"Impala (*Aepyceros melampus*) Associate with Olive Baboons (*Papio anubis*) for Feeding and Security in Tarangire National Park, Tanzania"

A Senior Thesis Presented to

The Faculty of the Department of Organismal Biology and Ecology,

Colorado College

By

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Bachelor of Arts Degree in Biology

22nd day of April, 2016

Abstract

Species commonly associate for feeding purposes and for security. In East Africa, impala and olive baboons are commonly found together; however, little research exists on this relationship. This study aimed to determine if impala associate with baboons by comparing the number of groups of impala and equally abundant warthogs with and without baboons. I found that impala associate more often with baboons than warthogs relative to their respective abundances. I sought to discover the function of this association and found that impala glean the fruits and flower buds of sausage trees after baboons eat, and sometimes I observed impala actively displacing baboons to eat sausage fruits and the sausage fruit leavings. Additionally, when sausage trees were present, impala often followed the baboon troop considerable distances. I often observed impala with baboons even when there were no sausage trees, therefore I suspect that impala associate with baboons for increased predator detection in addition to feeding. After comparing vigilance behaviors of impala with and without baboons, I found that impala with baboons spend less time actively vigilant. Overall, the results of this study indicate an association between impala and olive baboons and suggest that they associate with baboons both for feeding and for security.

Abstract (Kiswahili)

Viumbe kwa kawaida wanaka pamoja kwa malengo yao kula na kwa usalama wao. Katika Afrika Mashariki, swala pala na nyani kwa kawaida wanaka pamoja, hatahivo tafiti chache zimefanyika kuhusu usiano wao. Utafiti huu unalenga kufahamu kama swala pala wanaka na nyani kwa makusudi kwa kufananisha idadi ya makundi ya swala pala na ngiri wakiwa na wasipokuwa na nyani. Nimeona kuwa swala pala na nyani wanaka pamoja zaidi na mara nyingi zaidi ngiri, ikimaanisha kuwa wanaka pamoja kwa makusudi maalum. Pia, nilifikiri kufahamu sababu ya uhusiano. Baadhi ya swala pala wanafuata makundi ya nyani kwa umbali mrefu kidogo. Niliona kuwa swala pala wanakula mabaki ya matunda na vikonyo vya maua ya mti wa mlegea yaliochwa na nyani. Pia niliona swala pala kwa makusudi wakifukuza nyani ili kula matunda ya mti wa mlegea yaliochwa. Nimeona nyingi swala pala na nyani bila kuwepo mti wa mlegea, kwa hivio nimefikiri kuwa swala pala wanaka pamoja na nyani kwa kuongeza uwezo wakuona adui kuambali zadi kula. Nilijana tofauti wa swala pala kuwa na wasi wasi wa kuepo adui pasipokua na wakiwa na nyani.

Key Words: impala, olive baboons, association, sausage trees, gleaning, vigilance, commensalism, mutualism

Introduction

Commensalistic and mutualistic associations of species occur throughout all of the kingdoms across many species from algae and coral to legumes and mycorrhiza. Animals associate and form mixed-species groups for many reasons, but two of the most common reasons for species associations are for safety and nutrient acquisition (Morgan-Davies 1960).

Animals coalesce into both mixed species and monospecific groups for increased security. The dilution effect takes place in large groups because the likelihood of any one individual being caught is reduced when the total number of individuals increases. For example, Treherne and Foster (1982) found that the marine insect *Halobates robustus* aggregates primarily for anti-predator functions and that attacks per individual decreased significantly as group size increased. Another benefit of being in a group is that predators have lower success rates when hunting grouped prey than they do when hunting solitary individuals. Kenward (1987) found that goshawks had lower success rates when hunting pigeons in large flocks than solitary individuals or small flocks. They concluded that the primary reason for the difference was that the goshawk was less able to surprise the pigeons in large groups.

These same principles also likely apply to mixed species groups (Sridhar and Shanker 2009). Additionally, sometimes in a mixed species groups, there is an advantage to one of the species if that species is better at evading predators. It is also possible that a predator has a preference for one species over the other. This is the case with the mixed species herds of Thompson's and Grant's gazelles. A study found that cheetahs more often caught the smaller Thompson's gazelles, therefore reducing the rate of Grant's gazelle kills when in mixed species herds (Fitzgibbon 1990).

Animals that form mixed species groups also have the advantage of more individuals looking for and announcing danger. Many animal species use alarm calls to announce the presence of a predator to conspecifics (Caro 2005). A prey animal must be constantly vigilant or rely on others to inform them of danger in order to be survive. It would therefore be advantageous for an individual to use as many sources of information as possible. As a result, many species not only rely on conspecific alarm calls, but also heterospecific alarm calls to alert them to danger; this is commonly referred to as eavesdropping (Dall et al. 2005, Danchin et al. 2004, Valone 2007). Eavesdropping has been recorded in a variety of species including several primates (Ramakrishnan and Coss 2000, Fichtel 2004, Seyfarth 1990), ungulates (Kitchen et al. 2010), and rodents (Mueller and Manser 2008, Shriner 1998). By increasing the number of individuals looking for danger, eavesdropping increases the likelihood of detecting a predator in time to display the proper anti-predator response. Additionally, heterospecifics may have alternative methods for detecting predators that other species may lack, again increasing the likelihood of detection (Bshary and Noe 1997, Goodale and Kotagama 2005, Magrath et al. 2009). It has even been observed that some species—including ungulates and primates—actively associate with species that are more adept at detecting predators (Noe and Bshary 1997, Fitzgibbon 1990, Stridhar et al. 2009).

Another common reason for species to associate is for nutrient acquisition. These associations can be either mutualistic or commensal. Mutualistic associations for nutrient acquisition often come in the form of cooperative hunting. For example, when coyotes (*Canis latrans*) associate with badgers (*Taxidea taxus*), their prey had increased vulnerability allowing both the coyotes and badgers to have higher success rates (Minta 1992). Among herbivores, a common reason for association is for gleaning, the acquisition of plant matter by ground-dwelling animals from arboreal animals (Tsuji 2007). Gleaning relationships are usually considered commensal (Heymann 2014), with the gleaning individual benefiting, however, these relationships can sometimes be mutualistic when an arboreal animal derives some security benefit from the ground-dweller. One such example is with the hanuman langur monkeys (*Presbytis entelfsa*) and chital deer (*Axis axis*) in the Central Indian Highlands. Chital deer initiate associations with the langur monkeys to glean a variety of dropped vegetation. The chital deer and langur monkeys appear to recognize each other's alarm calls, with the chital deer reacting more strongly. Therefore, this relationship is classified as a asymmetric mutualism with the chital deer benefiting more than the langur monkeys (Newton 1989).

Baboons have been observed in association with a variety of ungulates. Senzota (1983) observed hyraxes eating remains of tree fruits left by baboons and Elder and Elder (1970) discovered bushbuck present during 35% of their total baboon sightings. Later, Allsopp (1978) confirmed the baboon-bushbuck association and attributed it to shared habitat, gleaning of acacia seedpods, and security afforded by the baboon "sentinels" in the trees. One of the earliest noted associations of baboons and ungulates is the association of olive baboons (*Papio anubis*) and impala (*Aepyceros melampus*) described by Morgan-

Davies (1960). In Lake Manyara Game Reserve in northern Tanzania (then Tanganyika), Morgan-Davies described the impala gleaning fruits and flowers dropped from *Acacia sieberiana* and *Phoenix reclinata.* Morgan-Davies further suggested that the relationship was secondarily for security.

In Tarangire National Park, Tanzania, I not only saw a clear association between the olive baboons and impalas, but also saw impala gleaning fruit from a previously unreported tree—sausage tree (*Kigelia africana*)—from the baboons, and examples of impala following baboons. Although the association between baboons and impala has been noted in the literature, it has been described exclusively qualitatively (Hall 1963, Poles 1955, Washburn 1961, Morgan-Davies 1960). Additionally, no research has investigated movement patterns near gleaning sources or differences in impala vigilance with and without baboons. To examine the baboon-impala association, I hypothesized:

1: If impala actively associate with baboons, then the impala will associate more often than a different, but equally abundant, species associates with baboons (relative to their respective abundances).

2: If impala associate with baboons for gleaning, then following behaviors will be exhibited more often when sausage trees are present.

3: If impala associate with baboons primarily for gleaning, then the impala will be observed associating with baboons primarily when there are sausage trees present.

4: If impala associate with baboons for increased predator detection, then impala associating with baboons will be less vigilant than impala not associating.

Methods

Study Site & Study Population

This study was conducted during October and November 2014 with the resident populations of impala, baboons, and warthogs in Tarangire National Park, Tanzania (3.83° S, 36.00° E). Tarangire National Park is savanna ecosystem dominated by grassland, open woodland, and dense woodland. This study was performed in the north of the park in the areas surrounding the Tarangire River (Figure 1). Observations were primarily made in open woodland habitats where the most abundant species observed included zebra, giraffe, impala, warthog, elephant, lion, cheetah, olive baboon, and vervet monkey.

Locating Baboons and Impala and Assessing Likelihood of Association

In order to determine if impala actively associate with baboons, I compared the number of groups of impala and warthogs (*Phacochoerus africanus*) with and without baboons. I used warthogs as a comparison species due to similar habitat preferences as impala, because other ungulate species were not sufficiently abundant, and because both species have diets that overlap minimally with baboons (impala: grazers and browsers; warthogs: grazers including rhizomes [Cumming, 1975]; baboons: selective omnivores [Hamilton *et al*., 1978], which during our study ate sausage fruits and picked seeds and perhaps insects from among grasses). When I found warthogs with baboons, I closely watched them to see if the warthogs had any negative interactions with the baboons that would cause avoidance; none were observed.

Typically, searches for baboons, impala, and warthogs took place between 0700-1300 and 1600-1800. Upon entering Tarangire National Park, I immediately commence our search for baboons and impala. Total searching time was recorded and included only time the vehicle was moving and I was actively searching for baboons, impala, and warthogs in suitable habitat. I recorded all sightings of groups of impala and warthogs with and without baboons (within 50 m). I defined ‘groups’ as one or more individuals of the same species and considered groups separate if the closest individuals were greater than 50 m apart. Using Microsoft Excel, I performed a chi-square test of independence to determine if impala associate with baboons more than warthogs relative to their respective abundances (expected values based off of siting counts of monospecific groups of impala and warthogs).

Troop-Herd Movement Patterns in Relation to Sausage Tree Presence

When I discovered a mixed-species group of impala and baboons (n=27), I observed them from safari vehicles using unaided eyes and binoculars. I recorded approximate troop size and impala herd size in addition to impala herd composition (females, males, juveniles, and sub-adults). Animals were generally < 50 m from me and never > *ca*. 100 m. Once per sighting, I recorded the movements of the impala and baboon groups. Each time the visually estimated centroid of the troop or herd moved greater than 10 m it was recorded on a diagram. If the majority of both the impala herd and the baboon troop moved greater than 50 m in the same direction, the encounter was classified as a following event. I also considered direct movement toward baboons by impala greater than 50 m away from static baboon troops to be a following event. If less than half of the herd followed or if the herd followed, but did not follow for greater than 50 m, the encounter was classified as a possible/partial follow. If the troop moved greater than 50 m, but the impala did not follow it was classified as a non-following event. If neither the troop nor the herd moved, then it was classified as a no-movement event. I observed 15 min minimum to *ca*. 30 min (when other researchers finished or when baboons moved out of sight) and did not analyze no-movement events because observation time affects this. Regardless of whether or not the encounter was classified as a follow event, the presence of sausage trees (within 30 m) was recorded.

I tested following events and non-following events relationship to sausage tree presence for significance using a chi-square test of independence.

Vigilance

I sought to determine if baboon presence affects impala vigilance by measuring the vigilance of associating and non-associating impala. One or two focal individual(s) were selected by random number (two when logistics and time allowed; with two individuals I averaged results to assure independence); for the impala with the baboons, the focal individual had to be within 5 m of a baboon. A five-minute focal follow was performed where time spent in each of three vigilance states was recorded (active vigilance, passive vigilance, and no/low vigilance). Active vigilance was defined as any time the impala's head was at or above shoulder level. Passive vigilance was when the impala's head was bellow shoulder level, but not feeding or drinking. No/low vigilance was when the impala were feeding or drinking (Vigilance definitions adapted from Hunter & Skinner 1998, Walther 1969, for photos see Appendix 1). One observer did the focal follow and announced behavioral changes, while another recorded. If the focal animal was not visible, no data were recorded until it became visible again. If a focal animal went out of eyesight for more than two minutes, the follow was terminated.

I tested for differences in actively vigilant with a two-tailed, random-groups t-test (variances not pooled; transformation with negative reciprocal of (percent + 0.5) to meet assumptions of normality and equality of variances; there was one zero value). I did not test other categories because they are not fully independent of actively vigilant.

Results

Impala and Baboon Association

I observed comparable numbers of groups of impala and warthogs, but impala occurred with baboons seven times more frequently than warthogs. Impala associated with baboons over 50% more often than expected, while warthogs associated with baboons less than 30% of expected (*P*=0.005, Fig 2). Reasons that warthogs do not associate with baboons were unknown.

Gleaning and Sausage Tree Presence

I sighted impala within 50 m of a baboon troop 27 times. Of the total sightings, 13 (48%) were in an area with sausage trees present, despite a relatively small portion of the study area having sausage trees. During many of the sightings with sausage trees, I observed impala directly approaching baboons with the fruits of the sausage tree or approaching areas recently vacated by a baboon eating a sausage fruit. Several times, I also observed impala feeding directly beneath newly blooming sausage trees while baboons ate the flower buds. The impala appeared to seek out the buds that the baboons dropped.

Following Events

I observed approximately equal numbers of definite follow events and non-follow events. Sausage trees were present during the majority of follow events—twice as often as expected. Additionally, impala never followed baboons when there were no sausage trees present (P=0.0002, Fig 3). Baboons never followed impala.

Vigilance

Impala not associating with baboons (n=41) spent nearly twice the proportion of time actively vigilant than impala associating with baboons (n=9, P=0.029). Additionally, impala with baboons spent a lower proportion time with no/low vigilance than baboons not associating with baboons (Fig 4).

Impala group size with and without baboons was not different (means 8.6+/-1.9 and 9.4+/-2.6 respectively, t=0.23, df=34, P=0.82, 2-sample t-test, square root transformation, variances not pooled) so dilution effects of impala cannot explain vigilance differences.

Discussion

The results of the impala, warthog, and baboon association counts supported the hypothesis that impala spend more time with baboons than warthogs do, relative to their respective abundances. This indicates that impala likely seek out the baboon troops. Often when baboon-impala mixed groups were discovered, the baboons would be in or near sausage trees. Whenever I discovered baboons actually up in the sausage tree, the trees were about to bloom and the baboons were eating the flower buds. The impala would congregate directly under the tree and I could see the impala eating the flower buds that the baboons dropped.

In late October to early November, most of the sausage trees are past their flowering stage and are bearing fruits, therefore most instances of gleaning occurred when the baboons were sitting under a fruiting sausage tree eating the fruits. Impala would walk among the baboons and nibble at items on the ground. They particularly targeted areas that were currently or had previously been occupied by a baboon. The occasional impala near sausage trees without baboons sometimes tried to eat sausage fruits but failed due to the tough skin (Hamilton et al. 1978). Apparently impala access an otherwise unavailable food resource, sausage flowers and fruits, by associating with baboons. I did not observe impala gleaning other foods from baboons.

During most observations of mixed groups, the impala and baboons did not interact with each other, but when the impala gleaned sausage fruits, they sometimes had confrontations of varying degrees of aggression. Most often male impala were the aggressors and would approach baboons with a sausage fruit. Sometimes, the males would even tilt their heads downward and approach horns first. Usually, the baboons quickly moved away from the impala, often taking their fruits with them. On several occasions, I observed a baboon or group of baboons retaliating at the impala and chasing it away. When chased, the impala would not flee far and would resume feeding activities relatively quickly (see photos in Appendix 2).

When they had opportunities to glean sausage fruits or flowers, impala frequently approached or followed baboon troops for relatively large distances (up to 200-300 m). These data suggest that impala are willing to invest time and energy to follow baboons only when there is the benefit of obtaining sausage fruits. Although impala followed baboons when sausage trees were present, fewer than half of the baboon-impala mixed group encounters had sausage trees present, therefore impala likely have a secondary motivation to associate with baboons.

The vigilance data support the hypothesis that impala near baboons are less vigilant and suggest that impala may associate with baboons for increased security. Although impala are still wary of predators when they are with baboons—spending an average of 9.6% of their time actively vigilant—they are able to spend less time looking for danger. Since vigilance is a tradeoff with feeding, impala likely increase their fitness by associating with baboons.

Baboons and impala share the same predators, leopards (*Panthera pardus*) and lions (*Panthera leo*), and live in similar woodland habitats; therefore it would be logical to predict that the impala may utilize the baboons for predator detection (Cowlishaw 1994, Radloff 2004). Washburn and DeVore (1961) suggested that impala may associate with olive baboons in part because baboons can more readily detect predators with their keen eyesight and high vantage point in trees. In 2010, Kitchen et al. demonstrated that adult impala are capable of differentiating chacma baboon (*Papio ursinus*) alarm calls from contest calls. It is therefore likely that impala can also recognize the alarm call of olive baboons.

Impala are likely less vigilant around baboons because they can eavesdrop on the baboons and therefore more quickly escape danger, however the baboons may also provide impala with indirect protection against predators like the cheetah (*Acinonyx jubatus*). Baenninger et. al. (1977) observed an anti-predator display in which several male baboons drove away a cheetah, which then targeted a group of impala. When the impala noticed the cheetah, they fled directly in the direction of the baboon troop, but stopped when were within 100 m of the troop and resumed feeding. Similarly, DeVore & Hall (1965) observed three cheetahs approach a mixed-species group of impala and baboons and although the impala became very alert, they did not run away. These anecdotes suggest that impala may also seek out baboons for their ability to repel or deter cheetahs and possibly other predators.

The results of this study indicate that impala actively form associations with olive baboons for feeding and for security, with the impala as beneficiaries. In a review Heymann (2014) asserted that most primate—non-primate associations are commensal in nature with the non-primate benefitting. Morgan-Davies (1960) also defined the relationship of baboons and impala as commensalism, with the impala benefitting by gleaning and increased security. Hall (1963) agrees and describes the chacma baboon's relationship to the impala as one of "mutual disregard".

Despite the multiple benefits impala gain by associating with baboons, it is possible that baboons also benefit from the association. Washburn and DeVore (1961) described the relationship as mutualistic and claimed that impala have a keener sense of smell than baboons. Additionally, they gave anecdotal evidence of baboons reacting to impala alarm calls. Baboons may also gain security by associating with impala because of differences in vulnerability to predators, as is the case with the mixed species groups of Thompson's and Grant's gazelles—where predators target the smaller Thompson's gazelles (Fitzgibbon 1990). It is possible that in areas with tree cover, baboons may be less susceptible to predators like lions and cheetahs than the impala because they can escape into the trees, therefore reducing the rate of predation of baboons when impala are present.

Further study is required on this relationship to fully understand the benefits conferred to each species by this association. In particular, research should be done to test the possible benefits, if any, the baboons gain from the association. At present the baboon-impala association appears to be an example of commensalism or at best an asymmetric mutualism, with the impala gaining high quality food and increased security from the baboons.

Acknowledgments

I would like to thank Jim Ebersole, Laura Higgs, Ayubu Elisamehe, Carol Maynard for their guidance and support. Thank you to Stephanie Klockenbrink, Marcel Andre, Malika Dale, and Risa Luther for their assistance in my data collection. A special thank you to Marcus Glomset for collaborating with me for the vigilance portion of my study. I would also like to thank all the Nyayo Discovery Limited staff, especially Kamu and Raja. Finally, thank you to Tarangire National Park, ACM, and the University of Dar es Salaam for allowing me this opportunity.

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Figures & Tables

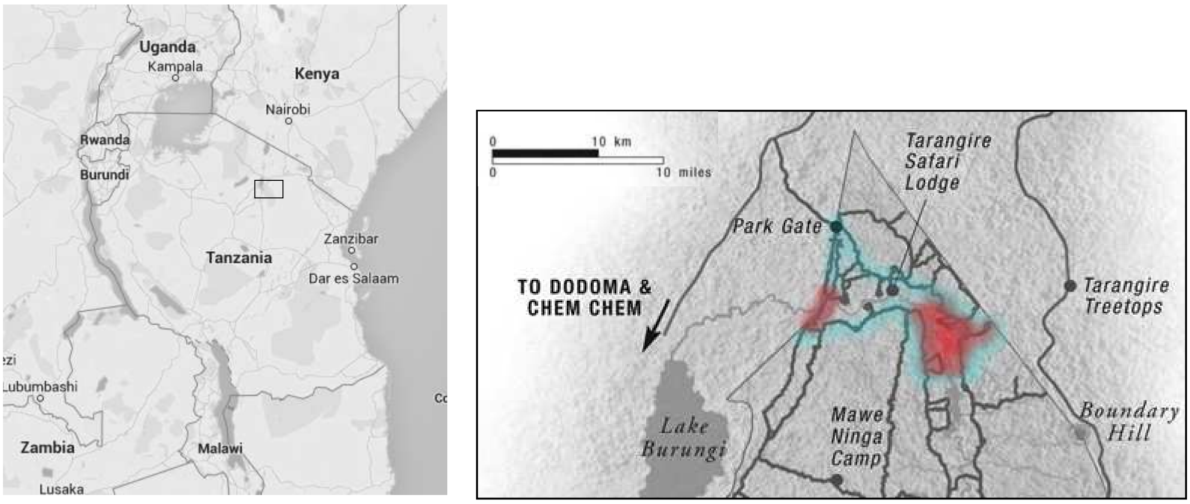


Fig 1- *Map of the northern end of Tarangire National Park.* This map shows the total search areas for baboons, impala, and warthogs (blue) and the areas where baboons were observed (red).
Google Maps 2014
Expert Africa 2012

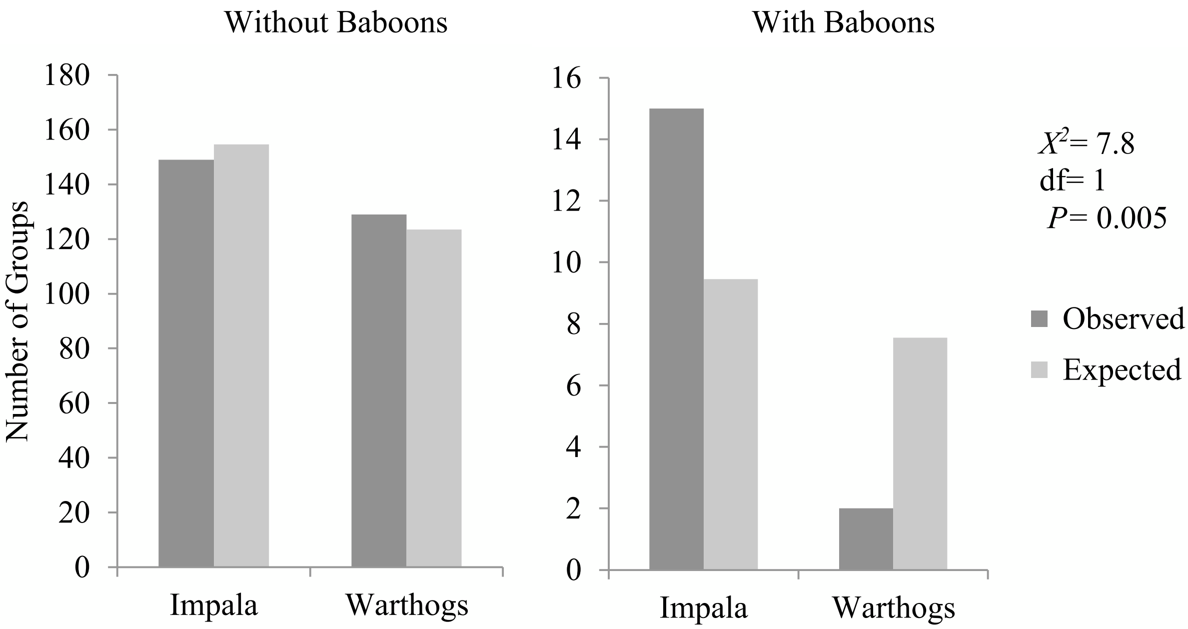


Fig 2- *Numbers of groups of impala and warthogs with and without baboons.* Expected values were calculated assuming independence of species and their association with baboons. The chi-square test of independence showed that impala and warthogs associate with baboons in different proportions than predicted by their abundances.

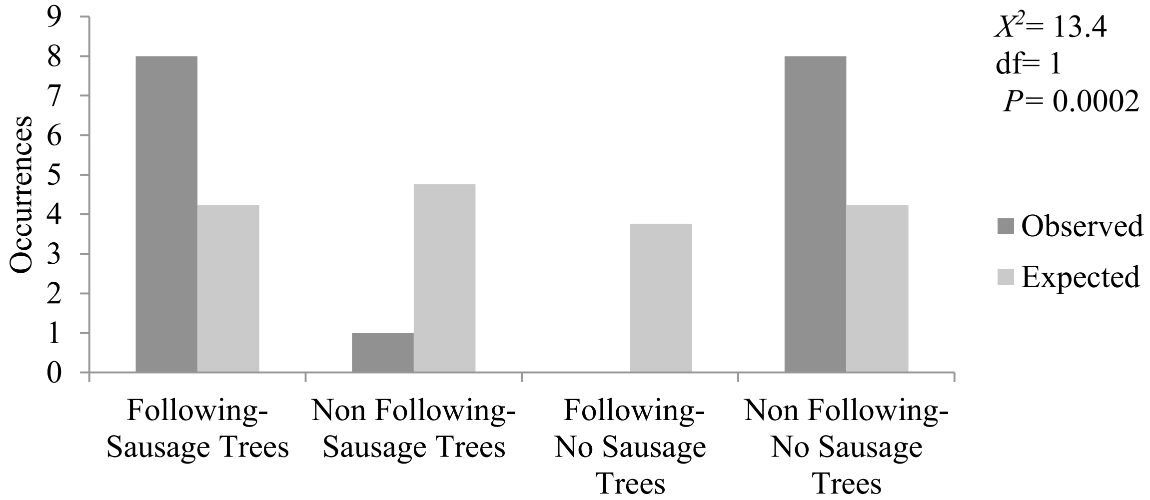


Fig 3- *Association of Following Events and Sausage Tree Presence*. Expected values were calculated assuming independence of following and presence of sausage trees. The chi-square test of independence showed that proportions of following and non-following events were different when sausage trees were and were not present. Note that the *P* value should be interpreted with caution since the total observations of 17 does not quite meet the 20 (four groups, mean expected value of 5) often given as the minimum for a chi square test.

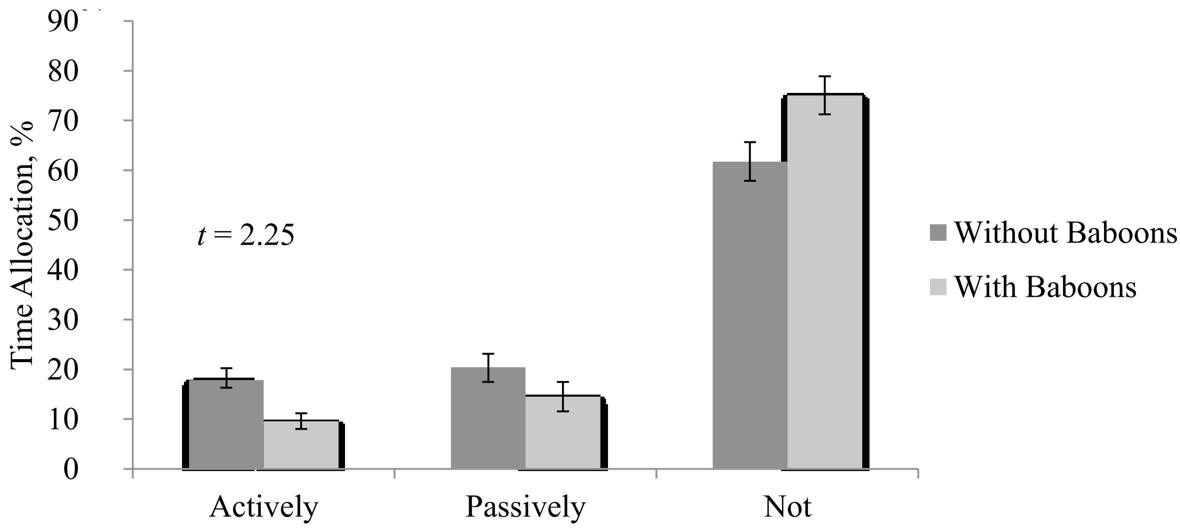


Fig 4- *Differences in Vigilance of Impala with and without Baboons.* This graph shows the mean (+/- SE) of percent time impala spent in three levels of vigilance with baboons (n=9) and without baboons (n=41) Only actively vigilant means were tested statistically (see text).

Appendix 1—Photos of Impala Vigilance Stances

Active vigilance

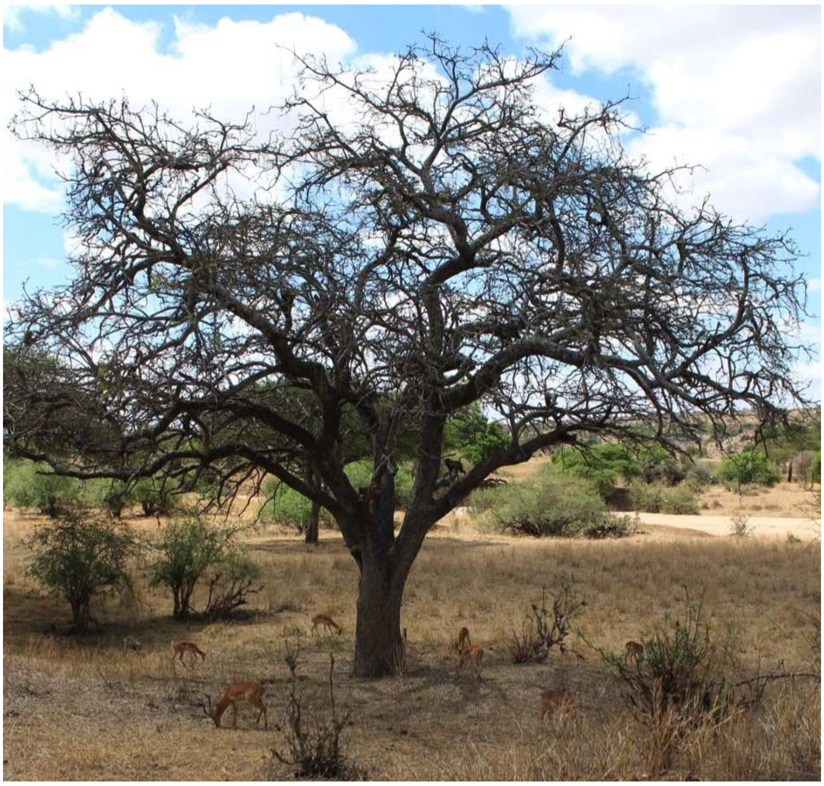
Passive vigilance

No/Low vigilance

Appendix 2—Photos and Videos of Impala-Baboon Encounters

Impala-baboon mixed group where no sausage trees were present.

Impala-baboon mixed group under a fruiting sausage tree.



Baboons in a flowering sausage tree while an impala herd feeds on the fallen flower buds.