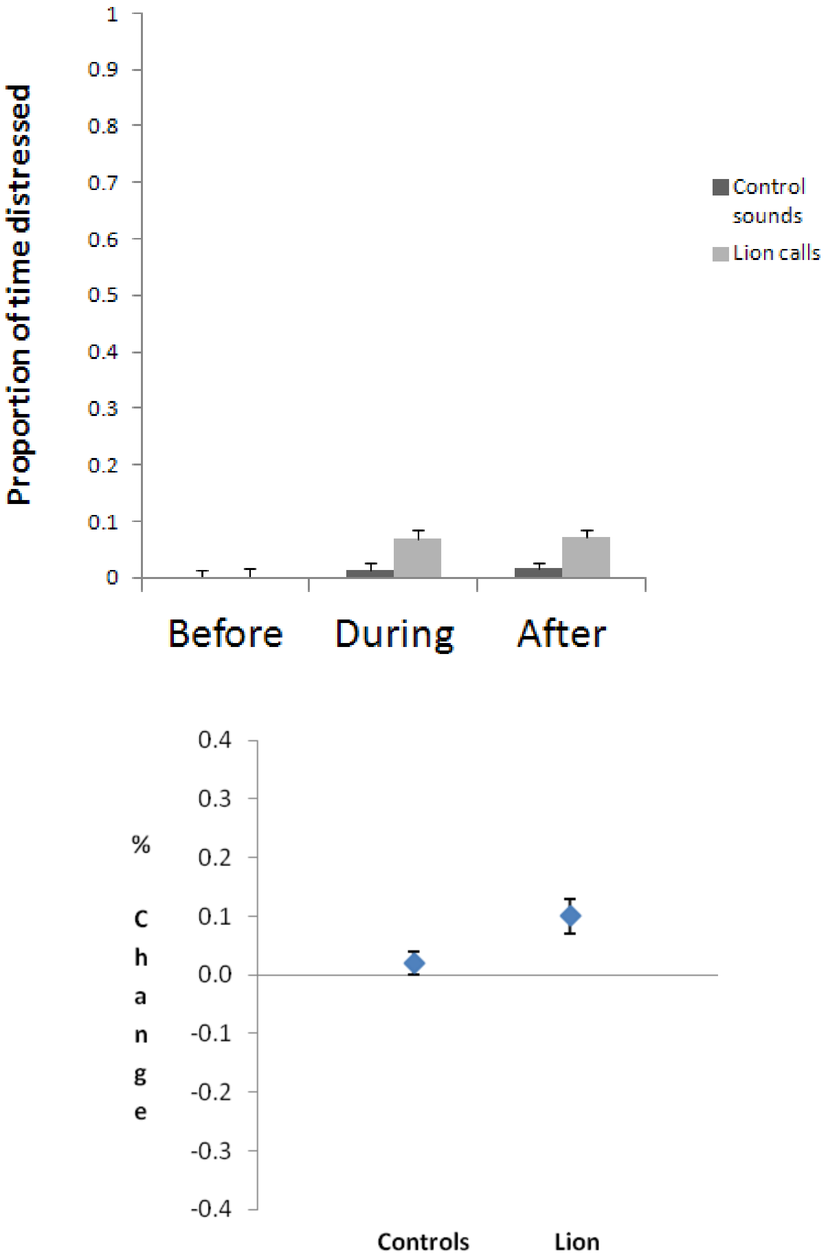


Figure 10. Distressed state behavior over control sounds compared to lion call trials. Proportion of time elephants displayed distress states over the course of control sound and lion call trials. The change in proportion of time in distress states from before to after sounds played (bottom). Bars are ± 1SE. (see Table 7e)

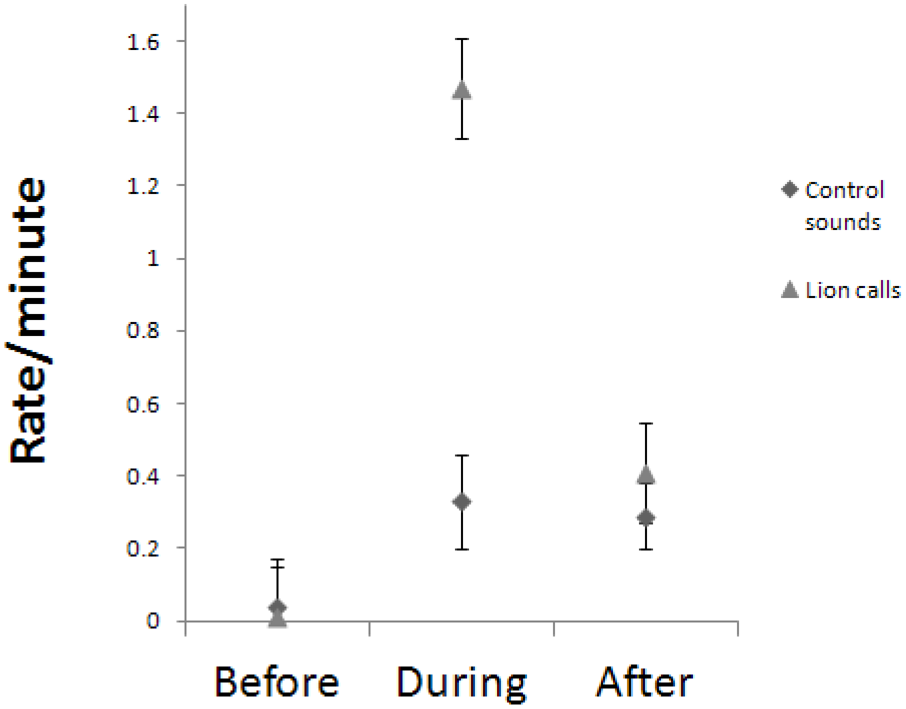


Figure 11. Rate of performing distress behaviors for control sounds compared to lion call trials. Bars are ± 1SE. (see Table 8c).

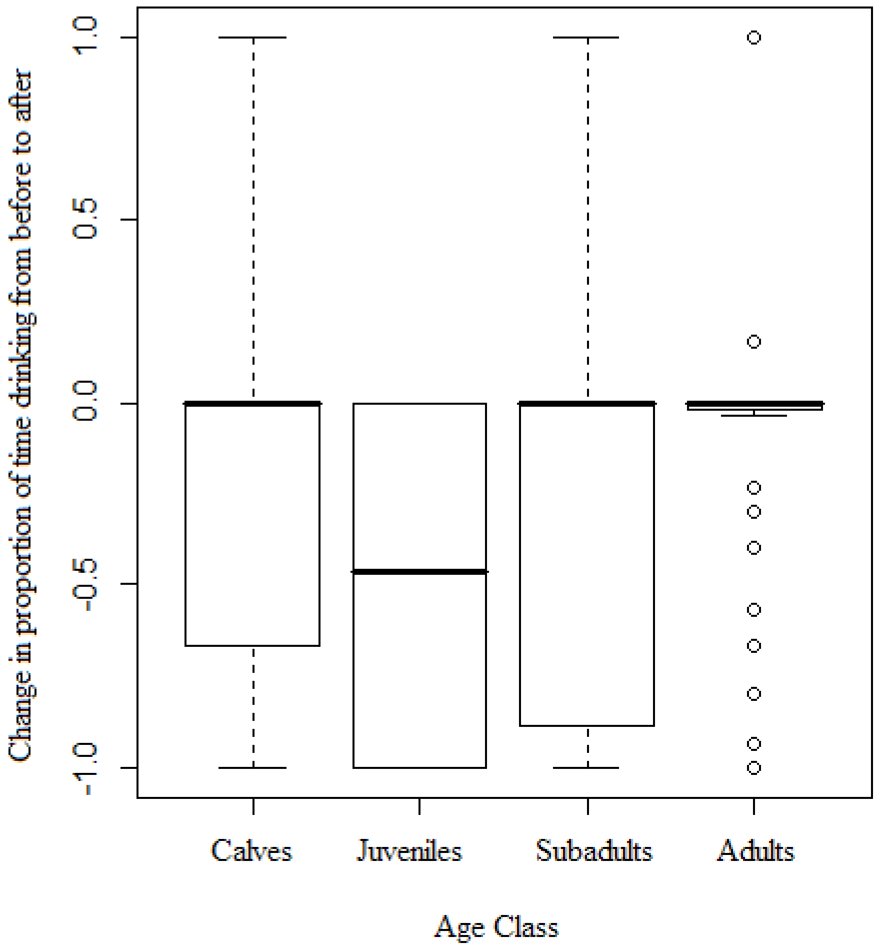


Figure 12. The change in proportion of time drinking from before to after lion calls played by developmental stages. Box plots show the middle quartiles (25-75%) of responses in boxes. The dark bold line represents the median value. The whiskers show the minimum and maximum excluding outliars (shown as the dots). (see Table 16)

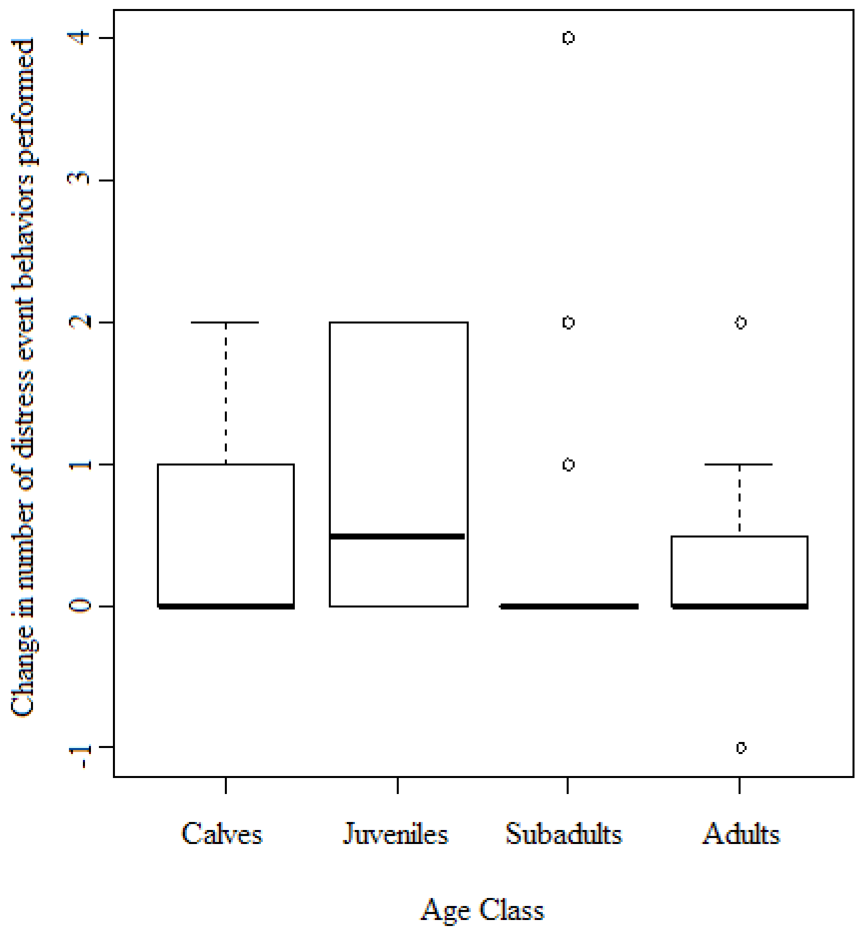
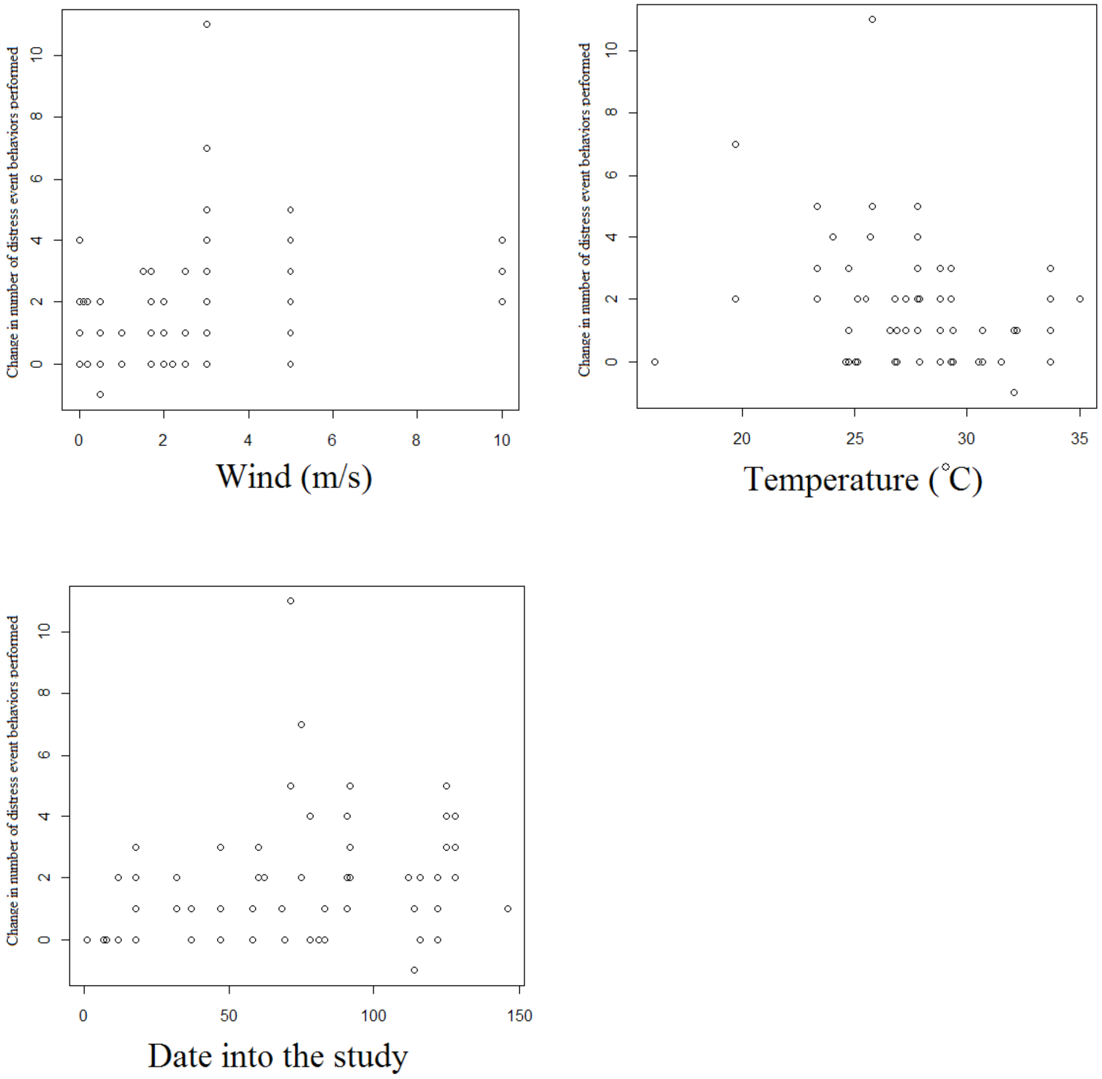


Figure 13. Change in the number of events elephants performed per 30 seconds from before the call to after by age class. Refer to Figure 12 for information on box plots. (see Table 16).

APPENDIX A



Appendix A. Change in distress behaviors from before to during the lion calls by uncontrollable factors.

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